

Population Structure and Dynamic Characteristics of Mangrove Plants in the Beilun River Estuary, Guangxi (Postprint)

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Abstract

This study examined four mangrove species in the Beilun Estuary National Nature Reserve of Guangxi: *Kandelia obovata*, *Aegiceras corniculatum*, *Avicennia marina*, and *Bruguiera gymnorrhiza*. Based on field plot surveys, we analyzed and predicted the population structure and dynamics of these four mangrove species using methods including height class and size class structure, static life tables, survival curves, time series analysis, and seven aggregation intensity indices. The objectives were to elucidate the structural characteristics and dynamic patterns of mangrove populations and communities, as well as their underlying driving mechanisms, thereby providing fundamental data and scientific basis for the conservation and restoration of mangrove ecosystems in Guangxi. The results indicated that *Bruguiera gymnorrhiza* and *Kandelia obovata* populations exhibited good regeneration, *Aegiceras corniculatum* regeneration faced certain resistance with relatively stable populations, while *Avicennia marina* populations showed poor regeneration with an obvious declining trend. The four mangrove species exhibited considerable differences in survival among different age classes, with survival rates and life expectancy generally decreasing with increasing age class. The survival curve of *Avicennia marina* populations belonged to Deevey Type I, where individuals could reach their average physiological lifespan; *Bruguiera gymnorrhiza* and *Kandelia obovata* populations belonged to Deevey Type II, with relatively consistent mortality rates across age classes; while *Aegiceras corniculatum* populations were intermediate between Deevey Type I and Type II, showing higher mortality during the juvenile stage that gradually approached typical levels after the middle-age stage. Time series analysis also demonstrated that future population numbers of *Avicennia marina* would decrease significantly, with populations gradually declining; future numbers of *Aegiceras corniculatum* would show a stable-to-declining pattern; while future populations of *Bruguiera gymnorrhiza* and *Kandelia obovata* would tend

to increase. Populations of different age classes for the four mangrove species mostly showed aggregated distributions, with aggregation intensity tending to decrease with increasing age class. These results demonstrate that the population dynamics of the four mangrove species in the Beilun Estuary are closely related to the successional stage of the community. The pioneer species *Avicennia marina* is in a rapid decline stage, *Aegiceras corniculatum* in the early-to-mid succession stage shows a stable-to-declining pattern, while *Kandelia obovata* and *Bruguiera gymnorrhiza* in the mid-to-late succession stage exhibit varying degrees of growth, reflecting that the surveyed mangrove community is currently in the middle successional stage. The *Avicennia marina* and *Avicennia marina* + *Aegiceras corniculatum* associations will gradually succeed into associations dominated by *Bruguiera gymnorrhiza*. Furthermore, mangrove population dynamics are regulated by multiple factors including reproductive characteristics, habitat conditions, intra- and inter-specific competition, and pest infestations.

Full Text

Preamble

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Population Structure and Dynamics of Mangrove Species in Beilun Estuary, Guangxi, Southern China

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Abstract

This study investigated the population structure and dynamics of four dominant mangrove species—*Kandelia obovata*, *Aegiceras corniculatum*, *Avicennia marina*, and *Bruguiera gymnorrhiza*—in the Beilun Estuary National Nature Reserve, Guangxi. Based on field surveys of permanent plots, we employed height class and size class structure analysis, time series analysis, and seven aggregation intensity indices to characterize and predict population dynamics. The results illuminate structural characteristics and dynamic patterns of mangrove populations and communities, providing fundamental data and a scientific basis for conservation and restoration of mangrove ecosystems in Guangxi.

Using survey data from 12 permanent plots (each 20 m × 20 m), we analyzed height class, size class, static life tables, survival curves, and time sequences to describe and predict population structure and dynamics. Seven aggregation intensity indices, including mean crowding index, clumping index, and patchiness index, were applied to analyze spatial distribution patterns across different size classes.

Height and size structure analyses indicated that *K. obovata* and *B. gymnorrhiza* had abundant seedlings and saplings, showing robust regeneration. *A. corniculatum* regeneration was hindered to some extent, with fewer adult plants, though seedling quantity and overall population remained relatively stable. *A. marina* showed poor regeneration with few individuals and no seedlings, exhibiting an obvious decline.

Static life table analysis revealed substantial differences in survival among age classes for the four species, with survival and life expectancy generally decreasing with age. Survival curve analysis showed that *A. marina* followed a Deevey Type I curve, with all individuals reaching average physiological lifespan and dying almost simultaneously. *B. gymnorrhiza* and *K. obovata* showed Deevey Type II curves, with relatively consistent mortality rates across age classes. *A. corniculatum* fell between Deevey Types I and II, with relatively high mortality in young age classes that gradually stabilized after middle age.

Time series analysis predicted that *A. marina* population would decrease; *A. corniculatum* would show a stable trend with slight decline as young individuals decrease and adults increase; and *B. gymnorrhiza* and *K. obovata* populations would increase due to good regeneration across age classes.

Calculations of seven aggregation intensity indices demonstrated that populations of different age classes mainly exhibited clumped distributions, with ag-

gregation intensity tending to decrease with age. Population dynamics were closely related to community succession stages. The pioneer species *A. marina* was in rapid decline; *A. corniculatum*, typical of early-mid succession, was stable with slight decline; and *B. gymnorrhiza* and *K. obovata*, typical of mid-late succession, showed various degrees of growth. These results suggest the studied mangrove communities are in middle succession stage, with *A. corniculatum* associations gradually succeeding to *B. gymnorrhiza*-dominated associations.

Population dynamics were regulated by multiple factors including habitat conditions, intra- and interspecific competition, and insect pests. The clumped distribution pattern was closely related to reproductive modes and habitat conditions, with decreasing aggregation intensity likely caused by self-thinning or thinning effects from intensified interactions.

Keywords: mangrove plant; population structure; spatial distribution pattern; time sequence analysis; Beilun Estuary

Introduction

Population structure and dynamics are core topics in ecological research. As the fundamental unit of species existence, adaptation, and evolution, populations serve as the link among individuals, communities, and ecosystems. Analysis of plant population structures can reflect current population status and reveal future dynamics. Mangroves are woody plant communities growing in tropical and subtropical coastal intertidal zones subject to periodic seawater inundation, representing critical coastal ecological zones that provide important services in wave attenuation, biodiversity maintenance, and coastal ecological security.

China's mangroves are mainly distributed in Guangdong, Hainan, and Guangxi, with Guangxi's mangroves primarily located in the Beibu Gulf coastal zone's Pearl Bay, Qinzhou Bay, and Yingluo Bay. Dominant species include *Avicennia marina*, *Aegiceras corniculatum*, *Kandelia obovata*, *Rhizophora stylosa*, and *Bruguiera gymnorrhiza*. However, Guangxi's mangrove ecosystems face numerous threats including habitat loss, fragmentation, pollution, and invasive species, with some areas showing gradual decline. From 1960-1976, Guangxi's mangrove area decreased by 22.16% from 9,062.5 hm² to 7,054.3 hm², averaging 0.53% annual loss. While artificial afforestation has stabilized and slightly increased mangrove area in some mudflats, natural mangroves continue facing reduction threats and require strengthened scientific research and conservation.

Previous studies on Guangxi mangroves have focused on restoration measures and large-scale spatiotemporal distribution changes, with limited recent community-level basic research. Given multiple environmental stressors, long-term ecological studies on mangrove structure and dynamics are urgently needed. The Beilun Estuary National Nature Reserve, located at the southwesternmost end of China's mainland coastline, contains the country's

s only contiguous border mangrove ecosystem, providing valuable samples for studying natural mangrove structure and function. However, ecological research on Beilun Estuary mangroves remains limited, particularly regarding population structure and dynamics.

This study analyzes population structure and dynamics of four dominant mangrove species (*K. obovata*, *A. corniculatum*, *A. marina*, and *B. gymnorrhiza*) using height class, size class, static life tables, survival curves, time series analysis, and spatial distribution patterns. The objectives are to elucidate structural characteristics, dynamic patterns, and driving mechanisms of mangrove populations and communities, providing fundamental data for conservation and restoration of Guangxi' s mangrove ecosystems.

1. Study Area

The Beilun Estuary National Nature Reserve (21°31'00" -21°37'30" N, 108°00'30" -108°16'30" E) is located in Fangchenggang City, Guangxi, bordering Vietnam to the southwest and the Beibu Gulf to the southeast, spanning Pearl Bay, Jiangping Islands, and Beilun Estuary. The reserve contains approximately 53 km² of mangroves. The climate is south subtropical maritime monsoon, with mean annual temperature of 22.3°C (extreme maximum 37.8°C, minimum 2.8°C), mean annual precipitation of 2,220.5 mm, and mean evaporation of 1,400 mm. The tidal regime is regular diurnal with mean tidal range of 2.22 m (based on Yellow Sea datum), mean water level of 0.34 m, mean seawater temperature of 23.5°C, and salinity of 23.1‰.

In addition to the four study species, the reserve' s mangrove flora includes *Rhizophora stylosa*, *Lumnitzera racemosa*, *Acanthus ilicifolius*, *Acanthus ebracteatus*, and *Excoecaria agallocha*.

2. Methods

2.1 Plot Setup and Survey

Based on comprehensive surveys of Beilun Estuary mangroves, we selected areas with relatively concentrated natural mangrove distribution in Pearl Bay in December 2015. Following mangrove distribution patterns across high, middle, and low intertidal zones, we established 12 permanent 20 m × 20 m plots with 10 m intervals. Each plot was divided into 10 m × 10 m subplots. All individuals with basal diameter ≥ 1 cm and DBH ≥ 1 cm were numbered and recorded by species, with height measurements. Seedlings with DBH < 1 cm were recorded by species and height only. Geographic coordinates, relative coordinates, disturbance levels, and soil properties were documented for each plot.

2.2 Height and Size Class Structure

Height classes were divided into five categories: Class I (0.0–1.0 m), II (1.0–2.0 m), III (2.0–3.0 m), IV (3.0–4.0 m), and V (4.0–5.0 m). While size class cannot directly represent age class, under similar habitat conditions, size class and age class show consistent responses to environmental gradients. When age data are unavailable, size class is commonly used as a proxy for age class analysis.

Given distinct growth habits among species—*B. gymnorrhiza* has a single main stem while *A. corniculatum* and *A. marina* are multi-stemmed shrubs—we used different classification schemes: *B. gymnorrhiza* was classified by DBH, while *A. corniculatum* and *A. marina* were classified by basal diameter. Size classes were defined as: Class I (<0.5 m height), II (0.5 m height), and for individuals 1 cm DBH, basal diameter increments of 2 cm defined subsequent classes.

2.3 Static Life Tables and Survival Curves

Following Wei et al.'s method, we compiled static life tables for the four species, using size class as a proxy for age class. Parameters included: standardized survival number (l), mortality (q), standardized mortality (Q), total survivors beyond size class (T), life expectancy (e), and logarithmic standardized survival number ($\lg L$). Survival curves were plotted with size class (x) on the x-axis and l on the y-axis.

2.4 Time Series Analysis

Time series analysis has proven effective for predicting plant population dynamics. We applied one-step moving average method to predict age structure changes. The formula is:

$$M_t^{(n)} = \frac{1}{n} \sum_{k=t-n+1}^t X_k$$

where M represents population size at age class t after n age-class intervals, X is individual number at age class k , and n is the prediction interval (2, 4, 6, and 8 age classes in this study).

2.5 Spatial Distribution Patterns

We used seven aggregation intensity indices to analyze spatial distribution patterns: mean crowding index (m), clumping index (I), patchiness index (m/m), Cassie index (CA), negative binomial parameter (K), and Green index (GI). Higher values indicate greater aggregation. These indices provide complementary perspectives to ensure result reliability. Detailed calculations follow standard ecological methods.

3. Results and Analysis

3.1 Population Height Structure

Only three species (*K. obovata*, *A. marina*, and *B. gymnorrhiza*) appeared in the plots, representing the dominant mangroves in Beilun Estuary. Height analysis showed most individuals were in Class I (0–1 m), comprising 64.60% of the total (324 individuals). Classes II, III, IV, and V accounted for 17.11%, 12.75%, 5.24%, and 0.30%, respectively.

A. marina height structure was dominated by Class I (1,911 individuals, 54.96%), with few individuals exceeding 4.0 m, indicating poor regeneration. *A. corniculatum* height structure concentrated in Classes I (1,291 individuals, 37.66%) and II (1,183 individuals, 53.36%), showing stable populations but regeneration obstacles. *K. obovata* showed a bimodal pattern with abundant seedlings and saplings, indicating good regeneration. *B. gymnorrhiza* exhibited a typical inverse pyramid structure with most individuals in Class I (733 individuals, 54.65%), demonstrating robust regeneration.

[Figure 1: see original paper] Population height structure of four mangrove plants in Beilun Estuary

3.2 Population Size Class Structure

Size class analysis revealed single peaks for *B. gymnorrhiza* and *A. corniculatum* populations. *A. marina* and *A. corniculatum* had maximum individual numbers in Class I (1,336 and 462 individuals, respectively). *K. obovata* showed two peaks. *B. gymnorrhiza* and *K. obovata* had complete size class structures, while *A. marina* and *A. corniculatum* lacked certain size classes, indicating decline trends. Compared with height structure, size class structure further confirmed that *A. marina* is a declining population, *A. corniculatum* shows gradual decline, while *B. gymnorrhiza* and *K. obovata* are growing populations.

[Figure 2: see original paper] Population size class structure of four mangrove plants in Beilun Estuary

3.3 Static Life Tables

Static life tables showed that survival numbers differed greatly among age classes, generally decreasing with age. Life expectancy also showed decreasing trends. *A. marina* mortality increased with size class, peaking at Class III. Negative mortality values occurred when Class I, II, and III individuals were fewer than the subsequent class, consistent with extremely low numbers in these classes. *B. gymnorrhiza* and *K. obovata* had relatively low juvenile mortality, while *A. corniculatum* showed high early mortality that stabilized after middle age. Life expectancy typically peaked at intermediate age classes then gradually declined.

Static life tables of four mangrove plants in Beilun Estuary

3.4 Population Survival Curves

Survival curves are classified into three Deevey types: Type I (most individuals reach average physiological lifespan and die simultaneously), Type II (constant mortality across age classes), and Type III (high juvenile mortality, low and stable later mortality). *A. marina* showed a Deevey Type I curve, with all individuals reaching average lifespan. *B. gymnorrhiza* and *K. obovata* showed Type II curves with relatively consistent mortality across age classes. *A. corniculatum* fell between Types I and II, with high early mortality that gradually stabilized after middle age. Maximum survival rates occurred at seedling stages for all species.

[Figure 3: see original paper] Survival curves of four mangrove plants in Beilun Estuary

3.5 Time Series Analysis

Time series analysis predicted that *A. marina* populations would decline across all age classes. *A. corniculatum* would show decreased young individuals but increased adults, maintaining stable populations with slight decline. *B. gymnorrhiza* and *K. obovata* populations would increase across age classes due to good recruitment, though growth rates would differ. Overall, *A. marina* will clearly decline, *A. corniculatum* will remain stable with slight decline, while *B. gymnorrhiza* and *K. obovata* will increase.

Time sequence analysis of age structure of four mangrove plant populations in Beilun Estuary

3.6 Spatial Distribution Patterns

All seven aggregation indices indicated clumped distributions for all four species across different age classes, except for random distribution in *A. marina* Class I and *A. corniculatum* Class I. Aggregation intensity generally decreased with age. This clumped pattern likely relates to reproductive characteristics and habitat heterogeneity. Decreasing aggregation intensity with age may result from self-thinning or density-dependent thinning due to intensified intra- and interspecific interactions.

Population distribution patterns of four mangrove plants in Beilun Estuary

4. Discussion

4.1 Mangrove Population Structure and Dynamics

Population structure is influenced by biological factors (intraspecific and interspecific competition, pests) and environmental conditions. Analyzing population structure helps infer dynamic processes and underlying ecological mech-

anisms, revealing survival status and regeneration strategies. Our integrated analyses consistently show that *A. marina* is a declining population, *A. corniculatum* is relatively stable but shows decline signs, while *K. obovata* and *B. gymnorrhiza* are growing populations.

A. marina, a pioneer species distributed in low intertidal zones, has cryptoviviparous reproduction and extensive root systems enabling rapid colonization of bare substrates. After pioneer community formation, reduced wave action and accumulated organic matter create conditions for other species, but changed salinity and light environments hinder pioneer seedling establishment. *K. obovata* and *B. gymnorrhiza*, with viviparous reproduction, gradually dominate in muddy habitats. The successional sequence appears to be: *A. marina* association → *A. corniculatum* association → *K. obovata* association → *B. gymnorrhiza* association → *Heritiera* and *Thespesia* association. Our results support this pattern, indicating the studied communities are in middle succession stage.

Biological factors also drive population dynamics. After *A. marina* forms monospecific stands, intraspecific competition for light, space, and nutrients intensifies, causing self-thinning. Interspecific competition with *K. obovata* also reduces *A. marina* survival and reproduction. Additionally, pest outbreaks significantly impact mangrove dynamics. The moth *Oligochroa cantonella* specifically feeds on *A. marina* leaves, causing severe defoliation and mortality, while rarely affecting *K. obovata* and *B. gymnorrhiza*. The observed declines in *A. marina* and *A. corniculatum* may relate to intensified competition and pest outbreaks, though this requires further verification.

4.2 Spatial Distribution Patterns of Mangrove Populations

Clumped distribution, the most common pattern in terrestrial forests, results from long-term adaptation to heterogeneous habitats, seed dispersal limitation, and competition. Our study shows clumped distributions across developmental stages, with intensity decreasing with age, consistent with studies from Shenzhen, Macao, Dongzhai Harbor, and Zhangjiang Estuary.

At local scales, clumped patterns relate to biological characteristics: viviparous *K. obovata* seedlings drop vertically near mother trees, increasing spatial aggregation. Cryptoviviparous *A. marina* and *A. corniculatum* have light, buoyant propagules, but clonal reproduction and microtopographic heterogeneity also create clumped distributions. Depressed microtopography can trap more propagules, enhancing aggregation.

Decreasing aggregation intensity with age is common in forest stands. As mangrove populations age, increasing resource demands intensify intra- and interspecific interactions, causing density-dependent thinning that reduces clumping. Most previous studies used small plots (10 m × 10 m or 20 m × 20 m), but spatial pattern accuracy depends on sampling scale and habitat type. We recommend establishing large-scale permanent plots (e.g., 100 m × 300 m) covering multiple intertidal zones and heterogeneous habitats, using point pattern analysis

or wavelet analysis to better resolve scale-pattern relationships and underlying mechanisms through long-term monitoring of flora, fauna, microorganisms, and environmental factors.

5. Recommendations for Mangrove Conservation and Management

To address natural mangrove degradation, we recommend: (1) Establishing mangrove resource databases and pest early-warning systems; (2) Implementing artificial tending measures for declining species, protecting young forests to improve survival and coverage; (3) Using natural mangrove structure as reference for developing near-natural restoration techniques; (4) Following the “right species for right site” principle, selecting appropriate species for different tidal zones; (5) Using mixed-species planting with native trees and shrubs to enhance structural complexity and stability.

Early afforestation focused on shrub species (*A. corniculatum* and *A. marina*), while recent efforts emphasize small trees (*K. obovata*) and exotic species (*Sonneratia apetala*). For degraded pioneer shrub communities, we should introduce taller late-successional species like *B. gymnorrhiza* and *R. stylosa* to create two-layered mixed stands following natural succession. For pure stands (e.g., *S. apetala*), thinning, pruning, and enrichment planting with native species can increase biodiversity and reduce pest damage, forming mixed communities such as *S. apetala*-*K. obovata* associations that enhance ecological benefits.

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