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Density-dependent spatial patterning of woody plants differs between a semi-arid and a mesic savanna in South Africa

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ABSTRACT

Savannas can be defined by the co-dominance of grasses and trees. Interactions between these two life forms are relatively well studied, whereas tree-tree interactions attracted increased attention only recently. However, the influence of woody plant density on tree-tree interactions is rarely considered. We studied tree-tree interactions in a semi-arid and a mesic savanna to test for differences between open and dense woody vegetation in relation to broad-scale environmental conditions. We applied spatial point pattern analysis to gain a better understanding of processes, such as competition, facilitation and disturbances, affecting the spatial distribution of trees. Competition between trees was most pronounced in dense vegetation, whereas facilitation effects were more common in open vegetation. Further, we found that factors shaping the spatial patterns differ with scale. At short tree-to-tree distances, results indicate limited seed dispersal as the most influential factor explaining the spatial distribution of trees. However, with increasing tree-to-tree distances, environmental heterogeneity in the semi-arid savanna and disturbances in the mesic savanna became more important. We conclude that studying tree-tree interactions in savannas should explicitly consider the actual woody plant density, especially when different savanna types are compared.

1. Introduction

Savannas represent the largest biome in South Africa as well as on the whole African continent (Rutherford et al., 2006). They are characterized by a continuous grass layer interspersed with scattered trees or shrubs (Scholes and Archer, 1997). The outstanding characteristic of savannas is the co-dominance of the two contrasting plant life forms trees and grasses (Scholes and Archer, 1997). Different savanna types can be classified with respect to the mean annual precipitation (MAP) they receive (Sankaran et al., 2005). In African semi-arid savannas, the MAP is generally < 650 mm/yr and the tree cover is primarily limited by the available soil moisture (Sankaran et al., 2005). The establishment of tree seedlings commonly depends on a sequence of favourable rainfall events and reduced tree-grass and tree-tree competition (Sankaran et al., 2004). Semi-arid savannas are therefore also referred to as climate-dependent savannas (Bond et al., 2003). In contrast, mesic savannas receive > 650 mm/yr MAP, and frequent disturbances such as fire or grazing and browsing are required to prevent canopy closure (Sankaran et al., 2005). Thus, mesic savannas are also referred to as fire-dependent savannas (Bond et al., 2003; Sankaran et al., 2004).

Savanna dynamics and especially the mechanisms allowing the co-dominance of trees and grasses are not fully understood and are still debated (Moustakas et al., 2010; Sankaran et al., 2004). While tree-grass interactions have been a major topic in savanna research (e.g. Accatino et al., 2010; Ward et al., 2013), tree-tree interactions are less commonly studied (House et al., 2003). Additionally, most case studies analysing tree-tree interactions neglect the actual tree density or cover as a potential factor influencing savanna structure (e.g. Meyer et al., 2008; Mureva and Ward, 2016; Pillay and Ward, 2012). However, in order to improve the understanding of savanna dynamics, an improved understanding of not only tree-grass interactions, but also of tree-tree interactions as one major vegetation layer is necessary. Also, studies are generally highly case specific with a lack of cross-site comparisons (House et al., 2003) and do not differentiate between different life-history stages (Sankaran et al., 2004; Ward et al., 2013). Therefore, one possible comprehensive study approach to better understand savanna dynamics is to include tree-tree interactions, different life-history stages and tree densities as well as different savanna types (House et al., 2003; Sankaran et al., 2004).

Such a study requires investigating the effects of tree-tree

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Table 1
Overview of summary statistics and null models used to address the hypotheses about different spatial patterning and tree-tree interactions in semi-arid and mesic savannas. For additional 278 information on the null models seeVelázquez et al. (2016) and Wiegand and Moloney (2014).

Hypotheses	Summary statistic and null model	Figure/Table
(i) The shift from a clustered pattern to a regular pattern with increasing tree height is more pronounced in the semi-arid savanna compared to the mesic savanna.	Univariate pair correlation function $g(r)$ with CSR for each height group.	Fig. 3 Fig. 5
(ii) The shift from a clustered pattern to a regular pattern with increasing tree height is more pronounced in denser vegetation compared to open vegetation.	Univariate pair correlation function $g(r)$ with CSR for each height group. Mark-correlation function $k_{mm}(r)$ with random marking. Correlation between distance to and mean size of 4 nearest neighbours.	Fig. 3 Fig. 4 Fig. 5 Fig. 6 Table 3 Table 4
(iii) Associations between small and large trees occur in both savanna systems	Bivariate pair correlation function $g_{12}(r)$ with antecedent conditions.	Fig. 7
(iv) Associations between small and large trees are primarily found in open vegetation compared to denser vegetation.	Bivariate pair correlation function $g_{12}(r)$ with antecedent conditions. Mark-correlation function $k_{mm}(r)$ with random marking. Correlation between distance to and mean size of 4 nearest neighbours.	Fig. 4 Fig. 6 Fig. 7 Table 3 Table 4

CSR: complete spatial randomness

interactions, e.g. competition and facilitation effects or seed dispersal limitation, on the spatial distribution of individual trees (Meyer et al., 2008; Mureva and Ward, 2016; Pillay and Ward, 2012). One proven method to study both the spatial distribution of trees and their density-dependent properties, such as position or size, is spatial point pattern analysis. The position (rooting point) of each tree is considered as a point in space and the properties of the overall point pattern such as local density, clustering or the distribution of tree characteristics in a local neighbourhood are analysed on a continuum of different spatial scales (Velázquez et al., 2016; Wiegand and Moloney, 2014). Analysing the point pattern allows deducing the underlying ecological processes forming the spatial pattern of trees (Law et al., 2009; Wiegand and Moloney, 2014). In the present study, the term 'tree' refers to trees and shrubs, whereas their individual rooting points define the spatial point pattern of the woody savanna component. There are three fundamental configurations of spatial point patterns: i) random, ii) clustered/associated or iii) regular/segregated, each of which has an ecological interpretation.

A random pattern of trees is commonly attributed to purely stochastic events without dominant processes shaping the pattern (Wiegand and Moloney, 2014). However, a random pattern may also result from non-random processes such as a superposition of different processes (e.g. limited seed dispersal and simultaneous competition) or represent an intermediate transitional state between clustering and regularity.

A clustered pattern of trees is commonly attributed to limited seed dispersal (Caylor et al., 2003; Meyer et al., 2008), vegetative propagation (Meyer et al., 2008) or a heterogeneous environment of favourable regeneration sites (Caylor et al., 2003; Meyer et al., 2008). Clustered patterns due to limited seed dispersal are mainly found for young, small trees (Meyer et al., 2008). Facilitation effects may be another reason for a clustered pattern. These facilitation effects include buffering against extreme temperatures, higher soil moisture and nutrient availability, an improved soil structure or protection from herbivory. Facilitation can also lead to an association between small and large trees, because smaller trees may benefit from the special micro-environment in the subcanopy of larger trees. Such effects are more common in arid and semi-arid ecosystems than in more moist environments (Flores and Jurado, 2003). In mesic savannas, clustering of trees may result from frequent fires or grazing and browsing impacts. Tree clusters suppress the grass growth and hence the fire probability and intensity, thereby limiting the ignition and spread of fires (Accatino et al., 2016; Skarpe, 1991). Consequently, small trees, which are most susceptible to fire (Scholes and Archer, 1997), are less likely to be killed by fire in the neighbourhood of larger trees as large trees reduce the fire intensity.

A regular pattern is commonly attributed to competition effects (Meyer et al., 2008). Competition is the negative influence on a tree exerted by one or several neighbouring trees (Fowler, 1986). At this, the weaker competitor is usually smaller in size or not able to establish or survive (Pielou, 1962; Shackleton, 2002). The latter can be the result of ‘density-dependent mortality’. Density-dependent mortality is often assumed to be more common in dense woody vegetation due to increased competition (e.g. dense forests), but can also be present in encroached or thickened savannas (Sea and Hanan, 2012; Wiegand et al., 2008). A regular pattern is expected for older, larger trees because of their increased competitive strength and space demand leading to a maximization of tree-to-tree distances between mature trees (Wiegand et al., 2006). If density-dependent mortality is present, the spatial pattern of small trees should be more clustered, whereas for large trees the spatial pattern should be more regular (in the following we refer to this change in patterning as ‘shift’ from clustered to regular with increasing tree size). However, density-dependent mortality may be more common in savanna systems without reoccurring disturbances because disturbances, such as fire and grazing or browsing, reduce tree-tree competition (Sea and Hanan, 2012) and promote clustering (Accatino et al., 2016; Skarpe, 1991).

To analyse tree-tree interactions comprehensively, we test four hypotheses about the spatial patterning of trees in different savanna types (semi-arid vs. mesic savanna) and with different tree densities each (open vs. dense vegetation) (Table 1). This approach allows us to learn about possible tree-tree interactions without relying on long-term field observations or experiments. The comparison of climatically different savanna types enables us to deduce the potential influence of broad-scale environmental conditions and to infer the importance of the disturbances and mechanisms being generally characteristic within these climates. The comparison of different tree densities allows us to analyse the degree to which point patterns and tree-tree interactions are density-dependent. We tested the following hypotheses:

(i) The woody savanna layer generally shows a shift from a clustered pattern of small trees to a regular pattern of larger trees likely, due to limited seed dispersal and competition. These patterns are more pronounced in the semi-arid compared to the mesic savanna as a result of less frequent fires.
(ii) The shift from a clustered pattern to a regular pattern is less pronounced in open vegetation compared to denser vegetation, due to competition being less important in open vegetation.