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Fire acting as an increasing spatial autocorrelation force: Implications for pattern formation and ecological facilitation

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ABSTRACT

Fire is an indissoluble component of ecosystems, however quantifying the effects of fire on vegetation is a challenging task as fire lies outside the typical experimental design attributes. A recent simulation study showed that under increased fire regimes positive tree–tree interactions were recorded (Bacelar et al., 2014). Data from experimental burning plots in an African savanna, the Kruger National Park, were collected across unburnt and annual burn plots. Indices of aggregation and spatial autocorrelation of the distribution of trees between different fire regimes were explored. Results show that the distribution of trees under fire were more clumped and exhibited higher spatial autocorrelation than in unburnt plots. In burnt plots spatial autocorrelation values were positive at finer scales and negative at coarser scales potentially indicating co-existence of facilitation and competition within the same ecosystem depending on the scale. The pattern derived here provides inference for (a) fire acting as an increasing aggregation & spatial autocorrelation force, (b) tree survival under fire regimes is potentially facilitated by forming patches of trees and (c) scale-dependent facilitation and competition coexisting within the same ecosystem with finer scale facilitation and coarser scale competition.

1. Introduction

Fire is and has historically been an important regulator of tree community structure in different ecosystems (Pausas and Keeley, 2009). In most cases fires are hard to predict and to control, and their spatial scale exhibits high variance spanning to different levels of magnitude of hectares. Thus, fires lie outside the typical examples of experimental design, and as a result analyzing their effects is often a hard task (Matossian et al., 2013; Van Mantgem and Schwilk, 2009). Theoretical studies have indicated that the spread of fire can be critically influenced by the density (Calabrese et al., 2010) as well as the spatial structure of trees (Bacelar et al., 2014).

Tree spacing can be random, regular, or aggregated (also known as clumped). The regular pattern is created by competition between aggregated neighbouring individuals and death of some of them (Moustakas et al., 2008; Wolf, 2005). In the absence of fire, clumped distributions can be formed by anthropogenic disturbances, soil patchiness, vegetative reproduction, limited dispersal capabilities, as well as gap regeneration – see (Moustakas et al., 2008) and references therein. Theoretically, assuming spatial homogeneity, the spatial distribution that provides optimal growth opportunities for all trees is achieved by equal tree spacing, i.e. regular tree distribution (Wolf, 2005). It has been reported that spatial autocorrelation did not greatly influence assessments of fire effects and that treatments designed to assess heterogeneity in forest conditions prior to the reintroduction of fire will likely be unnecessary (Van Mantgem and Schwilk, 2009). However, a recent study reports increased clumping of trees under more frequent burning, and thus providing inference for higher spatial autocorrelation in the spatial distribution of trees under more frequent burning (Bacelar et al., 2014).

Often unaccounted for in the past, positive (facilitative) and negative (competitive) plant interactions are now considered to have serious implications for population dynamics and ecosystem function (Brooker et al., 2008). Ecological facilitation and reciprocal competition have been often investigated in terms of the stress gradient hypothesis (Bertness and Callaway, 1994), which predicts an increase of positive interactions with increasing environmental stress (Bertness and Callaway, 1994; Blaser et al., 2013; Dohn et al., 2013). To date there are very few studies investigating the effects of fire frequency as a stress gradient on competitive–facilitative

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interactions on plants and the effects of fire are not necessarily straightforward: competition with established vegetation limits plant recruitment and fires create open conditions which can allow new species to establish (Bullock, 2009). However, facilitation theory suggests that destruction of vegetation will restrict germination and survival (Bullock, 2009). A theoretical study recently reported that fire frequency can increase positive tree–tree interactions (Bacelar et al., 2014).

Savannas are ecosystems comprising of a mixture of woody species (trees and bushes), grasses and forbs. They cover about a fifth of the global land surface and about half of the area of Africa, Australia and South America (Sankaran et al., 2005). Savannas are characterised by a continuous grass and a discontinuous tree layer. A savanna, where trees and grasses coexist (Kyriazopoulos et al., 2014), may be viewed as an intermediate ecosystem between grassland (grass dominance) and forest (tree dominance) with increasing precipitation resulting in a denser tree layer yet still discontinues in comparison to a forest (Moustakas et al., 2010; Sankaran et al., 2005). Fire is an indissoluble component of savanna ecosystems (Higgins et al., 2007). Savannas are mainly characterized by ground fires as fuel load derives mainly from grass biomass and such fires occur mainly in mesic or humid savannas (Govender et al., 2006).

The aim of this work is to quantify the effects of fire on tree size class distributions and spacing patterns and link pattern and process (Turner, 2001; Vicente et al., 2014) regarding tree–tree interactions (Bacelar et al., 2014). To that end size and spatial properties of trees in prescribed burning plots in a mesic savanna were compared with unburnt plots on the same location (Nesmith et al., 2011). Prescribed fires managed for resource objectives displayed similar patterns of fire severity, heterogeneity, and seedling and sapling survival with wildfires, creating post-fire conditions that approximate natural fires when assessed on a fine spatial scale (Nesmith et al., 2011). Data from experimental burning plots that included annual burning vs. no burning (control) for the past ~50 years (Govender et al., 2006; Higgins et al., 2007) were used.

The properties of trees examined included indices of aggregation as well as the spatial autocorrelation of their distributions. Two questions were addressed in this study: (i) are trees more aggregated in burnt than in unburnt treatments? This could be the result of fire-generated open conditions resulting in lower tree occupancy thereby leading to a higher aggregation (Karlson et al., 2011) Alternatively a higher aggregation in burnt plots could result from fire increasing positive tree–tree interactions (Bacelar et al., 2014) due to an increased stress gradient (Dohn et al., 2013) with fire as the stressor. (ii) Are tree distributions exhibiting higher spatial autocorrelation values in burnt plots? This would follow up from a potential higher aggregation in burnt plots (Fan and Myint, 2014).

2. Methods

Data were collected in the Kruger National Park (KNP), South Africa between February and March 2010. The park is situated in the savannas of north-eastern South Africa (Fig. 1), and covers an area of ~19,633 km^2. The vegetation in the park is mainly characterised by dense savanna dominated by Acacia and Combretum species. Within the park there are long-term Experimental Burning Plots (EBPs) where fire is manipulated as a treatment for the past ~50 years and thus KNP is an ideal environment for comparing fire effects on vegetation (Govender et al., 2006; Higgins et al., 2007). The experiment was laid out between 1954 and 1956. In 1979, some plots, in some landscapes were split to allow the implementation of additional treatments (Higgins et al., 2007); no data are analysed from these new treatments. The experiment is replicated four times within the Skukuza landscape (plots) within the park. The Skukuza landscapes are on granite soils and the mean annual precipitation is 550 mm. Each replicate plot consists of two different experimental treatments and each treatment is implemented in a 7-ha plot in a split-plot randomised design (Fig. 2a). The burning treatment includes annual burning every August (*F1*) which is the dry season, while the control treatment excludes fire (*F0*).

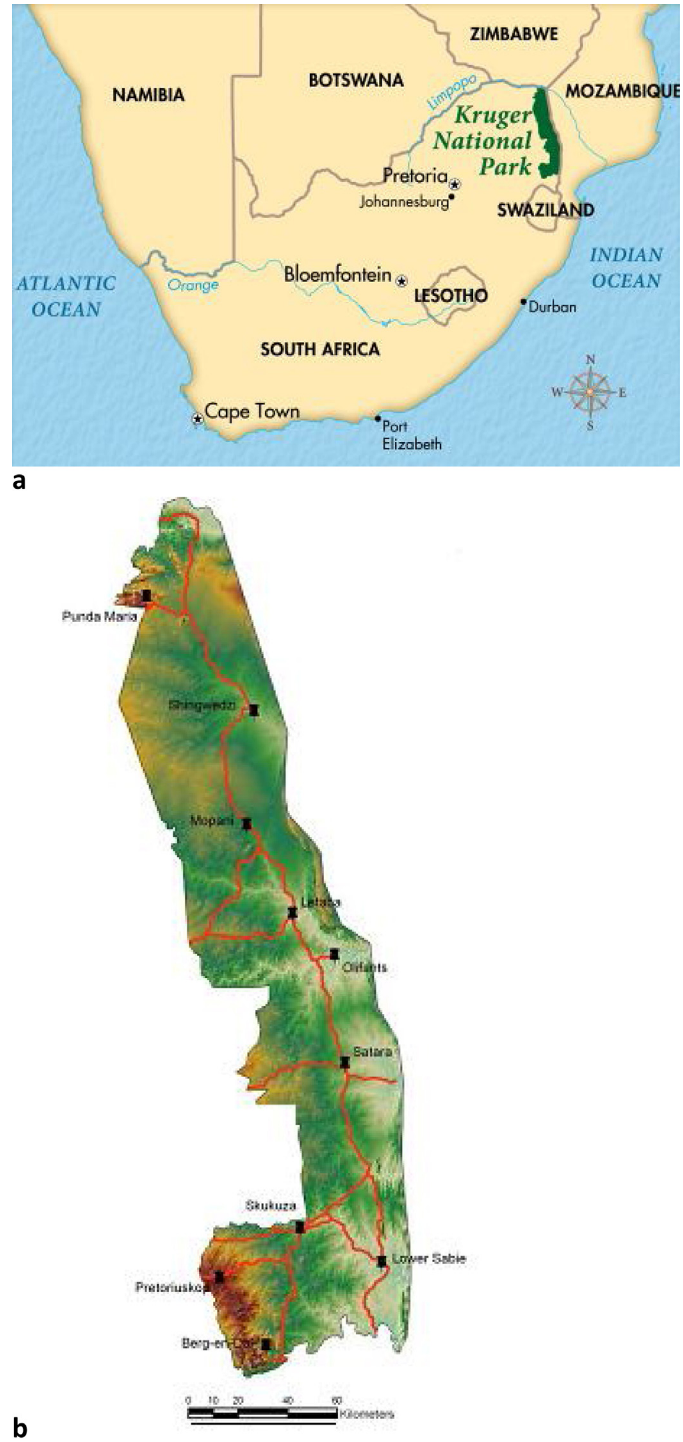

Fig. 1. Geographic location of the study area. The study was conducted in the Kruger National Park (KNP) in South Africa. (a) The location of the park in South Africa. (b) Geophysical map of the park. The experimental plots sampled are all located within a maximum distance of 60 km from Skukuza.

In each of the eight plots, four line transects of 200 m length each were drawn. Each transect was distanced 40 m from the