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Caught in a human disturbance trap: Responses of tropical savanna trees to increasing land-use pressure

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ABSTRACT

Increasing land-use pressure threatens the persistence of tree populations in West Africa's savannas. We do not fully understand yet why tree species respond differently to human disturbances, hampering the design of appropriate management strategies. To identify typical response pathways, we compared tree populations in three land-use types with increasing levels of human disturbance (protected forest, fallow and field). We analyzed size-class distributions (SCDs) of species and plant functional types, and compared the performance of juvenile and adult age-classes. Biomass was derived from biometric measurements via allometric equations. Higher land-use pressure increased juvenile proportions of plant functional types, but divergent responses were found for species: Juvenile proportions on fields were either very low (0%) or, in most cases, very high (>96%), leading to SCDs with significant negative slopes. While negative slopes are commonly interpreted as indicating populations with sufficient recruitment, they could also indicate growth suppression, particularly if size-classes are missing between juveniles and adults. This 'juveniles get trapped' pathway is well-recognized for near-natural savannas with a high incidence of fire ('fire trap') or wild browsers ('browse trap'), and is attributed to a high resprouting ability of trees. As resprouting constitutes a pre-adaptation to human disturbances, the trap concept should be extended accordingly. Species dominating in highly disturbed environments are either characterized by trait combinations allowing them to persist in a 'human disturbance trap', or they are actively protected. Our results advocate for designing management strategies that take into account how species' age-classes respond to disturbances. As the escape of juveniles to mature vegetation is a main demographic bottleneck for most Sudanian savanna species, it is essential to create escape opportunities.

1. Introduction

Dramatic increases in land-use pressure during recent decades have provoked a considerable decline of Africa's woody savanna vegetation (Lykke, 1998; Bollig and Schulte, 1999; Jurisch et al., 2013). This has profound consequences for services that humans derive from these ecosystems, as woody plants are the main source of energy and non-timber forest products for Africa's rural populations (Schumann et al., 2011; Linstädter et al., 2013). Land-use related disturbances such as woodcutting, browsing and fire greatly influence growing conditions for savanna trees (Sawadogo et al., 2005), and modify vital rates such as recruitment and mortality (Higgins et al., 2000). In West Africa's Sudanian savannas, human disturbances threaten the structure and persistence of tree and shrub populations on local and regional scales (Nacoulma et al., 2011). Fire, harvesting of timber, and browsing by domestic herbivores constitute the most important threats, even in protected areas (Traoré et al., 2013).

It is well-known how fire affects savanna tree populations (Higgins et al., 2000; Werner and Prior, 2013). Fire can be conceptualized as a disturbance that is in many aspects functionally analogous to vertebrate herbivory (Bond and Keeley, 2005; Staver and Bond, 2014): Like fire, herbivores may suppress seedlings and saplings, and large herbivores such as elephants may have an additional, negative effect on the performance and survival of small trees (Helm and Witkowski, 2012). It has been argued that, due to this analogy, the natural disturbance regime in savannas might have similarities with human disturbance regimes, particularly under communal land management (Linstädter, 2009). However, we still have a limited understanding of how tree populations respond to human disturbance regimes in West African savannas (Zida et al., 2009), which hampers the design of appropriate management strategies.

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In this context, the resilience of seedlings and saplings appears to play a crucial role. Juveniles may be either less or more resilient to disturbances than their adult conspecifics. If they have a lower resilience, a high mortality of juveniles may be the consequence, impairing sufficient regeneration (Mwavu and Witkowski, 2009; Zida et al., 2009). Particularly in case of recurrent fire, though, large numbers of suppressed small trees may accumulate in local tree populations (Werner and Prior, 2013). In these cases, a higher exposure of the understory to severe and recurrent disturbances (Zimmermann et al., 2010) goes along with a higher resilience of juveniles due to their better resprouting ability (Bond and Midgley, 2001; Jurisch et al., 2013). For a functional understanding of tree vulnerability toward human disturbances, it is thus crucial to evaluate the response of juvenile individuals, and to compare it to the responses of their adult conspecifics.

Another important step for a functional understanding of plant responses to disturbances is to identify functionally similar species (Lavorel et al., 1997; Linstädter et al., 2014). Here, a widely supported method is to aggregate species into plant functional types, or PFTs (Gillison, 2013). The underlying rationale is that species within a PFT share functional traits that show similar responses to the environment; in our case to disturbances. Both *a-priori* (deductive) classifications such as life-forms, and *a-posteriori* (inductive) approaches are used to capture disturbance responses (McIntyre et al., 1999). While deductive approaches draw from a general understanding of the system, inductive approaches rely on observations and experimental results. Despite their potential for advancing our understanding of tree responses to land-use effects, few studies have applied PFT approaches in West African savannas (see recent review for tropical deciduous forests in Chaturvedi et al., 2011).

Evaluating effects of land-use on woody vegetation across age-classes, species and/or PFTs is methodologically challenging. Most importantly, human disturbances have immediate and pronounced effects on tree individuals' biomass (Luoga et al., 2002), while effects on the basal area, density and structure of tree populations are less immediate and severe. This is partly due to local resource management strategies: Individuals are mostly pruned, coppiced or pollarded (Schumann et al., 2011; Sop et al., 2011), thus losing only part of their biomass. While studies on land-use effects in tropical forests frequently use biomass to complement other proxies (e.g. Gross et al., 2014), such studies are still rare for West African savannas, with the exception of some attempts to quantify carbon stocks (Fischer et al., 2011).

Another methodological issue is how juveniles are considered when evaluating effects of human disturbance on population structure. In West Africa's savannas, size-class distributions (SCDs) are often used for this purpose. This approach takes advantage of the fact that long-term effects of disturbance (and other drivers) leave imprints in tree population dynamics and size class structure (Peltzer et al., 2014). One assumption of SCD analysis is that a high proportion of small (juvenile) individuals characterizes a 'stable' tree population with sufficient regeneration, and leads to SCDs skewed toward the lower classes and an inverse J-shaped size distribution (Venter and Witkowski, 2010; Helm and Witkowski, 2012). Surprisingly, although the inclusion of juvenile individuals into SCD analysis is required for savanna trees (Lykke, 1998), many studies in West Africa's savannas test only adults' SCDs (e.g. Savadogo et al., 2007; Sop et al., 2011), referring to the approach proposed by Condit et al. (1998) for tropical forests. It remains unclear why juveniles were excluded from these studies, and what the consequences are for the interpretation of SCDs.

The main objective of our study is to improve our understanding why West Africa's savanna tree species respond differently to human disturbances, and to characterize functionally similar response pathways. It overcomes several caveats of previous studies. First, we analyze SCDs of all age-classes. Second, we assess the ecological performance of species' age-classes via their contribution to biomass. Third, to avoid bias, we evaluate land-use effects on all tree species with a high ecological importance. In this way we aim to identify species and/ or PFTs which are particularly vulnerable to increasing land-use pressure, to better understand what makes them vulnerable, and to derive implications for conservation and sustainable management. We hypothesize that (1) stand structure and ecological performance deteriorates with increasing land-use pressure; (2) PFTs and key species are differently affected by human disturbances, with effects being more pronounced for the juvenile age-class; and (3) response patterns of age-classes can explain why certain species or PFTs are particularly vulnerable.

2. Materials and methods

2.1. Study area

The study area is located in Burkina Faso's North-Sudanian savannas, between 11°21′ to 11°39′N, and 3°29′ to 3°16′W. Climate is semi-arid, with a mean annual precipitation around 900 mm yr^{-1}, and a rainy season between May and October (Bondé et al., 2013). Landforms consist of small rocky elevations surrounded by sedimentary basins (Butt and Bristow, 2013). Soils are mainly lixisols (Savadogo et al., 2007). The study area includes two protected forests (Bansié with 3 km^2; and Bahoun with 16 km^2). Outside protected areas, a mosaic of fallows, non-arable land, forest fragments and fields is found (Bondé et al., 2013).

2.2. Study design and data collection

We compared three typical levels of land-use pressure in West Africa's Sudanian savannas, i.e. forest, fallow and field. This sequence has been frequently used to evaluate increasing levels of human disturbance on the tree layer of West African savanna landscapes (e.g. Kelly et al., 2004; Kindt et al., 2008; Schumann et al., 2011). Fields represent the highest level of human disturbance (Schumann et al., 2011). They surround the homesteads ('village field'), and are continuously under cultivation. Besides agriculture, human disturbance include harvesting of non-timber forest products, fire, and livestock grazing in the dry season. Fallows – also called 'sylvopastoral areas' (Kindt et al., 2008) – represent an intermediate land-use pressure on the tree layer (Schumann et al., 2011). They have a continuous grass layer and are left for grazing. Moreover, harvesting of timber and non-timber forest products occurs (Kindt et al., 2008), mainly pruning and coppicing for livestock feeding. In the study area, fires are set by farmers once or twice during the dry season to promote the growth of palatable forage plants (Bondé et al., 2013).

As a reference ecosystem, we sampled in the protected Bahoun forest. Here, specific access rights are granted to local populations, e.g. picking leaves and bark for medicinal purposes, or collecting dead wood for domestic consumption (Thiombiano and Kampmann, 2010). Foresters apply annual early fire to minimize potential damages of late fire (Ouédraogo et al., 2009). Like in other protected areas in West Africa (Grégoire and Simonetti, 2010; Jurisch et al., 2013), illegal logging occurs. Since 2004 an increasing incidence of browsing was observable (O. Ouédraogo, pers. observ.). Still, human disturbance is lowest in this land-use type, compared to fallows and fields (Schumann et al., 2011). While forests and fields were easily recognizable, the identification of fallows of a sufficient age (>10 years) required the help of local farmers. Fallows and fields were located within a 5-km radius around forests.