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Exploring survival strategies of African Savanna trees by partial ordering techniques

Ulfia A. Lenfers*, Rainer Bruggemann, Thomas Clemen

Department of Computer Science, Hamburg University of Applied Sciences, Berliner Tor 7, 20099 Hamburg, Germany

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ABSTRACT

The resilience of savanna ecosystems to climate and land-use changes is an important ecological and management question. The term 'resilience' is used to refer to the ability of a tree species to survive in a specific location, even under changing environmental conditions. In this study, vectors of functional traits of selected savanna tree species are studied by applying partial order algorithms to them. Some ecological interpretations are obtained and are compared to published research. One finding is the high rates of nitrogen fixation for the leaves of *Acacia nigrescens*. In opposition to this well-known fact, we discovered that *Sclerocarya birrea* has a bigger average leaf area than the other four tree species. Additionally, we found high carbonate values within the leaf from *Colophospermum mopane*, *Combretum apiculatum*, and *Terminalis sericea*. These results correspond to different ecological strategies for the tree species in question. It became obvious that geometric structures gained from partial ordering show a very good correspondence to ecological strategies of these tree species. Concepts of partial order theory may therefore be helpful in ecosystem research.

1. Introduction

In order to survive, African savanna tree species have to deal with drought, fire, herbivores, and tree-grass competition (Archibald et al., 2005; Bohrer et al., 2014; Cardoso et al., 2016; Manning et al., 2006; Scholes and Archer, 1997). For this reason, the plant communities of savanna ecosystems change in a specific manner across time and space (Barbosa et al., 2014). Each species in the bi-stable savanna ecosystem (Staal et al., 2016) has its own strategy to respond to the variation of environmental configuration, disturbance, and climate conditions - the so-called ecological niches (February and Higgins, 2016; Neyret et al., 2016; Stevens et al., 2013). In our study, we focused on large deciduous trees. They form a keystone structure (Helm et al., 2009; Levick and Asner, 2013; Manning et al., 2006) and are functionally important for savanna ecosystems.

For the purposes of this study, we took data from Benjamin J Wigley et al. (2016a, 2016b) and selected five major tree species. All of them are common in many areas of the Lowveld in South Africa. The research focused on the comparison between *Sclerocarya birrea* (Marula) (Sb) with *Acacia nigrescens* (An), *Colophospermum mopane* (Cm), *Combretum apiculatum* (Ca), *and Terminalia sericea* (Ts). Marula, ecologically speaking, is one of the most important trees in the South African savannas (Helm et al., 2009; Jacobs and Biggs, 2002), as it provides food and shade for several groups of animals. The leaves are browsed by mammalian herbivores and insects, the bark is stripped by elephants, and the fruits are eaten by several wild animals (Shackleton, 2002).

Several investigations were also performed within the context of *Sclerocarya birrea* and provided a broad data basis (Emanuel et al., 2005; Helm et al., 2009; Jacobs and Biggs, 2002; Maroyi, 2013; Shackleton, 2002). All of this data was thoroughly analyzed with the use of conventional (multivariate) statistics. The key findings were, for example, the strong correlation between soil properties and spatial and temporal tree distribution (Wigley et al., 2016a, 2016b). The strong influence of precipitation within savanna ecosystems was verified as well (Sankaran et al., 2005).

In the context of ecological strategies and resilience, one of the key questions is to what extent tree species are able to optimize their growth and their stability within the savanna ecosystem. Additionally, the concept of inter-species competition has to be considered; i.e. which tree species is better adapted to which specific site or condition than another. This comparison is difficult to make because a singular (deterministic or even heuristic) goal function is unknown. To perform this analysis, a multi-indicator system must be scrutinized. In this study, several leaf traits extended by climate data are used as a vectorial information base. We were thereby able to keep the single indicator information separated, avoiding information loss due to any heuristic aggregation process. Such processes unavoidably merge the valuable information provided by each indicator due to the aim of getting a

* Corresponding author.
E-mail addresses: ulfia.lenfers@haw-hamburg.de (U.A. Lenfers), brg_home@web.de (R. Bruggemann), thomas.clemen@haw-hamburg.de (T. Clemen).

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reduced set of new indicators: in general, just a one-dimensional scalar. An appropriate analysis tool is provided by the theory of partially ordered sets (Bruggemann and Carlsen, 2006).

Partial order theory has been applied toward in many disciplines, e.g. to environmental chemicals, pollution, economic and socio-economic topics (Annoni et al., 2015, 2011; Fattore, 2008; Sørensen et al., 1998). To date, partial order theory has only been applied to few ecological studies (Patil and Taillie, 1982; Solomon, 1979). As far as we know, this study is the first attempt to combine elements of partial order theory with aspects of savanna ecology. In our study, we focused on the question of whether it is possible to extract different survival strategies of selected savanna tree species by applying methods from partial order theory.

The paper is organized as follows: The following section presents the origin and amount of data used here and gives a brief overview about methods of partial order theory. Applying these methods to the data led to a set of results that are described in Section 3. Various ecological strategies were derived from these results and respectively validated by a literature review. Finally, the last section of the paper summarizes our contributions and identifies areas for further research.

2. Material and methods

2.1. Study area

The study was conducted in the eastern part of South Africa (Fig. 1a). All sites are located in conservation areas confined within the region bounded by the coordinates −22°S, 29°W and −28°S, 32°W. The annual precipitation of this region is between 300 and 900 mm (Table 1).

Functional trait data were obtained from Wigley et al. (2016a, 2016b); please see the original paper for details.

Data analysis was focused on five tree species identified by Wigley et al. (2016a, 2016b) identified as the dominating woody species in Kruger National Park, a representative savanna ecosystem in South Africa. In correspondence to the selected tree species, nine distinct sites were chosen as depicted in Fig. 1a. We refer to Fig. 1a for site locations. A typical tree-grass savanna landscape and a leaflet from *Sclerocarya birrea* in springtime are shown in Fig. 1b.

2.2. Data preprocessing

It is necessary to restructure, join, and classify the sampled data in order to provide a base for the application of partial order theory. Our approach avoids artificial (i.e. non deterministic, process based) aggregation by deriving a single but composite indicator.

2.2.1. Data organization

As we are interested in discovering the interplay between sites, their characteristics and tree species, the data is organized as follows:

1) Set of tree species T: = Sb, An, Ca, Cm, Ts}.
2) Set of sites S: = {Hl, Nh, Nw, Mo, Po, SB, SM, SG, Ma}.

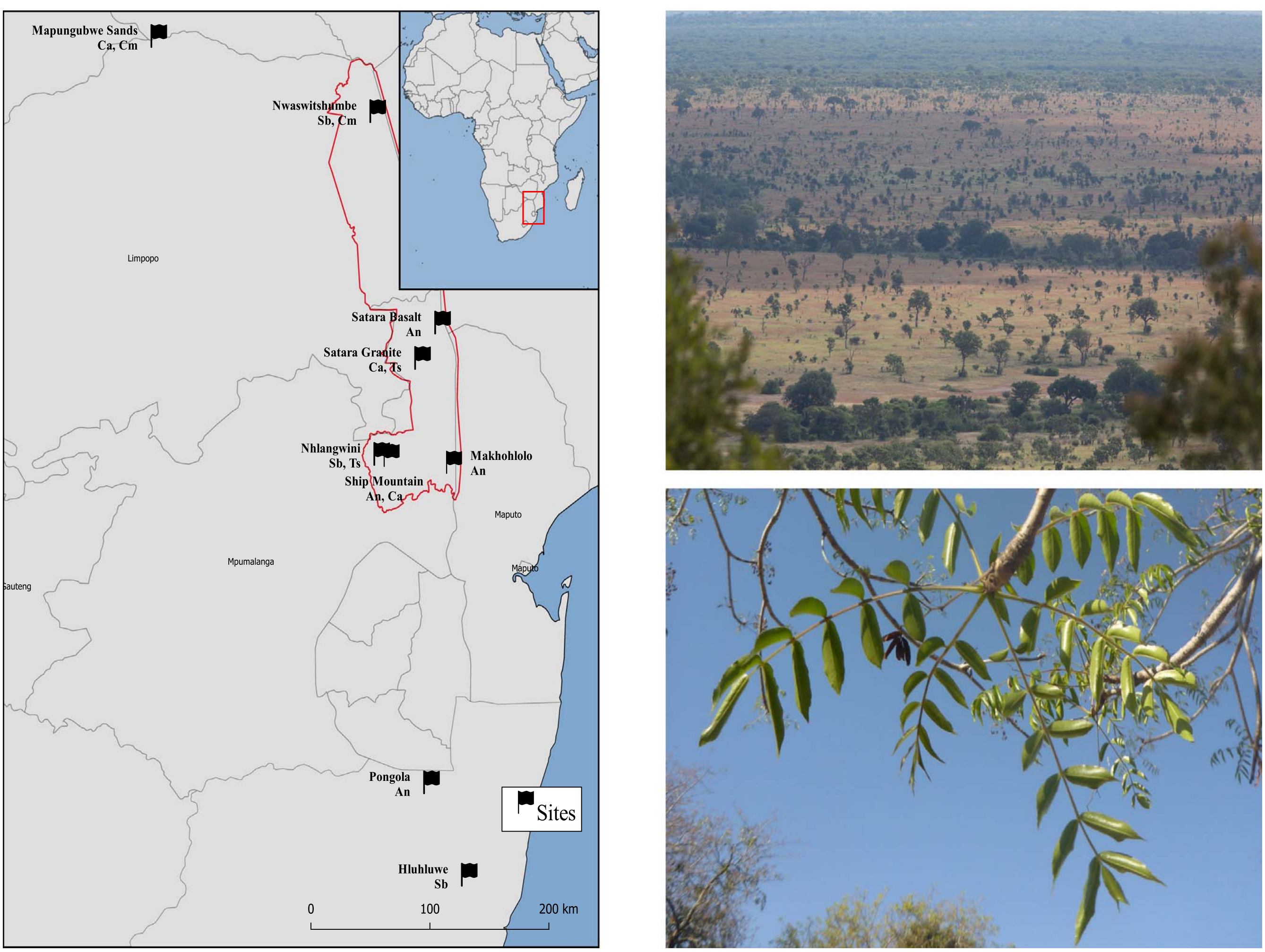

Fig. 1. a Data sites sampled by Wigley et al. (2016a, 2016b) and containing at least one of our selected trees.
b: Typical savanna with tree-grass landscape (above), flushing leaflet of *Sclerocarya birrea* in springtime (below).