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Spatial patterning and species coexistence: A case study using concentric circular vegetation patches in saline land

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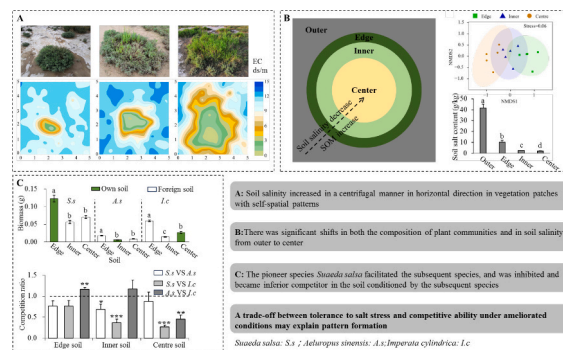
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HIGHLIGHTS

- Soil salinity increases outward from the center in vegetation patches with self-spatial patterns.
- Significant shifts in plant communities and soil salinity occur from the patch's edge to its center.
- Pioneer species aid but become less competitive in soil conditioned by subsequent species.
- Trade-off between salt tolerance and competitive ability may explain pattern formation.

GRAPHICAL ABSTRACT



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ABSTRACT

Spatial patterns in plant community structures within stressed ecosystems have drawn much attention in the field of ecology. However, the mechanisms underlying spatial formation and its impact on species coexistence and diversity remain controversial. In this study, we investigated concentric circular vegetation patches in coastal saline land, and analysed the spatial patterning of plant communities and associated soil physicochemical properties. Thereafter, we tested how the soil conditioned by plant communities from different locations within the vegetation patches influence the species growth and inter-specific competition. Our results show soil salinity enlarges in a centrifugal manner in horizontal direction in all patches. Soil salinity decreased and species diversity increased along with the increase of patch size. In addition, we found significant shifts in both the composition of plant communities and in soil physicochemical properties from outer to center. The results indicate that the pioneer species *Suaeda salsa* facilitated the subsequent species. However *Suaeda salsa* was inhibited and became inferior competitor in the soil conditioned by the subsequent species. We infer that the less-visible spatial patterns of soil physicochemical properties at small scales create ecological niches for specialized species, allowing them to coexist but not mix. We suggest that a trade-off between tolerance to salt stress and competitive ability under ameliorated conditions may underlie mechanisms of pattern formation in small scale.

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Our findings lend support to the idea that soil stress constraints community assembly and triggers spatial patterns, which, in turn, buffer the stress on plant communities and enhance species diversity.

1. Introduction

Vegetation patches often exhibit regular spatial patterns that can be important for ecosystem processes and functioning in terrestrial ecosystems (Aguiar and Sala, 1999). These spatial patterns arise from interactions between species, communities and the environment, particularly in stressed environments like arid ecosystems (Christopher, 1999; Rietkerk et al., 2004) and salt marshes (Koppel et al., 2004). The mechanisms underlying spatial formation and its impact on species coexistence and diversity remain controversial in ecology.

The formation of spatial self-organization patterns of vegetation and their impact on ecosystem functions have been fascinating topics in ecology. Various regular or irregular forms of spatial self-organization patterns, such as spotted, striped, and labyrinth patterns, have been reported since the 1990s (Christopher, 1999; Bonanomi et al., 2014). A large body of literature has proposed several mechanisms for these patterns, including oscillating consumer-resource interactions, localized disturbance-recovery processes and scale-dependent feedback (Cross and Hohenberg, 1993; Fernandez-Oto et al., 2014; Getzin et al., 2016; Rietkerk and Van de Koppel, 2007). Most of the spatial self-organization patterns were found and studied in stressed environments, such as ring-type patterns in Australian and Namibian dryland ecosystems (Pringle and Tarnita, 2017; Juergens, 2013; Getzin et al., 2016), and concentric ring patterns in Chinese salt marshes (Zhao et al., 2021). These studies all emphasize the role of localized ecological interactions on generating striking large-scale spatial patterns in ecosystems.

Compared with homogeneous moderate soil conditions, a vegetation generally shows stronger interactive relationships with the soil in harsh environmental conditions (Zhang et al., 2019). Many scholars believe that the deterministic process of plant community construction is, to a large part, the result of ecological filtering in harsh environments (Drake, 1991). Environmental stresses on plant communities may result in community reassembly and trigger self-organization in spatial patterns of biota and resources, which is predicted to alleviate these stresses (Bera et al., 2021; Pringle and Tarnita, 2017). Previous studies mainly focused on large landscapes and the overall relationship between vegetation patches and the environment. Analyzing the synergistic changes between plants and soil, as well as the changes in plant communities within patches, can provide new insights into patch formation and function.

In many ecosystems, spatial patterned vegetation patches are dynamic as both the positioning and the species composition change over time (Stewart et al., 2013). By continuous mapping quasi-circular patterned vegetation patch dynamics, Shi et al. (2021) reported that the total area of a vegetation patch increased, and the location showed a certain regularity, although the expansion was irregular. Vegetation patches exhibit significant fertility island effects that are not found in saline bare soil areas (Liu et al., 2019), and some soil properties exhibit regular changes from the perimeter to the center of the patch. Another study conducted by Zhao et al. (2021) indicated that the different locations within a vegetation patch can be envisaged as representing different phases of plant establishment, with the center representing the late-establishment phase and the outer areas representing the pre-establishment phase. They also reported that nutrient depletion plays a key role in explaining the concentric rings patterns, as nitrogen fertilization mitigates depletion stress and shifts plant growth from negative to positive in the center of patches. Vegetation and soils coevolve through a feedback process: changes in soil conditions influence the plant component, which, in turn, leads to further changes in the soil, and vice versa (Ehrenfeld et al., 2005; Mora and Lázaro, 2013). Thus, analyzing the internal heterogeneity of vegetation patches may be

very effective in inferring recruitment dynamics from current structure and the underlying mechanisms of pattern formation.

Coastal saline land is often the research object of spatial patterns and community assembly because of the simple structure of the plant community. In this region, vegetation patches are randomly embedded in a large area of bare land.

By analyzing 63 quadrats, the previous study (Yang et al., 2023) indicated that *Suaeda salsa*, *Aeluropus sinensis* and *Imperata cylindrica* were dominant species in this region. *Imperata cylindrica*-dominated communities were consistent in the development of plant communities in this study area, with high plant diversity. In the present study, three dominant types of vegetation patches have been identified in the study site (Fig. 1): (1) those mono-dominated by *Suaeda salsa* (SDP, Fig. 1b); (2) *Aeluropus sinensis* dominated in center and encircled by a ring of *Suaeda salsa* (ADP, Fig. 1c); and (3) those dominated by *Imperata cylindrica* in the patch center (IDP, Fig. 1d). The diameter of the patches dominated by *S. salsa*, *Aeluropus sinensis* and *I. cylindrica* were about 2.5, 3.5 and 4.5 m, respectively. In the patches with *I. cylindrica* as the dominant species, there is an obvious phenomenon of species stratification in horizontal direction: *I. cylindrica* occupies the center, *Aeluropus sinensis* is present in the transition area, and *S. salsa* is present on the edge of the patch containing the bare land. We named the four locations as center, inner, edge and outer (bare land). These patches are excellent research targets due to their simple community structure and unique spatial self-organization characteristics. Here, we attempt to answer the following questions: (i) whether soil salinity and species diversity are affected by the expanding of the vegetation patch; (ii) how soil properties and inter-specific competition drive the formation of spatial pattern.

In this study, we evaluated the changes of soil salinity and species diversity among the three types of vegetation patches. We used IDP to analyse spatial patterns of the plant community and the associated soil physicochemical properties, due to its most complex structure. Then, we test how the soils conditioned by plant communities from different locations within the vegetation patches influence the species growth and inter-specific competition. In addition, we evaluated the colonization ability of species by examining the density of germinated plants. Our hypotheses are: 1) patterns in soil properties are associated with aboveground visible patterns of plant communities; 2) the competitive ability of plant species changes with changing soil characteristics; and 3) there is a trade-off between colonization in outer and competitive ability in center of patch.

2. Materials and methods

2.1. Study location and field survey

A Field study was carried out at the coastal saline land near Bohai Bay, located in Haixing County, Hebei province, North China (117°57'17"-117°58'31"E, 38°16'83"-38°17'59"N). The study site is approximately 24.8 km away from the coastline and currently rests atop a shallow groundwater table (0.9–1.5 m layer) maintaining a high salinity range (10–40 g L⁻¹) (Ju et al., 2019). Vegetation patches are randomly embedded in a large area of bare land.

Firstly, to explore the spatial variation of soil salinity in different vegetation patches, a square grid-sampling scheme (5 × 5 m) was imposed on each type of vegetation patch (Fig. S1). The samples were collected from 100 sample points in a regular grid with 0.5 m between adjacent points. At each point, soil samples were collected at depths of 0–10 cm using a soil auger, and the soil electrical conductivity (EC) was measured in a 1:5 soil-water suspension.

Thereafter, we chose five of each typical patches (SDP, ADP and IDP), to investigate the changes of soil salt content and species diversity among the circular plant patches. Here, we placed a 40 × 40 cm sample quadrat at the center (2 m in diameter of the central area to eliminate the impact of patch size effect) of each chosen patches. Floristic lists and density were recorded at each quadrat. Simpson' diversity index (Ds) were selected to evaluate species diversity (Simpson, 1949):

$$Ds = 1 - \sum_{i=1}^s p_i^2$$

where P_i is the ratio of the i th kind number and the total number of sample (in accordance with abundance). Soil samples in each quadrat were collected down to 40 cm and separated into 3 layers in depth (0–10 cm, 10–20 cm, 20–40 cm).

Finally, five IDPs with obvious species stratification in horizontal direction and a diameter ranging from 4 to 6 m were selected to study the spatial patterning and species coexistence in fully developed circular patches. A 40 × 40 cm quadrat was set at each location (edge, inner and center) within each vegetation patch (Fig. 1d). Data on plant species presence, density, frequency and canopy cover percentage were recorded. The importance value (IV) is a comprehensive quantitative indicator of the status and role of a species in a community. In this study, the importance value index was used, as defined in Giliba et al. (2011):

$$\text{Importance value index} = \text{Relative abundance} + \text{Relative frequency} + \text{Relative canopy coverage}$$

where Relative abundance was calculated as the percentage of the number of a certain species to the total number of all species, Relative frequency was calculated as the frequency of a certain species in all quadrats to the sum of all species frequencies, Relative canopy coverage was calculated as the percentage of coverage of a certain species in a community compared to the sum of all coverage.

Using the five IDPs, we also examined the changes of soil properties associated with the above-ground plant communities at different locations within vegetation patches and bare land (outer, edge, inner and center). We randomly took one soil core (3 cm in diameter, 10 cm in height) in each quadrat. To determine the soil bulk density, we inserted a 100 cm³ ring cutter into the surface soil to collect soil samples.

2.2. Soil characteristics

Gravimetric soil water content was measured based on fresh weight of the soil samples and weight after oven-drying at 105 °C. The main soil cations (sum of Na⁺ and K⁺, Ca²⁺, Mg²⁺) and anions (Cl⁻, HCO₃⁻, SO₄²⁻) contents were measured by titration methods. The soil total salt content was calculated as the sum of the ions (Guo and Liu, 2014). We dried the soil samples taken from the 100 cm³ ring cutters to obtain the soil bulk density. Soil organic matter content was analysed colorimetrically according to Sims and Haby (1971).

2.3. Soil legacy effects on species growth and inter-specific competition

We conducted a greenhouse experiment at the Center for Agricultural Resources Research, Institute of Genetic and Developmental Biology, Chinese Academy of Sciences, at Shijiazhuang, Hebei Province, China (38°1'2"N, 114°31'47"E). The aim was to investigate plant-soil feedback effects using samples collected from the natural patches. The strength of this method lies in the fact that plants have influenced the soil for a long period of time under natural conditions (Brinkman et al., 2010). Soil collected from three locations (edge, inner and center) in five

vegetation patches was sieved (<0.5 cm) to remove coarse fragments and then homogenized. The soil collected from the same location within each of the five patches was thoroughly mixed and pots (5 cm × 5 cm) were filled with 300 g soil weight (on a dry weight basis). Twenty-four pots were filled with the soil from each location. Eight pots were planted with *S.s.*, *A.s.*, or *I.c.* in monocultures, respectively. Four plants were planted in each pot (intra-specific competition). Overall, the monoculture part of the experiment included 3 locations × 3 plant species × 8 replicates (Fig. S2).

In addition, we planted the species in inter-specific competition. Twenty-four pots were filled with the soil from each location; and eight pots were planted with *S.s.* + *A.s.*, *S.s.* + *I.c.*, or *A.s.* + *I.c.* in mixtures on the soil, respectively. Two plants of each species were planted in each pot. Overall, the interspecific part of the experiment included 3 locations × 3 plant species pairs × 8 replicates. Seeds of the three species were collected from the study site in the preceding year, were surface sterilized in 3 % sodium hypochlorite solution for 1 min, rinsed, and germinated on sterile glass beads in a climate chamber at 20 °C (16 h/8 h, light/dark). Ten-days-old seedlings were transplanted into each pot. Other plants that emerged from the soil were removed from each pot to keep a consistent number for the same species. For both experiments, all pots were randomly re-positioned every two weeks and watered regularly without fertilizer application. The soil water content in each pot was checked (80 % of field capacity) twice a week by weighing the pots.

After 60 days growth, aboveground plant biomass was clipped at the soil surface and weighed after oven-drying at 70 °C to a constant weight.

2.3.1. Calculations of the competition ability

To test the competitive ability of species when grown together with another species, the competition ratio (CR) (Grace, 1995) was calculated with the following equation:

$$CR_A = RY_A / RY_B$$

where, RY_A and RY_B represent the relative biomass of plant A and B, and

$$RY_A = Y_{AB} / p_A Y_A$$

Y_{AB} refers to the biomass of plant A when plant A and B grow together; Y_A and Y_B are the biomass of plant A and B grown in monoculture; and p_A is the proportion of plant A in the mixture. When $CR_A > 1$, the competitiveness of species A is greater than that of species B; When $CR_A = 1$, species A and B have equal competitiveness; When $CR_A < 1$, the competitiveness of species A is less than that of species B.

2.4. Seedbank test

The colonization ability comprises not only the dispersal ability of seeds but also the successful establishment of seeds. *A.s.* and *I.c.* can be propagated by both seeds and propagules, especially at small scales. Within vegetation patches, species possess the capability to disperse seeds or propagules to various locations within and among the patches. The germination ability reflects a plant's capacity to tolerate the environment and the potential for successful colonization. To assess this, we randomly took three soil cores (10 cm in diameter, 10 cm in height) at each location within each vegetation patch. These soil cores were transferred to pots that were placed in the greenhouse. The soils were then stirred to encourage the germination of remaining seeds or propagules. Sufficient water and light were provided and greenhouse temperature was controlled at 25 ± 3 °C. Then we recorded the species identity and density of all germinating plants in each pot every 10 days for a period of 90 days.

2.5. Statistical analysis

The soil EC spatial distribution maps were constructed using the ordinary kriging method in the software Surfer 12.0 (Golden Software Inc., Colorado, US).

We performed all subsequent statistical analyses in R version 4.1.3 (R Core Team, 2022). We analysed difference in soil salt content among the three types of patches using linear mixed-effects models with patch, soil depth and their interaction as main effects and patch replicate as a random effect. We used lmer in LME4 for linear mixed-effect model (Bates et al., 2015). We assessed the significance of main effects using the function anova in lmerTest (Kuznetsova et al., 2017) and examined pairwise contrasts using the function emmeans in the package emmeans (Lenth, 2019) with the Tukey method *P*-value adjustments for multiplicity. We used the nonparametric Kruskal-Wallis test in post hoc comparisons to test the differences about species diversity among the three types of patches.

We visualised dissimilarity in plant community composition between locations within vegetation patches using nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distances and tested for effects of location with PERMANOVAs (999 permutations) using the package vegan (Oksanen et al., 2022). Compositional dissimilarities among locations (beta diversity) were partitioned into replacement and richness difference components using the package adespatial. We show the beta diversity comparisons (using Jaccard similarity index) for plant communities among locations by triangular plots.

We used a nonparametric Kruskal-Wallis test for post hoc comparisons to test for differences among soil physicochemical properties at different locations within vegetation patches (outer, edge, inner and center). One-way ANOVA was used to analyse the soil effect on plant biomass. A one-sample *t*-test was used to analyse whether the competition ratio differed from 1. One-way ANOVA was used to analyse the difference of density of the three species in soil collected from different location on the 90th day after the establishment of seedbank experiment.

3. Results

3.1. Changes in soil salinity and species diversity with patch types

As shown in Fig. 2a soil EC values beneath vegetation patches was lower than that in bare land. In three vegetation patches, EC values increased in a centrifugal manner in horizontal direction. There was no obvious spatial variation at the edges of each grid which displayed high EC values and that corresponded to the bare land.

From bare land to SDP, ADP, and then to IDP, vertical salinity reduction was significant, and the distribution pattern of salt in the profile significantly changed (Fig. 2b). In bare land, the accumulation of salt in the topsoil was evident, and soil salt content decreased significantly when soil depth increased. In SDP, the accumulation of salt in topsoil was inexistant and there was no significant difference in soil salt content in the 0–40 cm soil depth in SDP. Compared to ADP, the

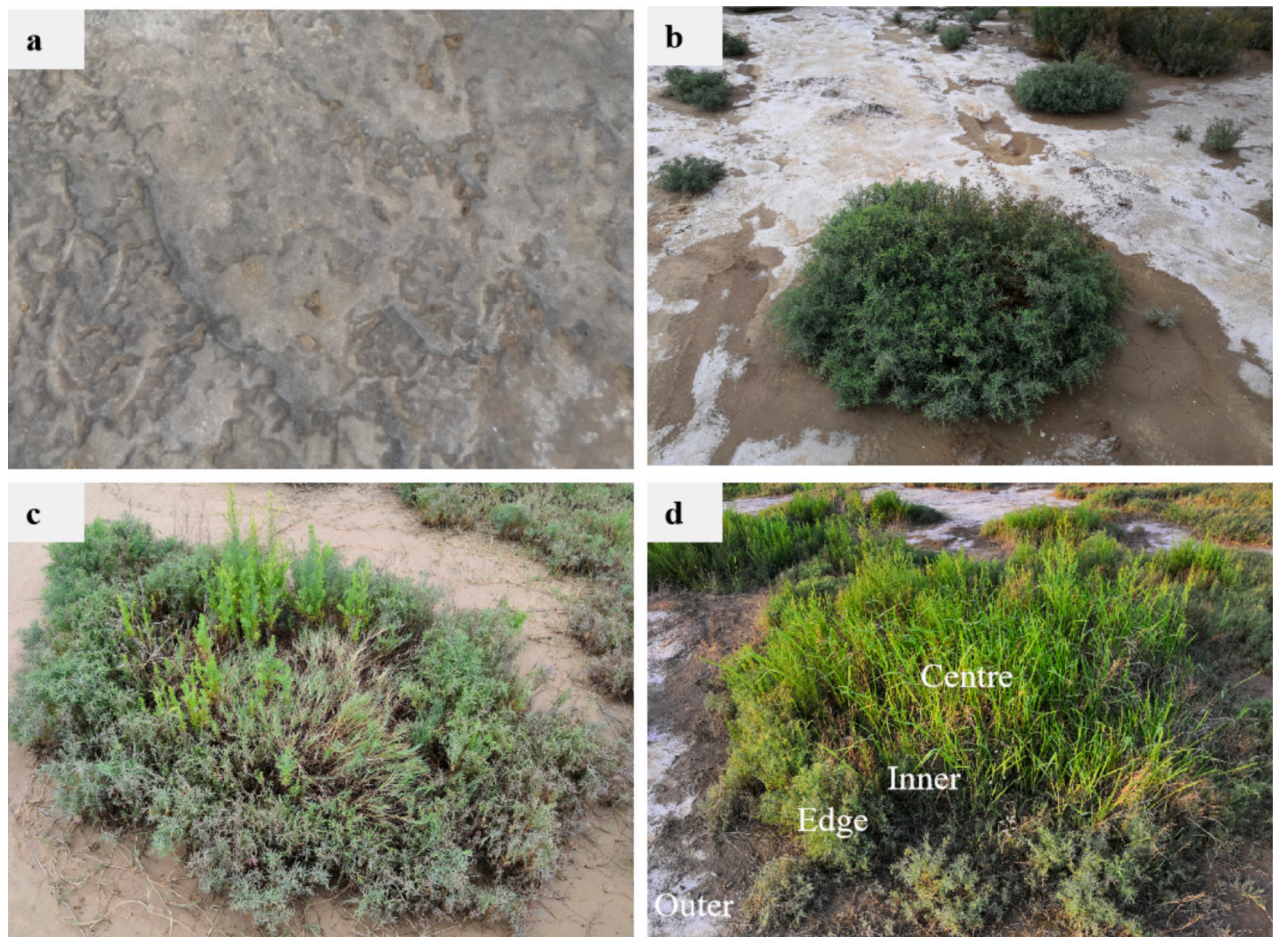


Fig. 1. Spatial patterned vegetation patches and bare land at the study site. (a) Bare land. (b) *Suaeda salsa*-dominated patch. (c) *Aeluropus sinensis*-dominated vegetation patch. (d) *Imperata cylindrica*-dominated vegetation patch. In (d) sampling zones across this concentric circular pattern vegetation patch are also indicated. Species stratification in horizontal direction: *I. cylindrica* occupies the center, *Aeluropus sinensis* dominate the transition zones (inner), and *Suaeda salsa* is distributed at the edge.

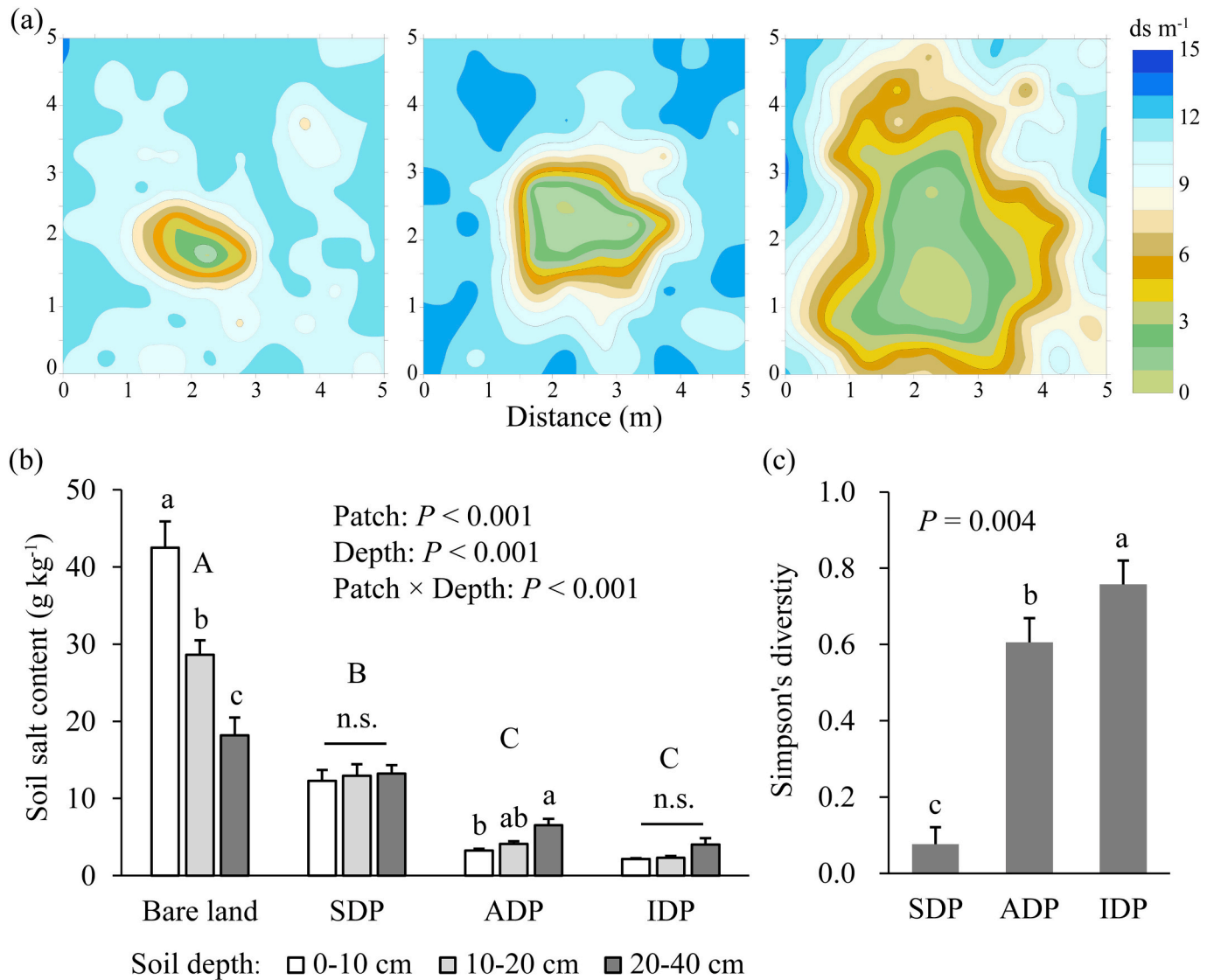


Fig. 2. Changes in soil salinity and species diversity with patch types. SDP, *Suaeda salsa*-dominated patch; ADP, *Aeluropus sinensis*-dominated vegetation patch; IDP, *Imperata cylindrica*-dominated vegetation patch. (a) Spatial variation of soil EC in the three types of patches ($n = 1$). (b) Changes in soil salinity, statistics presented in the upper part of panel are the overall effects of the patch type, soil depth and their interactions from a mixed linear model. Shown are mean $\pm$ SE ($n = 5$) and results of multiple pairwise comparisons, where upper case letters indicate significant differences for patch type and lower case letters for depth. n.s. indicates no significant difference detected. (c) Changes in species diversity, statistics presented in the upper part of panel are the overall effects of the patch type. Shown are mean $\pm$ SE ($n = 5$) and results of multiple pairwise comparison, different letters indicate significant differences for patch type.

differences of soil salt content between soil layers in IDP weakened.

From SDP to ADP, and then to IDP, plant species diversity significantly increased (Fig. 2c).

3.2. Plant composition at different locations within vegetation patches

The composition of plant communities in fully developed IDPs shifted significantly within vegetation patches from edge, to inner, to center, as shown in the NMDS ordination (Fig. 3a). Permutational multivariate analysis of variance (PERMANOVA) indicated a significant difference in species composition among locations ($P = 0.001$; Table S1). Beta diversity analyses revealed that the richness difference process was higher, contributing 68.57 %, than the species replacement process which contributed 31.43 %, (Fig. 3b). From the edge to the inner, and the center, the dominant species shifted from *S.s.* to *A.s.*, and *I.c.* (Table S2). The number of species increased from edge to center, and the importance value of the dominant species decreased.

3.3. Soil properties at different locations within vegetation patches

Soil properties showed regular changes from outside bare land to the patch center (Fig. 4). The soil water content beneath vegetation was significantly higher than that of bare land (outer). Soil salt content and bulk density displayed a decreasing trend from outer to the center. In contrast, SOM gradually increased from the outer area to the center of the patch (Fig. 4).

3.4. Species growth and inter-specific competition in soil from different locations within vegetation patches

S.s. plants and *A.s.* plants produced significantly more biomass in edge soil than in inner and center soil (Fig. 5; for *S.s.*, $F = 28.67$, $df = 2$, $P < 0.001$; for *A.s.*, $F = 49.81$, $df = 2$, $P < 0.001$). In the case of *I.c.* plants, the highest biomass was found in edge soil, followed by center soil, and the smallest in inner soil (Fig. 5; $F = 115.30$, $df = 2$, $P < 0.001$).

S.s. exhibited a lower competition ratio when grown in inner soil

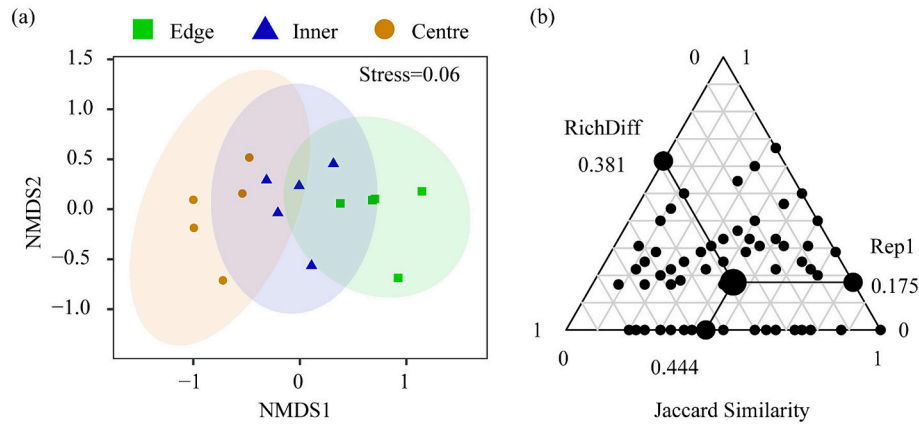


Fig. 3. Dissimilarity in species composition at different locations within vegetation patches. (a) NMDS ordination based on species dissimilarity among communities at the three locations. Dots and ovals of the same color correspond to same locations within patches. The value of NMDS stress is also shown. (b) Triangular plots of beta diversity comparisons (using Jaccard dissimilarity index) for communities among locations. Each point represents a pair of sites. Its position is determined by a triplet of values: Jaccard similarity, Repl (replacement) and RichDiff (richness difference) and each triplet sums to 1. The mean values of Jaccard similarity, Repl and RichDiff are also shown as larger dots.

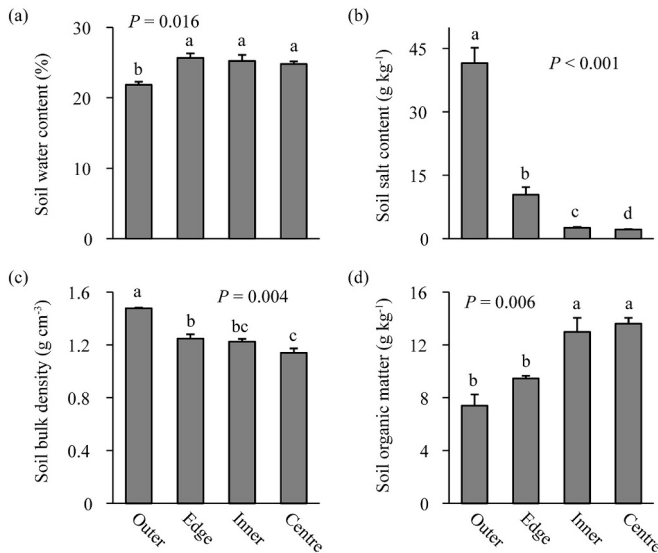


Fig. 4. Soil physicochemical properties at different locations within IDP. Statistics presented in the upper part of panel are the overall effects of the location. Shown are mean $\pm$ SE ($n = 5$) and results of multiple pairwise comparisons, different letters indicate significant differences. P values are also shown, based on One-way ANOVA.

(conditioned by an *A.s*-dominated community) both in competition with *A.s* and *I.c* (Fig. 6). Moreover, the competition ratio of *S.s* was significantly lower than that of *I.c* when they competed in the center soil (conditioned by an *I.c*-dominated community, $P < 0.001$). The competitive relationship between *A.s* and *I.c* reversed depending on the soil condition. In the edge soil (conditioned by a *S.s*-dominated community), the competition ratio of *A.s* was significantly greater than that of *I.c* ($P < 0.01$). However, when they grew together in the center soil (conditioned by an *I.c*-dominated community), the competition ratio of *A.s* was significantly lower than that of *I.c* ($P < 0.01$).

3.5. Seedbank test

The seedbank revealed that only *S.s* emerged in outer soil (Fig. 7). The density of *S.s* plants that germinated in the soil collected from the edge was significantly higher than that in other locations ($P < 0.001$). There was no significant difference in the density of *A.s* plants in edge,

inner and center soil ($P = 0.062$). No germination of *I.c* was detected in outer and edge soil. In inner soil, the density of *I.c* plants was significantly higher than in edge soil ($P < 0.001$).

4. Discussion

The study of interactions between plant species and their environment, as well as into interspecific interactions, can offer valuable insights into the formation and function of spatial self-organization patterns of vegetation (Rietkerk et al., 2004). In this study, we investigated vegetation patches with concentric circle spatial patterns in coastal saline land in China. We tested the horizontal and vertical distribution of soil salinity and the variation of species diversity among patches with different sizes. Our results show that EC values increase in a centrifugal manner horizontally in all patches. Soil salinity decreased and species diversity increased with the increase in patch size.

We used IDP to analyse spatial patterns of the plant community and the associated soil physicochemical properties, due to its most complex structure. Our results show significant shifts in both the composition of plant communities and in soil physicochemical properties from outer to center. We then tested how the soil conditioned by plant communities from different locations within the vegetation patches influence the species growth and interspecific competition. Our results show that *S. salsa* which is located at the edge of patches faced growth inhibition in inner and center soils, and the competitive ability was significantly lower than that of the other species in both inner soil and center soil. However, only *S. salsa* can germinate and grow in bare soil, while the other species performed best in the soil conditioned by *S. salsa*. and could not propagate or germinate in bare land according to the field observation and seed bank test.

In addition, the competition ability of *A. sinensis* and *I. cylindrica* was reversed as the soil shifted from edge to center. We infer that a trade-off between tolerance to salt stress and competitive ability under ameliorated conditions may be an underlying mechanism of pattern formation at small scales. Our findings support the idea that soil stress constraints community assembly and triggers spatial patterns, which, in turn, buffer the stress on plant communities and enhance species diversity (Bera et al., 2021; Pringle and Tarnita, 2017).

Spatial information on the differences of vegetation patches is a prerequisite for characterizing the spatial patterning of vegetation patches and understanding the relations between ecological and physical processes (Wang et al., 2007; Armas et al., 2008). In vegetation patches, EC values exhibited concentric circle structures, and increased from the center to the outer regions (Fig. 2a). This can be interpreted as

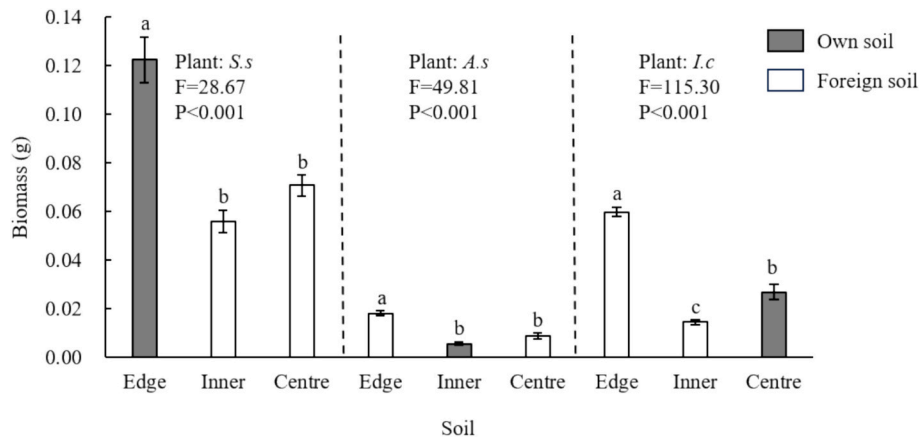


Fig. 5. Soil legacy effect on plant growth. S.s, *Suaeda salsa*; A.s, *Aeluropus sinensis*; I.c, *Imperata cylindrica*. Error bars indicate mean ± SE (n = 8). F and P values from One-way ANOVA are also shown.

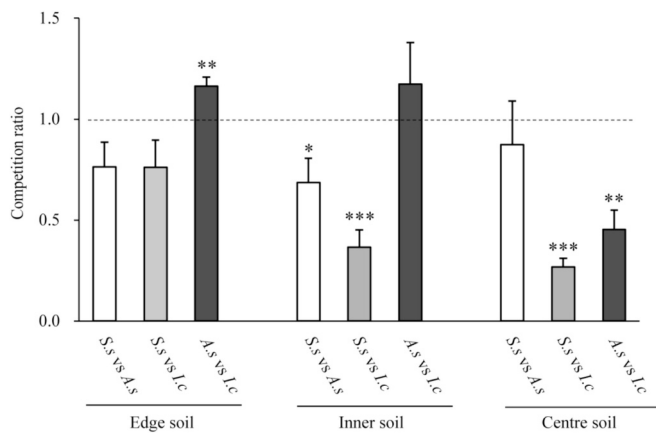


Fig. 6. Soil legacy effect on interspecific competition. S.s, *Suaeda salsa*; A.s, *Aeluropus sinensis*; I.c, *Imperata cylindrica*. Competitive results of three species in mixed sowing (1:1) in the soil conditioned by S. s dominated community (edge), A. s dominated community (inner) and I. c dominated community (center). The competition ratio >1 means the front species is more competitive than later, competition ratio <1 means the later species is more competitive than front. Error bars indicate ± SE (n = 8). Asterisk (*) indicates that the response differed significantly from 1: *P < 0.05, **P < 0.01, ***P < 0.001.

an effect of the time that the zone has been colonized by plants. Although the above-ground vegetation in SDP appears homogeneous, the soil salinity is heterogeneous. Soil salinity decreased and species diversity increased along with an increase of patch size. Consistently with previous reports, soils beneath vegetation patches exhibited higher soil water content and more organic matter and lower soil bulk density than soils from bare land (Fig. 4; Li et al., 2021; Liu et al., 2019). Studies have suggested that there is a source-sink relationship of resource (runoff, erosion products and nutrients) redistribution between patches of biological soil crust and vegetation (Ludwig et al., 2005). Vegetation patches intercept runoff, erosion products, organic matter, nitrogen and dissolved nutrients from biological soil crust patches, resulting in fertility islands (Butterfield and Briggs, 2009). By intercepting runoff, reducing soil bulk density and increasing hydraulic conductivity, vegetation patches promote water infiltration and salt leaching (Xia et al., 2019). The reduction of salt content is a prerequisite for the amelioration of other soil physicochemical properties (Yang et al., 2023) and an increase in species diversity (Zhang et al., 2007). In our case, IDPs showed the most complex structure and the highest species diversity, making them the best material for analyzing spatial patterns of plant community and the associated soil physicochemical properties.

Our results show significant shifts in both the composition of plant communities and in soil physicochemical properties from outer to center in IDP. The location within a vegetation patch can be envisaged as the establishment phase of plants (Zhao et al., 2021), with the center, inner, edge and outer representing late-establishment, mid-establishment, early-establishment and pre-establishment phases of plants, respectively. Our data indicate that *S. salsa*, *A. sinensis* and *I. cylindrica* are the dominant species from edge to inner to center, respectively. Community dissimilarity among locations infers that richness differences play a major role, which means that the loss of species or variation in ecological niche quantity was caused by changes in abiotic conditions. Our results shows a decreasing trend in soil salt content and bulk density from outer to the center, while soil organic matter gradually increased (see Fig. 4). These patterns of soil properties may contribute to niche differentiation (Weiher et al., 2011). The adaptation of plants is highly responsive to environmental variation, even when the variation is small, resulting in the development of a set of specialized species (Frías-Ureña et al., 2022). The present study indicates that spatial self-organization patterns involve not only spatial distributions of the plant community but also less-visible spatial patterns of soil properties.

We show that the growth and inter-specific competition of the tested plant species varies across soils from different locations. *S. salsa* faced growth inhibition in inner and center soils. As a halophyte, the optimal salt concentration for *S. salsa* growth is between 15 and 20 g/kg dry soil (Song et al., 2008; Li et al., 2010). The lower salt concentration in inner and center soil might be unfavorable for the growth of *S. salsa*.

Furthermore, the competitive ability of *S. salsa* was significantly lower than that of *A. sinensis* or *I. cylindrica* in both inner soil and center soil. The upper limits of distribution of halophytes into less saline or nonsaline habitats are often determined by competition (Ungar, 2008). Consequently, for *S. salsa* it is difficult to colonize the center of the patch, which is already partially occupied by *A. sinensis* or *I. cylindrica*.

Meanwhile, only *S. salsa* can germinate and grow in bare soil according to the results of our soil seed bank test. It is widely accepted that tolerance to abiotic stress and facilitation dominate in the early stages of vegetation establishment on bare land (Castillo et al., 2021). Studies have indicated that growth of *S. salsa* altered the distribution of soil salt in vertical profiles, inhibiting the surface salt accumulation. (Song et al., 2008) Our data show that when plants were grown in monoculture, all species performed best in the soil conditioned by *S. salsa*. Thus, we suggest that *S. salsa* acts as the pioneer species and facilitates subsequent colonizing species.

The salt tolerance of *A. sinensis* and *I. cylindrica* is low, and these two species mainly rely on tillers (Ding et al., 2011; Liu et al., 2019). It is likely due to inhibition of propagation or germination, *A. sinensis* or *I. cylindrica* cannot grow in bare land soil (see Fig. 7). The above result

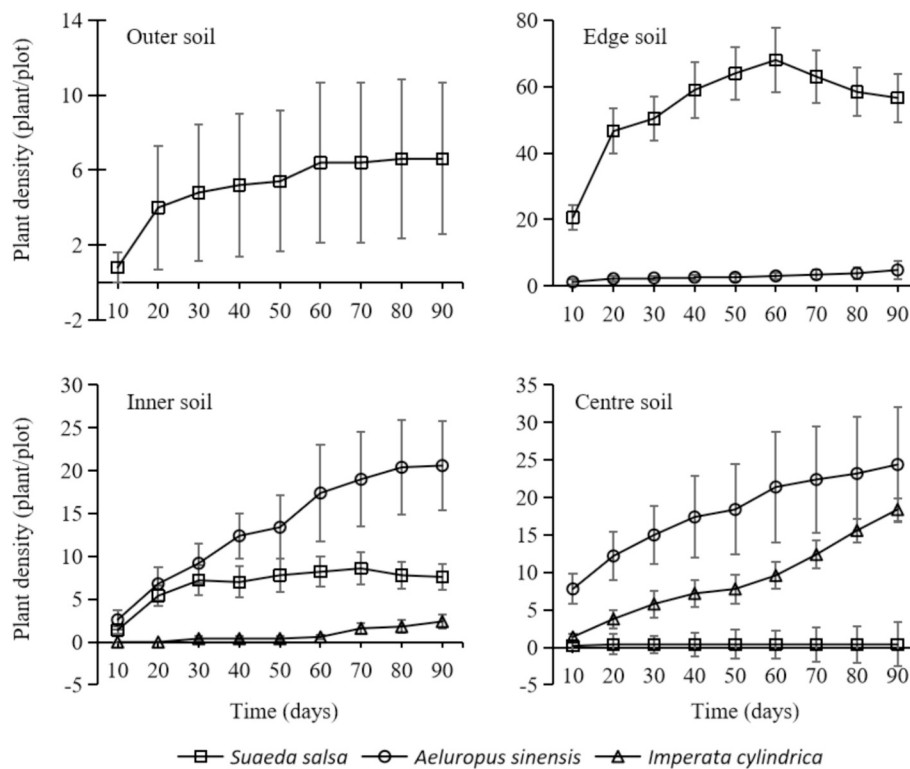


Fig. 7. Plant germination from soil samples collected at different locations within vegetation patches. Only the three dominant species are presented. Mean is shown ($\pm$ SE), $n = 5$ for each location.

may explain the striking phenomenon that *S. salsa* is located at the edge of the patches dominated by other species, and acts like a fence separating them from the bare land. Soil physicochemical properties in the center and transition area were relatively homogeneous. At relatively small spatial scales, competitive interactions can play an important role in influencing plant distributions (Yang et al., 2014). The competition ratio of *A. sinensis* was significantly greater than that of *I. cylindrica* in the edge soil, but reversed in the inner soil. At the patch center, *I. cylindrica* might rapidly propagate and alter the soil conditions, resulting in *A. sinensis* being squeezed out of the center position (evidenced by the lower competition power of *A. sinensis*). Apart from the variations in salt concentration, other aspects of soil properties (e.g. soil microbiome) may largely differ in different zones within the circular patches. Understanding the relationship between the dominant halophytic plants and soil microbiota will further help us decipher the mechanisms of plant community formation in coastal saline ecosystems (Ma et al., 2024).

Overall, we infer that the less-visible spatial patterns of soil physicochemical properties at small scales provide ecological niches for specialized species, allowing them to coexist but not mix. Otherwise, in a homogeneous low salt environment, *S. salsa* may be eliminated from the community due to competitive exclusion. Thus, a trade-off between tolerance to harsh conditions and competitive ability under more favorable conditions may underly the pattern formation that is occurring at these small scales. We suggest that the concentric circular pattern in this study buffered the salt stress on plant communities and enriched species coexistence in patch. Similarly, we acknowledge that vegetation and soils coevolve through a feedback process (Ehrenfeld et al., 2005). We suppose that the entire patch would expand in a centrifugal manner, constantly occupying bare land, changing soil conditions and community composition. Further studies are needed to track patch dynamics over larger time scales. Our study deepens our understanding of the link between spatial self-organization and species coexistence. Such insights are important for advancing ecological research set out to understand

patterns in harsh environments, and lay the foundation for local ecosystem management, including conservation, restoration, and sustainable use.

CRediT authorship contribution statement

Ce Yang: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kai Guo:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Xiaohui Feng:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Xiaojing Liu:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **T. Martijn Bezemer:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data sets used for analyses in this study have been deposited in the Science Data Bank with the identifier doi:10.57760/sciencedb.11694.

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Appendix A. Supplementary data

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