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Original article

Regeneration of *Rhizophora mucronata* (Lamk.) in degraded mangrove forest: Lessons from point pattern analyses of local tree interactions

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ABSTRACT

Spatial structural patterns emerging from local tree interactions influence growth, mortality and regeneration processes in forest ecosystems, and decoding them enhance the understanding of ecological mechanisms affecting forest regeneration. Point-Patterns analysis was applied for the very first time to mangrove ecology to explore the spatial structure of *Rhizophora mucronata* regeneration in a disturbed mangrove forest; and the pattern of associations of juvenile–adult trees. *R. mucronata* trees were mapped in plots of 50 m × 10 m located at the seaward, central and landward edge along 50 m wide transect in the forest, and the mapped patterns were analysed with pair correlation and mark-connection functions. The population density of *R. mucronata* differed along the tidal gradient with the highest density in the central region, and the least near the shoreline. The study revealed that short distance propagule dispersal, resulting in the establishment of juveniles in closed distance to the mother trees, might not be the driving force for distribution of this species. The spatial structural pattern of *R. mucronata* population along tidal gradient showed a characteristic spatial aggregation at small scale, but randomly distributed as the distances become larger. There was a distinct spatial segregation between recruits and adult trees, and hence spatially independent. Though, adult–adult trees associations did not show a clear spatial segregation pattern; the recruit–recruit species associations exhibited significant clustering in space. Although habitat heterogeneity might be responsible for the local scale aggregation in this population, the effect of plant–plant conspecific interactions is more probable to inform the long-term structure and dynamics of the population of *R. mucronata*, and ditto for the entire forest.

1. Introduction

Mangrove forest species mostly thrive in harsh environment at the land–sea interface; and it is suggestive that environmental conditions vary along land–sea gradients, informing the species specific natural constellation in optimally favourable zones based on their habit and tolerance to prevailing conditions. Species distribution and spatial structure in mangrove forests are informed by the synergistic and/or antagonistic influences of temperature, salinity, tidal inundation, soil texture, pH, geomorphology, propagule predation, among others (Smith 1992). Coalescing with these factors in determining the forest spatial structure are recurrent natural disturbances (wind, cyclones, flooding, tsunamis, etc.) and human-induced pressure (including purposeful forest management). Albeit, mangrove ecosystems continue to undergo structural and compositional changes (Reddy and Roy, 2008); and the spatial pattern of the current vegetation provides a good indicator for the processes underlying such changes.

Earlier scientists articulated that the spatial patterns of tree configuration describing the structural characteristics of forest ecosystems often reveal the pattern of successional development in plant communities (Levin, 1992; Getzin et al., 2008; Eichhorn, 2010; etc.); and can provide insight into the intrinsic ecosystem processes and functional diversity in the system (Luo et al., 2012). The competition or facilitation processes resulting from tree association and interactions do result in specific spatial patterns (Grabarnik and Sarkka, 2009). Getzin et al. (2006) also opined that different spatial patterns may reflect species abilities to survive intra and inter-specific competition during succession. In essence,

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forest spatial patterns, in combination with other factors, influence growth, mortality and regeneration processes, and thereby play significant role in forest ecosystem dynamics (Dieckmann et al., 2000; Grabarnik and Sarkka, 2009). Invariably, analysis of the spatial structural pattern of a given forest ecosystem makes way for increasing understanding of the history, ongoing ecological processes and functions, and future trajectories of forest development (Moorcroft et al., 2001).

The total area covered by mangroves in Kenya was once estimated to be 55,280 ha, but now 45,590 ha with an estimate cover loss of about 18% between 1985 and 2010 (Kirui et al., 2012). With increasing population, economic development, agricultural expansion, urbanization and technology and concomitant over-exploitation of mangrove resources, clear-cutting, hydrologic modification and pollution among others, impacts of human activities on the mangrove forests become more pronounced (Bosire et al., 2008; Duke et al., 2007). Also, climate change anomalies (e.g. fluctuation in sea surface temperature and sea level rise, extensive siltation and sedimentation, altered biogeochemical cycles, etc) work synergistically with anthropogenic pressure to further compromise the ecological integrity of mangroves and the intrinsic ecosystem goods and services (Olagoke, 2012).

In the case of Tudor creek, the mangrove forest has suffered significantly from combined impacts of recurrent human pressure and disturbances from climate-driven Indian Ocean Dipole (IOD) of 1997/98 and 2006, as evidenced by the reduction in areal extent, change in species distribution, biomass loss, canopy damage and gap creations, and irrefutable alteration to stand structure; but also with evidence of viable natural regeneration (Mohamed et al., 2008; Olagoke, 2012). Surveys on vegetation structure indicated that *Rhizophora mucronata* was the dominant species in the forest (Olagoke, 2012 and literature cited therein). It is *ipso facto* worth to examine the spatial pattern of the most abundant species, *R. mucronata* in this rejuvenating mangrove forest to decipher the pattern of regeneration, and the association of juvenile to adult trees, while advancing possible explanation on the processes underlying local to large scale distribution of this species. With Tidal Sorting Hypothesis (TSH) in mangrove systems (Rabinowitz, 1978), or the general opinion that mangrove zonation results from species physiologically aligning to edaphic and habitat conditions, and the expected environmental heterogeneity along tidal gradient, a varying population distribution and spatial structural pattern along tidal gradient was hypothesized in this disturbed forest.

This study therefore aimed at investigating and comparing spatial distribution pattern of *R. mucronata* population along tidal gradients, and determine whether: (1) the species demonstrates a consistent regeneration and distribution pattern, or the spatial structure is formed by tidal gradient; and (2) juvenile positively benefit in the neighbourhood of adult or co-juvenile tree, at fine to coarse scale, irrespective of the position along the tidal gradient.

2. Methodology

2.1. Description of the investigated site

The study was conducted in a rejuvenating degraded mangrove forest in Tudor Creek (4°02′04″S; 39°40′27″E), located at the northwest of Mombasa Island in the coastal province of Kenya. Tudor creek extends some 10 km inland with two main seasonal rivers, Kombeni and Tsalu, draining over 45,000 and 10,000 ha respectively. It is characterized by a 20 m mean depth single narrow sinuous inlet that widens inland to a central 5 m depth basin, covering an area of 637 ha and 2235 ha at low- and high water spring tides respectively (Mohamed et al., 2008). Sediments covering the forest mainly comprise mud, and sand in some parts (ibid). Mangrove forest is distributed over an area of 1465 ha, composed of *R. mucronata*, *Avicennia marina* and *Sonneratia alba* with no distinctive display of species zonation (Mohamed et al., 2008; Olagoke, 2012). Map of Tudor Creek showing the study location and image of the typical appearance of investigated site is shown in Fig. 1

The climate of the study is under the influence of semi annual passage of the inter-tropical convergence zone (ITCZ) and the monsoons in two distinct seasons (Mohamed et al., 2008). The Northern Easterly Monsoon (NEM) and the Southern Easterly Monsoon (SEM) manifest between December and March, and May and October respectively. The pattern of average monthly rainfall and temperature distribution from 2004 to 2011 in Mombasa where the study area resides is presented in Fig. 2.

2.2. Plot location and field measurement

We carried out field survey and forest measurements to assess mangrove structure and spatial pattern across this site between February and April 2012. For this purpose, we relied on the results of classified satellite SPOT imagery data of 2009 and information from vegetation analyses of our field survey (Olagoke, 2012) in selecting a representative study location for entire forest.

For tree measurement, three rectangular plots of 50 m × 10 m were selected in a 50 m wide transect along the tidal land–sea gradient; the first (Seaward; 3°58′57″S, 39°36′45″E) and the third plots (Landward; 3°59′06″S, 39°36′41″E) located near the shoreline and landward side respectively with consideration for edge effects, and the second plot (Central; 3°59′01″S, 39°36′43″E) at the centre. The plots were partitioned into grids of 10 × 10 m to facilitate accurate and efficient measurement of tree coordinates. Assessment of diameter at breast height (DBH, 1.3 m) and height, and the x and y coordinates (reference to the right hand corner of the plot) of the position of all *R. mucronata* trees having DBH ≥2.5 cm was done within the 10 m × 10 m sub-plots. Juvenile with height greater than 40 cm and DBH lower than 2.5 cm were also mapped based on their respective x and y coordinates in each quadrat. Measurement was restricted to this juvenile size class as sampling of tiny seedlings may lower the accuracy and efficiency in tree mapping. All mapped stems were systematically classified into two DBH size classes, including (1) recruits – all regeneration class with no measured DBH and saplings below 5 cm DBH, and (2) adult trees with DBH ≥5 cm. This classification is based on subjective and arbitrary cut-off chosen to allow for comparisons between size classes.

2.3. Data analysis

2.3.1. Methodological approach for spatial statistics

Spatial patterns describing the general distribution of *R. mucronata*, and the intra-specific associations at varying distance scales r (m) were explored with both univariate and bivariate pair-correlation functions (pcf), and mark connection functions (mcf) (Perry et al., 2006; Getzin et al., 2008). The pcf is a normalized distance-dependent density function that describes spatial relationships of neighbouring points, defined by the x, y position of their stems, or point types, defined by stem diameter, species type, growth stage, etc (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). It describes the probability of observing a pair of points separated by a distance r, divided by the corresponding probability for a Complete Spatial Randomness (CSR); and it is expressed as:

$$g(r) = \frac{K'(r)}{2\pi r} \quad \text{for } r \geq 0 \tag{1}$$

where $K'(r)$is the derivative of Ripley's K-function (Ripley, 1977; Wiegand and Moloney, 2004; Wiegand et al., 2007; Law et al.,