Postprint: Aggregated Distribution Pattern and Characteristics of Suaeda corniculata Population in Qinwangchuan Salt Marsh Wetland

Authors: Wang Xiaopeng, Zhao Chengzhang, Wang Jiwei, Zhao Lianchun, Wen Jun

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Abstract

Multi-scale aggregation and changes in patch characteristics of plant populations represent the result of coordinated adaptation to environmental conditions. Using pair-correlation function and null model approaches, four sample plots were established according to soil salinity distribution patterns across microtopographic gradients. Within each 2 m × 2 m quadrat, 400 small grids were installed to record plant individuals and collect soil samples, thereby analyzing the intrinsic features of aggregated spatial patterns in Suaeda corniculata populations along a soil salinity gradient in the salt marsh wetlands of Qinwangchuan, Lanzhou. The results revealed that within the aggregated distribution range of S. corniculata populations, two critical scales of aggregation phenomena emerged: aggregation or superposition of small-sized patches formed composite large-scale clusters, manifesting as an overall nested double-patch distribution. With decreasing soil salinity, the size of large patches in the population' s clustered distribution tended to increase, whereas size differences among small patches remained insignificant. The number of large patches decreased markedly, while the number of small patches varied with population size, exhibiting a declining trend across the entire gradient. The average number of individuals per small patch gradually decreased, and the average number of small-scale patches contained within composite large patches also showed a decreasing trend. Under the background of soil environmental heterogeneity in inland salt marsh wetlands, the gradient variation in patch characteristics within the clustered distribution of S. corniculata populations reflects adaptive adjustments in individual plant morphology and structure, as well as the outcome of gradient shifts in positive and negative ecological relationships, sheltering effects, and self-thinning effects within the population.

Full Text

Preamble

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Aggregated Spatial Patterns and Characteristics of *Suaeda corniculata* in Qinwangchuan Salt Marsh

Wang Xiaopeng[1], Zhao Chengzhang[1],*, Wang Jiwei[1], Zhao Lianchun[1], Wen Jun[2]
[1]College of Geography and Environmental Science, Northwest Normal University; Gansu Provincial Wetland Resources Protection and Industrial Development Engineering Research Center, Lanzhou 730070, China
[2]Faculty of Science, Dingxi Campus, Gansu University of Chinese Medicine, Dingxi 743000, China

Abstract

Multi-scale clustering and variation in cluster characteristics represent the outcome of plants' collaborative adaptation to environmental conditions. Using pair-correlation functions and null model methods, we established four 2 m × 2 m sample plots according to soil salinity distribution patterns across microtopography. Each plot was divided into 400 cells (10 cm × 10 cm) to record plant individuals and collect soil samples. We analyzed the intrinsic characteristics of aggregated spatial patterns in *Suaeda corniculata* populations along a soil salinity gradient in the Qinwangchuan salt marsh wetland of Lanzhou.

Our results revealed that *Suaeda corniculata* populations exhibited complex spatial patterns with two critical scales of clustering. Small-scale clusters aggregated and superimposed to form composite large-scale clusters, showing a nested double-cluster process across all scales. As soil salinity decreased, the size of large-scale clusters tended to increase while small-scale cluster sizes showed no significant differences. The number of large-scale clusters decreased significantly, whereas the number of small-scale clusters increased with population size. The average number of individuals per small cluster gradually declined, and the average number of small clusters within each large cluster also showed a decreasing trend across the salinity gradient. Under the background of soil environmental heterogeneity in inland salt marsh wetlands, these gradient variations in cluster characteristics reflect adjustments in plant morphology and composition, representing the outcome of gradient transformation in population ecological relationships, protection effects, and self-thinning.

Keywords: aggregated spatial patterns; *Suaeda corniculata*; salt marsh; soil salinity; multiple clustering; cluster characteristics

Introduction

Spatial distribution patterns of plant populations reflect ecological adaptation capacity and environmental plasticity mechanisms, facilitating characterization of ecological processes and identification of key factors influencing pattern formation and dynamics. Aggregated distribution, where individuals form groups or clusters, represents a fundamental pattern in plant populations. Within aggregated distributions, individuals cluster at small scales, with these clusters further superimposing or aggregating to form larger-scale population-level patterns. Populations typically exhibit multi-scale clustering phenomena, with large- and small-scale clusters combining to create distinct spatial structures that vary dynamically with scale. These patterns represent adaptive strategies to different habitats and involve specific ecological processes.

Soil salinity in salt marsh wetlands constitutes a critical environmental factor affecting plant distribution and reproduction, influencing seed germination and consequently constraining individual numbers and distribution ranges. Under salt stress, populations develop morphological sizes and biomass accumulation adapted to their habitats, altering ecological relationships both within and among clusters and triggering changes in survival strategies and competitive relationships. Studying the intrinsic characteristics of aggregated distribution provides an important approach for understanding population co-adaptation to habitats.

Suaeda corniculata is an annual, succulent halophyte belonging to the family Chenopodiaceae, growing in saline or salt-affected soils with prostrate or erect stems. As a pioneer species for saline wetland restoration, it exhibits strong salt tolerance. Current research on plant spatial patterns and habitat adaptation has primarily focused on soil moisture, micro-topography, soil texture, and density-dependent factors, with most studies examining population pattern dynamics along environmental gradients and clustering characteristics at single scales. However, understanding remains limited regarding multi-scale spatial patterns of wetland plants under soil salinity conditions and cluster characteristics within aggregated distributions. This study investigates *Suaeda corniculata* populations in a typical inland salt marsh wetland using pair-correlation functions and different null model methods to analyze multi-scale aggregated distribution patterns across salinity gradients. We address two key questions: (1) How are large- and small-scale clusters spatially structured within population aggregated distributions? (2) How do cluster characteristics vary along salinity gradients? Our aim is to enrich understanding of plant population pattern responses and ecological processes to soil environmental conditions, providing a basis for wetland ecosystem function optimization and vegetation restoration.

1. Study Area and Methods

1.1 Study Area Description

The study area is located in the Qinwangchuan National Wetland Park in the southern Qinwangchuan Basin of Lanzhou City, Gansu Province (103°35 38 –108°38 37 E, 36°23 59 –36°27 56 N). The basin, situated on the southern edge of the Wushaoling fold mountains, slopes gradually from northeast to southwest with an overall gradient of 1/80–1/100. Characterized by a typical continental arid climate, the region receives an average annual rainfall of 265 mm with evaporation reaching 1879 mm. Groundwater flows near the surface, creating natural brackish inland salt marsh wetlands with evident salt patches on the surface. The soil is secondary salinized, with dominant vegetation including *Suaeda corniculata*, *Tripolium vulgare*, *Tamarix austromongolica*, *Elaeagnus angustifolia*, *Phragmites australis*, *Salicornia europaea*, *Salsola collina*, and *Poa annua*.

Based on field surveys, we selected a low-lying area (200 m × 50 m) with relatively flat surface in the conservation and restoration zone of the park. The terrain slopes slightly from northeast to southwest, forming a depression at the northeastern edge of the sample belt. Soil salinity distribution follows micro-topographic patterns: higher elevations with good drainage have lower groundwater tables and less salt accumulation, while depressions with poor drainage have higher groundwater and salt content. This creates a redistribution of soil salinity across micro-topography. Following this pattern from northeast to southwest, we established a salinity gradient and set up four sample plots (I, II, III, IV) based on uniform community appearance.

1.2 Sampling Design and Survey Methods

Each plot measured 2 m × 2 m and was divided into 400 cells of 10 cm × 10 cm. Using the lower left corner as the origin point, we recorded the precise location of all individuals within each small quadrat. We measured cover, density, and aboveground biomass for all species in each plot. Soil samples were collected from each plot at 10 cm intervals from the surface to 1 m depth using ring cutters. Samples were air-dried indoors, and soil salinity was measured using the electrical conductivity method. Fifty grams of soil were mixed with 250 mL of water (5:1 ratio), shaken for 3 minutes, and filtered using a Buchner funnel until the extract was clear. Electrical conductivity was measured using a DDS-11C portable conductivity meter (Shanghai Leici Instrument Factory).

1.3 Point Pattern Analysis

1.3.1 Pair-Correlation Function The pair-correlation function $g(r)$, a modified Ripley' s K function, avoids the cumulative effect of traditional K functions and provides more detailed characterization of spatial distribution patterns. The function form is:

$$g(r) = \frac{K'(r)}{2\pi r}$$

where K’ (r) is the derivative of Ripley’ s K function. Confidence intervals at the 95% level were obtained through Monte Carlo simulations using maximum and minimum values to determine significant deviations from null models.

1.3.2 Null Models Selecting null models with clear ecological meaning is crucial for spatial point pattern analysis, as different research questions require different null hypotheses. To reveal spatial pattern characteristics of dominant populations in inland salt marsh wetlands, we selected three progressively related models based on previous research: Complete Spatial Randomness (CSR), Poisson Cluster Process, and Double-Cluster Process.

Complete Spatial Randomness (CSR) Model:
CSR represents a homogeneous Poisson process where individuals are distributed independently with equal probability at any location. This model is typically used to test for uniform or clustered distribution patterns.

Poisson Cluster Process (Thomas Process):
Building upon CSR, this model assumes randomly and independently distributed cluster centers with density . Points within clusters follow a Poisson distribution with intensity , and their locations relative to cluster centers follow a bivariate Gaussian distribution with variance ^{2}. The cluster scale approximates the cluster radius, with determining cluster size. This model detects single-scale clustering but cannot identify nested structures.

Double-Cluster Process:
This multi-generation extension of the Poisson cluster model incorporates two distinct spatial scales. When populations show CSR with small-scale clustering, the Poisson cluster model can analyze large-cluster characteristics. When large clusters contain nested smaller clusters, the double-cluster model is applied. The function expression is:

$$g(r) = 1 + \frac{1}{4\pi\sigma_1^2\rho_1}\exp\left(-\frac{r^2}{4\sigma_1^2}\right) + \frac{1}{4\pi\sigma_2^2\rho_2}\exp\left(-\frac{r^2}{4\sigma_2^2}\right)$$

where and represent large- and small-scale cluster sizes, respectively; and are cluster center densities; and other parameters share meanings with the Poisson cluster model.

1.4 Data Processing

Plant individual coordinates were collected using GetData Graph Digitizer 2.22. All statistical analyses and mapping were completed using Programita 2014 and Origin Pro 8.6 software for point pattern calculations under different null models.

2. Results

2.1 Biological Characteristics of *Suaeda corniculata* in Response to Salinity

Soil salinity is a key factor affecting *Suaeda corniculata* growth and development. Electrical conductivity measurements showed a decreasing trend from plot I to IV, validating micro-topographic redistribution of soil salinity. Biological characteristics varied significantly across salinity gradients: population density initially increased then decreased, while cover and aboveground biomass showed consistent decreasing trends. In high-salinity plots (I, II), plants primarily exhibited prostrate growth, whereas in low-salinity plots (III, IV), erect growth dominated. *Tripolium vulgare* density decreased with salinity, but individual plant size and cover increased, with natural height showing no significant variation across the gradient .

2.2 Intrinsic Characteristics of Aggregated Spatial Patterns

Analysis Based on Complete Spatial Randomness Model:
The $g(r)$ values for plots I, II, and III exceeded confidence intervals at scales of 0–41 cm, 0–37 cm, and 0–75 cm, respectively, indicating aggregated distributions. As scale increased, populations gradually shifted to random or uniform distributions. Plot IV showed aggregation only at 32–44 cm, with random distribution at other scales [Figure 1: see original paper].

Analysis Based on Poisson Cluster Model:
The Poisson cluster model revealed that $g(r)$ exceeded confidence intervals at 1.5–4.5 cm, 0–5.5 cm, 1–8.5 cm, and 0–12.5 cm for plots I–IV, respectively, indicating small-scale clustering within aggregated distributions. Small clusters superimposed and aggregated to form composite large-scale clusters, suggesting multi-scale aggregation and nested double-cluster structures. Parameter simulations showed good fit, with composite large-cluster numbers (A) decreasing as population size increased [Figure 2: see original paper].

Analysis Based on Double-Cluster Model:
The double-cluster model confirmed inferences from previous analyses. Large-cluster size parameters ( ) significantly deviated from confidence intervals, with all plots conforming to the double-cluster model. This revealed a spatial structure where large clusters nested numerous small clusters, showing two critical scales of aggregation. Small-cluster size ( ) remained relatively stable, while the number of small clusters per large cluster (A) decreased across the salinity gradient. As soil salinity decreased, large-cluster size increased while the number of small clusters within each large cluster declined [Figure 3: see original paper].

3. Discussion

3.1 Spatial Combination Characteristics of Clusters in Aggregated Distributions

Population aggregation reflects positive ecological relationships within populations, resulting from interactions between biological characteristics, intra- and interspecific relationships, and habitat conditions. *Suaeda corniculata* seeds disperse and concentrate near maternal plants after release, creating localized aggregations. In high-salinity zones, salt stress strongly inhibits seed germination and seedling survival, particularly during the most vulnerable seedling stage. Photosynthesis and nutrient absorption are suppressed, reducing growth rates and causing plant dwarfism. At this stage, intraspecific facilitation dominates as individuals support each other to withstand adverse conditions, with small neighbor distances and obvious community dominance.

As salinity decreases, salt inhibition weakens, and *Tripolium vulgare* becomes more competitive. *Suaeda corniculata* cover and biomass decrease, plants normalize, and interspecific competition intensifies. The dominant factor shaping positive ecological relationships shifts from salinity stress to competition. At larger scales, high-density clustering leads to competition and self-thinning, causing populations to fragment into multiple clusters and exhibit negative ecological relationships. This nested double-cluster pattern, where large-scale clusters overlay random distributions, aligns with findings from Wiegand et al. [5, 28, 29].

3.2 Multi-scale Cluster Characteristics Along Salinity Gradients

Gradient variation in cluster characteristics results from combined effects of seed dispersal, salinity stress, and intraspecific competition. In high-salinity plots (I, II), abundant seed banks, high germination rates, and plant dwarfism create conditions for numerous small, dense clusters within large clusters. As salinity decreases, plant normalization increases spatial occupation and individual distances, reducing the number of small clusters within large clusters due to intensified intraspecific competition. Large-cluster size increases while small-cluster size remains relatively stable, reflecting adaptive adjustments in plant morphology and composition. The gradient transformation from positive to negative ecological relationships, coupled with shifts in population niches and resource competition, drives these characteristic changes.

4. Conclusion

Spatial combination characteristics and scale-dependent variations in cluster features represent adaptive processes of *Suaeda corniculata* populations to environmental heterogeneity, integrating seed dispersal, soil salinity inhibition, and intra- and interspecific relationships. Our findings demonstrate that populations adjust plant morphology and composition along salinity gradients to enhance survival and spatial colonization ability. This drives gradient transformation between positive and negative ecological relationships, with corresponding shifts in cluster spatial organization. Salinity inhibition directly affects population density and cluster numbers, while adjustments in population niches and competitive abilities alter cluster nesting and dimensions. Along decreasing salinity gradients, the primary drivers of ecological relationships and cluster formation gradually shift from salinity stress to interspecific competition. Multi-scale analysis of aggregated distribution patterns effectively reveals ecological processes in specific habitats, though more complex patterns such as cluster-cluster superposition and double-cluster-random distribution overlays require further investigation.

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Note: Figure translations are in progress. See original paper for figures.