Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2016:26

Fire dynamics in savanna woodlands of Tanzania: spatial and temporal patterns and relationships with woody species

Branndynamikk i savanneskog i Tanzania: mønstre i tid og rom og sammenhenger med forvedete arter

Beatrice Christopher Tarimo

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to Ase and Chris

for the choice of right priorities

for the sacrifices you gracefully made

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January 2016.

ÅS, NORWAY.

Abstract

Fire is an important ecological factor that influence the composition, structure and distribution of tropical savannas. Fire has been part of tropical savannas throughout recorded history. These savannas experience more frequent and extensive fires annually than any other biome. Anthropogenic uses of fire play a key role in defining fire regimes in African savannas. Human drivers are likely to regulate the future of African savanna fire regimes under changing climate conditions. Despite the great insights provided by decades of research, including long-term experimental fires, spatial and temporal patterns of fires and associated relationships with woody species remain uncertain. This is partly due to the limited spatial coverage of earlier studies, limited representation of human burning practices, and lack of historical fire records. In this PhD thesis, I characterize the fire regime in the savanna woodlands of Tanzania and assess the relationship between this regime and spatial differences and temporal changes in woody plant community properties. To achieve this, I utilize satellite data and woody plant communities and employ image analysis techniques, multiscale spatial ordination, and univariate and multivariate analyses.

In Paper I, I show that long-term (~40 years) spatial characteristics of fires, including fire return interval, burning season, burned patch sizes and extents suggest frequent, small-sized fires characterize the fire regime. Large-sized fires are very rare and occur more frequently in drier than in wetter parts of the savanna woodland. Wetter parts of the woodland experience a higher fire activity, at shorter return intervals and shorter annual fire season than drier parts of the woodland. Land use changes influence ignitions and spread of fires; the expansion of agricultural areas has a striking spatial conformity with the reduction of fire activity. The sizes of fires, return intervals, season of burning and spatial extents are generally consistent across time.

Fire appears to be an important driver of the spatial differences in species diversity and composition (Paper II and Paper III). This spatial difference in species composition was significantly related to fire, although the relationship was not strong and did not show clear patterns (Paper II). Woody species tend to occur in spatial clusters, probably as a protection mechanism against frequent fires, and mostly at large spatial scales (scale range successively between 0.29 – 5.87 km). On a wider spatial extent (~12 – ~337 km), spatial differences in species richness was related to the frequency of historical fires and density of recent fires (Paper III). Similarly, spatial differences in the change in species composition between 1977 and 2012 increased with fire frequency. In all cases, the results suggest that the influence of fire on the spatial variation in woody species diversity and composition is amplified by land uses, particularly the severity of past utilizations.

On a temporal scale, fire is a key driver of changes in the diversity and composition of woody species (Paper III). Species richness increased with the frequency of historical fires between 1977 and 2012. This increase in species richness caused a convergence of species composition at the large spatial scale, thus fire contributed to homogenizing the woody species composition. The differences among sites in the extent of species replacement between 1977 and 2012 increased with fire frequency. Both the frequency of historical fires and the density of recent fires contributed in determining the species compositional space occupied by sites in 2012. Overall, the magnitude of change in species composition between 1977 and 2012 decreased with increasing frequency of historical fires. Similar to the spatial differences in species composition, the influence of fire on the temporal changes in community properties was modified by the severity of historical utilizations.

The fire regime portray a regular spatiotemporal pattern during each fire season. This pattern, combined with the understanding of contrasting effects of early and late dry season fires on savanna vegetation and soils, can potentially facilitate fire management initiatives for various purposes. Moreover, woody species tend to persist in frequently burned sites. However, the combined effect of fire and land uses impose higher risks to woody plants. Results presented in this thesis will inform management strategies and priorities aiming at reduced biomass burning emissions, biodiversity conservation, and preservation and enhancement of carbon stocks.

Keywords: Anthropogenic fires; Burned area; Frequency-size distribution; Disturbance; Fire history; Miombo; Moran’s eigenvector maps; Re-sampling; Spatial patterns; Taxonomic homogenization; Temporal patterns; Woody plants.

Sammendrag

Brann er en viktig økologisk faktor som påvirker artssammensetning, vegetasjonsstruktur og utbredelse til tropiske savanner, og har vært en viktig del av tropiske savanner gjennom historisk tid. Disse savannene opplever hvert år hyppigere og større branner enn noe annet biom. Menneskets bruk av brann spiller en nøkkelrolle i Afrikas brannregimer, og menneskelig påvirkning vil trolig være en viktig regulerende faktor for branner på Afrikas savanner under endrede klimatiske forhold. Selv om vi vet mye om brannpåvirkning på savanneøkosystemer; gjennom årtier med forskning, inkludert, langsiktige eksperimentelle branner, er vår kunnskap omkring de romlige og tidsmessige mønstrene i branndynamikk og brannenes sammenheng med forvedete arter fremdeles usikker. Dette skyldes delvis en begrensing i den romlige utbredelsen til tidligere studier, et begrenset antall studier på forskjellige typer av branner og mangel på historiske data over brannhyppighet og utbredelse. I denne doktorgradsavhandlinger karakteriserer jeg brannregimet i savanneskog i Tanzania, og undersøker sammenhengen mellom dette brannregimet og romlige forskjeller og tidsmessige endringer i samfunnsegenskaper for forvedete arter (trær og busker).

For å oppnå dette har jeg brukt data fra satellitter og fra forvedete plantesamfunn, samt brukt billedanalyseteknikker, fler-skala romlig ordinasjon og univariate og multivariate statistiske analyser.

I det første arbeidet (Paper I) viser jeg at langsiktig (ca. 40 år) romlige egenskaper ved branner, inkludert brannfrekvens, sesong og størrelse, tyder på at branner i hovedsak er små, men opptrer hyppig på savannen i Tanzania. Store branner forkommer svært sjeldent og da oftere i tørre enn i mer fuktige savanneområder. Fuktig savanneskog er utsatt for mer hyppige branner over et kortere tidsrom enn tørrere savanneskog. Endringer i landbruk påvirker brannregimet; utvidelse av jordbruksområder har en sterkt reduserende effekt på brannhyppighet og størrelse av branner. Brannregimet i savanneskog i Tanzania har endret seg lite de siste tiårene.

Brann ser ut til å være en viktig pådriver for romlige forskjeller i artsdiversitet og sammensetning (Paper II and Paper III). Denne romlige forskjellen i artssammensetning er signifikant relatert til brannregime, selv om sammenhengen ikke er sterk og ikke har et tydelig mønster (Paper II). Forvedete arter forkommer hovedsakelig i klynger, trolig som en beskyttelsesmekanisme mot hyppige branner, og hovedsakelig på en stor romlig skala (skala mellom 0.29 – 5.87 km). På en større romlig utbredelse (~12 – ~337 km) er romlige forskjeller i artsrikdom relatert til hyppighet på historiske branner og tetthet av nylige branner (Paper III). I tråd med dette økte tidsmessige endringer i artssammensetning fra 1977 til 2012 med brannfrekvens. Disse resultatene tyder på at påvirkningen fra branner på den romlige variasjonen i artsdiversitet og sammensetning hos forvedete arter er forsterket av landbruk, spesielt graden av tidligere utnyttelse av naturresursene.

Brann er en nøkkelfaktor som påvirker endringer i artsdiversitet og sammensetning over tid i savanneskog (Paper III). Artsrikdom økte med hyppighet av historiske branner i tidsrommet fra 1997 til 2012. Denne økningen har før til en konvergens i artssammensetning på en stor romlig skala. Brann har således bidratt til en homogenisering av artssammensetningen av forvedete arter. Forskjellen mellom områder i graden av artserstatninger fra 1977 til 2012 økte med brannhyppighet.

Både hyppigheten av historiske branner og tettheten av nylige branner bidro til å påvirke artssammensetningen som ble målt i 17 områder i 2012. Størrelsen på endring i artssammensetning fra 1977 til 2012 sank med økende hyppighet av historiske branner. Effekten av brann på tidsmessig endring i samfunnsegenskaper i et område var modifisert av den tidligere landbruksaktiviteten i området

Brannregimet i savanneskog i Tanzania har et regulært mønster i tid og rom hver brannsesong. Dette mønsteret, kombinert med en forståelse av motstridende effekter av brann tidlig og seint i sesongen på savannevegetasjon og jordsmonn, kan bidra til å forbedre brannforvaltningsinitiativer med forskjellige hensikter. Selv om forvedete arter ser ut til å tåle hyppige branner, kan den samlede effekten av brann og landbruk representere en stor risiko mot sammensetningen av forvedete arter i savanneskog. Resultatene i denne avhandlingen kan brukes til å forbedre forvaltningsstrategier og prioriteringer som har til hensikt å redusere utslipp fra brenning av biomasse, bevare biodiversitet og sikre lagring og framtidig økning av karbon i afrikanske savanneskoger.

Nøkkelord: Menneskeskapte branner; Brannområder; Frekvens-størrelse fordeling; Forstyrrelse; Brannhistorikk; Miomboskog; Moran’s eigenvektor kart; Re-sampling; Romlige mønstre; Taksonomisk homogenisering; Tidsmessige mønstre; Forvedete planter.

List of papers

This thesis consists of the following papers that are referred to by the roman numerals I – III

I Tarimo, B., Dick, Ø. B., Gobakken, T. & Totland, Ø. (2015) Spatial distribution of temporal dynamics in anthropogenic fires in miombo savanna woodlands of Tanzania. *Carbon balance and management*, 10, 1-15.

II Tarimo, B., Totland, Ø., Klanderud, K. & Eldegard, K. Relationships between woody plant species composition and recent fire history across spatial scales in Tanzanian savanna woodlands. *Submitted to Journal of Vegetation Science, September 2015*.

III Tarimo, B., Eldegard, K., Klanderud, K. & Totland, Ø. Anthropogenic fires and land use increase small–scale species diversity and cause large–scale homogenization of species composition in savanna woodlands. *Manuscript*.

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1. Introduction

The occurrence of fire and the relationship between recurrent fires and the distribution and composition of tropical savanna woodlands plays a key role in the understanding of current and potential ecosystem properties (Vitousek 1994). Tropical savannas cover extensive areas in both Africa, South America and Australia; they are home to diverse plant and animal communities, support about one-fifth of the world human population, and experience more frequent and extensive fires than any other biome (Mouillot & Field 2005; Shlisky et al. 2009). Fire is a long-standing driver of vegetation patterns across the globe (Bond et al. 2005; Bowman et al. 2011). In African savanna woodlands, fire is regarded as a key component of the ecosystem, playing important roles from the time of the emergence and spread of savannas to the current state, with a codominance of trees and grasses (Higgins et al. 2000; Bond et al. 2003; Beerling & Osborne 2006; Pereira et al. 2012). Studies in the past decades, including long-term experimental fires, have provided great insights into the influence of fire on both the woody and grassy components of savannas (Laris & Wardell 2006; Furley et al. 2008). Nevertheless, spatial and temporal patterns of fires and associated influences on woody species in African tropical savannas remain uncertain, partly due to the spatial coverage and a limited replication in earlier studies (Furley et al. 2008), and a lack of historical fire records. Consequently, African savannas contribute the highest uncertainties to the global carbon budget and future biodiversity trends (Williams et al. 2007; Chazdon et al. 2009; Ciais et al. 2011). Therefore, there is still a large need for a better understanding of the dynamics in these habitats. However, most of African savannas are under various forms of human utilization, making them un-attractive to research efforts compared to pristine and less-utilized habitats (Fazey et al. 2005). Human utilization in African savanna woodlands will likely increase in the future, implying a continued risk to the less-utilized habitats (Tilman et al. 2001). However, African savanna woodlands cover large areas and have a high potential for natural regeneration. Accordingly, informed restoration activities in these savanna woodlands can have high potentials for mitigating ongoing global change (Chazdon et al. 2009). Restoration activities in tropical savannas are likely to be practical at local scales, because of the heterogeneity in the spatial mosaics in savannas that comprise vegetation patches and human modified landscapes. The need for a better understanding of the dynamics in savanna woodlands is thus greater at local scales.

The occurrence of fire and the response of plant communities to recurring fires vary across spatial and temporal scales within savannas (Mbow et al. 2000; Turner 2010; Levick et al. 2012). This variation may result from the landscape pattern that influence the spread of fires, and annual rainfall patterns that influence grass biomass production and thus the availability of fuel for fires (van der Werf et al. 2008; Archibald et al. 2010). Studies from African and Australian savannas have demonstrated the traditional patchy burning pattern across the spatial extents of savannas during each annual fire season (Russell-Smith et al. 2003; Laris 2005; Tarimo et al. 2015). In these savannas, traditional fire management practices are suggested to be beneficial because they fragment the landscape early in the dry season to prevent large, extensive and destructive fires later on in the season (Laris 2002; Bowman & Murphy 2010; Russell-Smith et al. 2013). Traditional fire management has been widely practiced across savannas throughout history. However, changes in these burning practices have occurred with the introduction of contemporary fire management, e.g. in association with colonial settlers in African savannas (van Wilgen et al. 2000; Laris & Wardell 2006). Although these contemporary practices were confined within a few selected areas, such as national parks, they largely influenced the inception and design of public policies on fire management and thus subsequent burning practices. Furthermore, changes in human demography and social, cultural and economic settings in the recent past have facilitated both increases and decreases in the density of fire ignitions and spatial extent of areas affected by fire (Le Page et al. 2010; Bowman et al. 2011; Grégoire et al. 2013; Andela & van der Werf 2014). These changes are largely undocumented, with a few exceptional cases, such as the Kruger National Park in South Africa (van Wilgen et al. 2000). An understanding of the variation in burning patterns across spatial and temporal scales, and how these patterns relate to the distribution and composition of woody species, is an important prerequisite to the management of these savanna woodlands.

2. Rationale and research objectives

Fire regimes (see section 3.2 for definition) in tropical areas are likely to change following climate change, with prospective increases and decreases in fire activity (Bowman et al. 2009; Krawchuk et al. 2009). Changes in fire regimes have direct influences on ecosystems (Bond & Keeley 2005), and fire represents an increasingly crucial driver of change in tropical savanna woodlands. Determining the change in fire regimes, and thus the likely effects of this change on ecosystem properties, requires an understanding of reference regimes, which are generally not well known (Bowman et al. 2011; Archibald et al. 2012). Furthermore, the complex feedback mechanisms between fire, vegetation and climate (Hoffmann et al. 2002; Lehmann et al. 2014; Beringer et al. 2015), may cause a large variability in fire activity across spatial and temporal scales. A record of historical fires is a necessity in the quest for an understanding of the changes in fire regimes, their influence on vegetation patterns, and feedbacks with climate.

Moreover, practical initiatives to reduce biomass-burning emissions, and safeguard carbon stocks and biodiversity, may require alteration of burning practices. These initiatives are challenged by the limited understanding of the likely influence of strategic changes in recurrent fires to support mitigation of the effects of global change on vegetation. An understanding of the relationship between long-term fires and spatial and temporal variability in woody plants community properties may contribute to more informed management initiatives.

Therefore, the objectives of this study are to

i. Assess changes in the spatial and temporal patterns of fire in savanna woodlands of Tanzania for the past ~40 years.

ii. Assess the influence of recent historical fires (~40 years) on the composition of woody species in savanna woodlands across spatial scales and along disturbance gradients.

iii. Assess the influence of recent historical fires and land uses (~40 years) on the temporal change in woody plant community properties.

3. Background and concepts

Savannas are characterized by a codominance of trees and grasses, with a continuous grass layer and a discontinuous tree layer. An important distinction of savannas from other plant communities with coexisting woody and grassy species is that most of the savanna species are intolerant to shade and thus require an open canopy. The ratio of the density of trees and grasses vary considerably within savannas, primarily due to variability in annual rainfall and edaphic characteristics, which influence soil moisture content. Moreover, atmospheric CO_2 is increasingly recognized as an important driver with a direct influence on this coexistence through the C_3 and C_4 photosynthetic pathways (Bond & Midgley 2012). Together with these primary drivers, fire and herbivory by both livestock and wildlife are important secondary drivers of the coexistence. Their influence vary with soil moisture content, which influence grass biomass production. Consequently, fire and herbivory are regarded as essential for the coexistence of trees and grasses in mesic savannas but may have little influence on this coexistence in arid and semi-arid savannas (Sankaran et al. 2005; Lehmann et al. 2008; Midgley & Bond 2015).

3.1. Pyrogeography in African savannas

The most extensive and high-density annual fires in the tropics occur in African savannas. In general, the occurrence of fire requires combustible fuels, conducive climates and sources of ignition (Moritz et al. 2010). African savannas are characterized by a high annual grass biomass production (i.e. fuels), distinct wet and dry seasons where the dry season extends for up to 7 months (climate) and the high dependency of local communities on forest resources for their livelihoods (ignitions) (van der Werf et al. 2008; Bowman et al. 2009; Krawchuk et al. 2009). These characteristics facilitates the consistently high annual fire activity in African savannas.

Burning in tropical African savannas lasts for the whole duration of the dry season, whereas parts of Africa north and south of the equator are characterized by a distinct annual fire season. At the continental scale, the season extend from November to April in parts of Africa north of the equator, and between May and November south of the equator (Dwyer et al. 2000). During the fire season, burning progresses from north to south and from west to east, in parts of Africa north and south of the equator, respectively (Dwyer et al. 2000; Mbow et al. 2000; Tarimo et al. 2015). The timing and direction of spread of fires during the fire season may provide opportunities to manage fires successively across space, given differences in the effects on vegetation between early and late season fires.

Individual fires generally burn small patches at a time, which progressively cover large spatial extents during each fire season (Laris 2005; Tarimo et al. 2015). In addition to the traditional burning practices, small-burned patches are associated with land uses, which may influence the location and timing of ignitions and the spread of fires (Laris 2011; Grégoire et al. 2013; Andela & van der Werf 2014). Protected areas in African savannas, where human uses are restricted, are exceptions to the persistence of small-burned patches. The homogeneous and continuous fuel accumulation in protected areas facilitate a greater control by climate on the fire regime, which results into larger fire sizes and in some cases more frequent fires (Archibald et al. 2010; Devineau et al. 2010; FAO 2013).

3.2. African savanna fire regimes

A fire regime encapsulate the recurring long–term patterns of fire characteristics that distinguish fires occurring in one area from those occurring in another area. The main fire characteristics that define a fire regime include type, size, frequency, intensity and severity, extent and season of fires (Bond & Keeley 2005; Cochrane & Ryan 2009). The most common type of fire in African savannas are surface fires, which burn through the understory, and are fueled mainly by grasses and surface litter. Accordingly, the threat to vegetation is confined within the flame height, which depends on the height of dominant grasses. The season of burning is important because of the contrasting influence of fires on vegetation when they occur early or late during the dry season. Late dry season fires are more intense and thus more severe than early dry season fires. These characteristics vary locally across African savannas but in all cases, the current fire regimes are mainly human driven with a very low frequency of natural fires. Based on the severity of fires, the fire regime may generally be described to constitute a mixed severity regime due to the variation in sensitivity to fire among savanna plant species (Brown & Smith 2000; Cochrane & Ryan 2009). Thus, the regime is characterized by frequent fires that can either be of high intensity and large or less intense and small (Archibald et al. 2013).

Fire regimes experience change over time, although changes in African savanna fire regimes are probably less dramatic compared to other biomes (Bird & Cali 1998; Giglio et al. 2010; Archibald et al. 2012). The drivers of these changes in fire regimes, which are explained in Shlisky et al. (2009), include climate change, agriculture and livestock ranching, rural and urban development, energy production, fire exclusion and suppression, invasive species, plantations and arsons. In addition, changes in human burning practices in response to socioeconomic needs can substantially influence changes in fire regimes (Butz 2009; Laris 2013).

3.2.1. Opportunities, threats and challenges associated with fire regimes

The occurrence of fire may provide both opportunities and threats to plant communities, which may range from the level of individuals to the transformation of habitat conditions. The ability by humans to manage fires has led to different management practices. These practices have evolved over time with an increase in the understanding of the role of fire in different plant communities (van Wilgen et al. 2000; Bowman et al. 2011; Archibald et al. 2012). However, the role of fire, the change in the global environment and climate, and associated feedbacks with fire regimes, are still largely unknown, thus a persistent challenge to the manipulation of fire regimes (Bowman et al. 2009).

Fire management choices have the potential to maintain biodiversity and suppress woody encroachment when undesirable (Chidumayo 1997; Laris 2002; Shlisky et al. 2009). In addition, management practices may limit the control by climate over fire regimes, thus preventing destructive fires (Archibald et al. 2010; Bird et al. 2012). On the other hand, fire management choices may cause loss of woody cover and biodiversity, spread of invasive species, and contribute significant amounts of biomass burning emissions (Bowman & Murphy 2010). In African savannas, contemporary fire management has proven difficult to implement, partly due to limited capacity and the high dependency on the savannas for rural livelihoods. On the other hand, traditional fire management is generally advocated across savannas, as the most ecologically sound alternative to contemporary fire management (Bowman & Murphy 2010).

3.3. Fire and savanna vegetation patterns

Fire has been part of savannas throughout recorded history (Bird & Cali 1998; Bowman et al. 2009; Archibald et al. 2012). Among the well-documented relationships between fire and vegetation dynamics in savannas is the potential of fire to change the tree–grass density ratios (Higgins et al. 2000; Sankaran et al. 2005; Lehmann et al. 2014; Levick et al. 2015). Fire is also considered a key driver of savanna and forest distributions as alternative vegetation states (Ratnam et al. 2011; Staver et al. 2011a; Staver et al. 2011b). At a global scale, the extent of savannas would be greatly reduced in the absence of fires (Bond et al. 2005). Thus changing fire regimes may result into substantial changes in habitats. The influence of fire on savannas vary across spatial and temporal scales and differs among size classes of woody species (Gillson 2004; Levick et al. 2012; Moustakas 2015). Thus, on an individual level, seedlings and saplings are at a higher threat to the damage by fire and gain more protection as they mature to adults, e.g. by developing a thicker bark that insulate the trees (Chidumayo 1997; Hoffmann & Solbrig 2003).

Although savanna woodlands – particularly in moist habitats – are maintained by fire, the vegetation pattern has an influence on the timing and progression of burning across spatial extents during the fire season (Sankaran et al. 2005; Laris 2013). This has promoted the argument that it is not fire that is driving vegetation patterns but it is the vegetation pattern that has a control over the occurrence of fire (Laris 2008, 2013). The feedbacks between fire and vegetation patterns are complex since they occur within a matrix of other drivers, including climate and human utilization (Lehmann et al. 2014; Midgley & Bond 2015).

3.4. Conceptual framework

Savannas are dynamic systems that are characteristically heterogeneous across spatial and temporal scales (Skarpe 1992; Higgins et al. 2000; Lehmann et al. 2008; Lehmann et al. 2009). The dynamics in savannas have persistently motivated decades of research that has provided both theoretical and empirical explanations to these dynamics. These explanations generally fall into two categories, either competition for available resources, such as the Walter's two layer hypothesis, or constraints on the establishment of individuals; i.e. demographic bottlenecks (Sankaran et al. 2004; Sankaran et al. 2005; Bond 2008; Midgley et al. 2010; Moustakas et al. 2010; Ward et al. 2013). Although there is both support and disputation to these explanations, it is widely accepted that the relative importance of the key drivers of the dynamics differ between dry and moist savanna (Higgins et al. 2000; van Langevelde et al. 2003; Sankaran et al. 2005; Lehmann et al. 2009; Higgins et al. 2010; Ward et al. 2013). In recent years, it has been suggested that the dynamics in savannas are best understood when both resource availability and demographic constraints are considered, and both spatial and temporal scales are explicitly taken into account (Skarpe 1991; Jeltsch et al. 1996; Whittaker et al. 2001; Favier et al. 2012). Assessments that are scale-specific are important because the key drivers of the dynamics in savannas are changing over time and operate at variable spatial scales (Lehmann et al. 2008). One scale–specific framework that is important to savannas is the patch dynamics framework (Wu & Loucks 1995; Scholes & Archer 1997; Gillson 2004; Wiegand et al. 2006; Meyer et al. 2007; Favier et al. 2012). In this framework, the link between processes within a community and patterns resulting from these processes at different spatial scales is emphasized. Thus, a number of factors that operate at variable spatial scales maintain the vegetation pattern over time at the landscape-scale, and facilitate variable vegetation patterns at the patch-scale within this landscape (Wu & Loucks 1995; Gillson 2004; Favier et al. 2012). Patches can take variable sizes and forms. However, the interrelationships between smaller and larger spatial scales is important to an individual or a group of patches, because of potential feedbacks between these scales (Levin 1992; Wu & Loucks 1995). Individual patches within savannas may comprise treeless grasslands, open savannas, closed savanna woodlands and even forest patches, depending on the drivers dominant in each patch (Bond 2008; Favier et al. 2012). The variation in the drivers may potentially maintain or cause a shift from one savanna state to another, such as from a grassland to a woodland (Jeltsch et al. 2000; Higgins & Scheiter 2012). The patch dynamics framework has facilitated an understanding of the savanna vegetation mosaic where abrupt changes in the tree–grass ratio are evident within similar climatic and edaphic conditions (Favier et al. 2012). It has been suggested that these abrupt local changes are caused by differences in the type and intensity of disturbances between the patches and the variability of these disturbances across the primary drivers, i.e. climate, soils and atmospheric CO_2 (Beckage et al. 2009; De Michele et al. 2011; Favier et al. 2012; Higgins & Scheiter 2012).

The distinction between natural processes and disturbances in African savannas is difficult, due to their long history of anthropogenic use and the likely influence of fire and herbivory during their historical spread (Bond et al. 2003; Goldammer & Stocks 2011; Heckmann et al. 2014). However, it is clear that the current human-driven fire regime has deviated from natural fires (Le Page et al. 2010; Archibald et al. 2012). Likewise, fragmentation resulting from land uses, such as wood harvesting and the transformation of savanna woodlands for agricultural expansion, are clearly disturbances. Transformation of landscapes to agricultural uses has been part of ecosystems throughout history, e.g. from the 7th century in northeastern Tanzania (Heckmann et al. 2014). Most of this expansion, and other land use changes in the tropics, has probably occurred within savannas, since savannas were not part of earlier efforts to biodiversity conservation that may have acted to restrict human use in tropical forests (Bond & Parr 2010). In Africa, about two-thirds of the expansion in permanent agricultural areas between 1700 and 1992 occurred in savannas and grasslands while the remaining one-third occurred in forests and woodlands (Ramankutty & Foley 1999). It is clear that these disturbances have persisted for a longer time and at larger spatial extents than can be covered by this study. The patch dynamics framework facilitate assessment at variable spatial and temporal scales (Fig. 1), within the spatial and temporal extents of this study (Wu & Loucks 1995; Gillson 2004).

3.5. Climate change, distribution of savanna woodlands and feedbacks

The availability of soil moisture, i.e. annual rainfall, within savannas has always been central to the hypotheses explaining the dynamics in savanna ecosystems (Sankaran et al. 2004; Staver et al. 2011a). The distribution of savannas and forests is predicted by the amount of annual rainfall, such that dominance by savannas occurs at low mean annual precipitation (MAP; < 600 mm) and by forest at higher precipitation (MAP > 2500 mm) (Sankaran et al. 2005; Staver et al. 2011b). At intermediate levels of MAP, fire is required to maintain open canopies. The fire-vegetation interaction comprise feedback mechanisms between fire, woody species and grassy species along a rainfall gradient. Although savanna fire regimes are human driven, rainfall seasonality determines when and where ignitions can occur. Consequently, climate change likely influences both the relative tree–grass density ratios and fire regimes in savannas, and the feedbacks between fire and vegetation patterns.

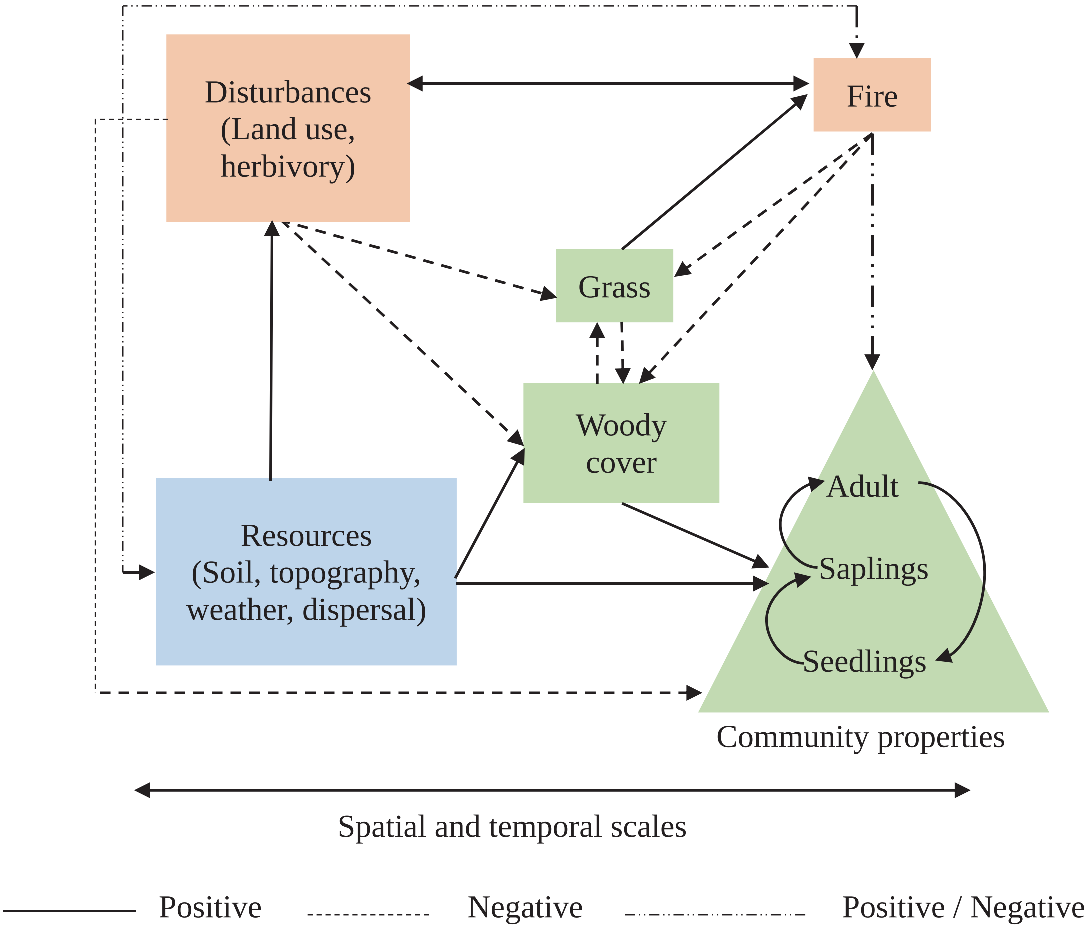

Fig. 1. Conceptual framework. Interactions between woody plants in African savanna woodlands at different size classes (green triangle) and the influence of background tree-grass coexistence (green boxes), resources (blue box) and disturbances (orange boxes). Scale vary across historical datasets and spatial extents of each study.

Among the changes associated with the ongoing climate change are variability in rainfall patterns and an increase in the atmospheric carbon dioxide, CO_2 (Bond & Parr 2010). Recently, rainfall variability alone has been associated with a decrease in woody cover in wet savannas (Holmgren et al. 2013). Similarly, increases in atmospheric CO_2 facilitates an increase in woody cover but has no direct influence of grass biomass (Bond & Midgley 2012; Higgins & Scheiter 2012; Midgley & Bond 2015). On the other hand, fire contributes to carbon emissions through biomass burning, which may increase atmospheric CO_2 levels (van der Werf et al. 2003). Thus, fire may indirectly facilitate an increase in woody cover through the increase in atmospheric CO_2. However, fire poses a demographic bottleneck to woody species by suppressing seedlings from reaching the reproductive adult stage (Hoffmann & Solbrig 2003). Consequently, there are likely feedbacks between fire, vegetation and climate change that may maintain savannas or suppress either of its components, i.e. trees or grasses. In addition, the historical spread of C_4 grasses that characterizes African savannas is attributed to low atmospheric CO_2 levels and the current continuing rise in atmospheric CO_2 will likely favor trees over C_4 grasses, thus influence fire activity (Vitousek 1994; Cerling et al. 1997; Beerling & Osborne 2006; Bond & Parr 2010; Ward et al. 2013; Midgley & Bond 2015). Indeed, the recent tendency to increased woody density in savannas, i.e. wood encroachment, has been associated with increases in CO_2 (Bond & Midgley 2012). Certainly, a better understanding of future vegetation patterns in African savannas requires an understanding of the synergistic influence of future changes in disturbances, atmospheric CO_2 and climate (Midgley & Bond 2015).

Fragmentation of tropical forests and savannas through harvesting and clearance for human uses has increased substantially in the recent decades. Clearance of savanna woodlands facilitate conducive weather conditions for ignition and spread of fires, i.e. a decrease in rainfall and humidity and an increase in temperature and wind speed (Hoffmann et al. 2002). Thus, clearance is associated with increased fire activity, which in turn may cause further reduction of woody cover (Hoffmann et al. 2002) and then interrupt the vegetation–fire feedbacks.

Although these complex interactions are not addressed in this study, their role in the dynamics of savannas is recognized. It is the hope of this study to contribute information on the relationship between spatial and temporal patterns of fires and woody species.

4. Methods

This section provides additional details to the information already presented in the materials and methods sections of each paper (see Paper I, Paper II and Paper III).

4.1. Study area

Savanna woodlands extend over ~90% of the vegetated areas in Tanzania. They support the majority of human livelihood activities and thus burning practices. Datasets from large spatial extents were required for a representation of the variation in the interrelationships between burning practices, plant community properties, human utilization and abiotic conditions across spatial and temporal scales. Consequently, the study area (Fig. 2) consist of the extent of miombo woodlands in Tanzania (Paper I), Kilosa and Kilwa districts in eastern Tanzania (Paper II), and Katavi and Rukwa regions in western Tanzania (Paper III). Study sites in eastern Tanzania were selected for a larger research project to represent different socioecological and cultural conditions that influence the use of fire. On the other hand, initial analyses of satellite data indicated a higher density and frequency of fire across most of western Tanzania than in eastern Tanzania. Subsequently, the study by Kikula (1979; 1986) came to my attention, and it formed the basis for the selection of sites in western Tanzania.

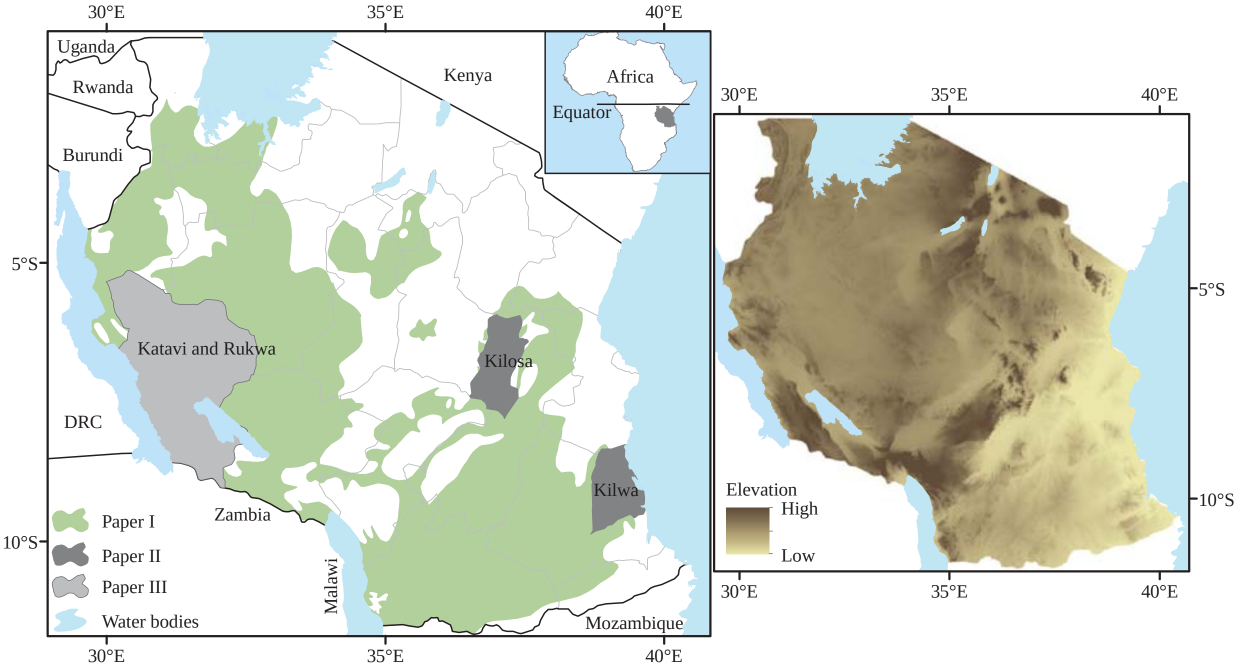

Fig. 2. The spatial distribution, extent and terrain of the study area: miombo woodlands (green), districts (Kilosa and Kilwa) and regions (Katavi and Rukwa) in Tanzania. Regions represents a higher administrative level than districts, and comprise a number of districts. Elevation data were sourced from the Shuttle Radar Topography Mission (SRTM; LP DAAC 2014).

The climate across the study area is mainly the tropical savanna climate of the Köppen–Geiger climate classification system with some parts occurring in the hot desert, hot semi–arid and humid subtropical climates of this classification (Peel et al. 2007). The topography consist of both flat, rugged and mountainous terrain, where the east occurs at lower elevations than the western and southwestern parts of the study area (Fig. 2). Sites in Kilwa district occur at the lowest elevations and are on relatively flat slopes. Conversely, there is a higher terrain variability within and between sites in Kilosa district and in Katavi and Rukwa regions than in Kilwa district (see for instance Fig. 8).

The main vegetation type across the study area is miombo woodlands, classified into drier and wetter miombo that occur in the eastern and western parts of the study area, respectively (Fig. 4 in Paper I). The woodland is, in general, a moist savanna woodland characterized by the dominance of woody species belonging to the genera *Brachystegia*, *Julbernardia* and *Isoberlinia*, and an understory comprising of shrubs and the light demanding C_4 grasses from the genera *Andropogon*, *Hyparrhenia* and *Loudetia* (Frost 1996; Chidumayo 1997). Miombo woodlands are extensive, but patchy in distribution, intermixed with other vegetation formations including dry forests, swamp and riparian forests, mopane woodlands, thickets and grasslands (Chidumayo 1997). In addition, the drier miombo borders the Zanzibar–Inhambane vegetation formation (Fig. 1 in Paper II), which is similarly characterized by intermixed patches of forests, bushlands, thickets, woodlands and grasslands (Moll & White 1978; White 1983). Therefore, the species composition of each site may comprise individuals from these associated vegetation types. Both miombo woodlands and the Zanzibar–Inhambane vegetation formation have long histories of human utilization (Moll & White 1978; White 1983; Chidumayo 1997).

Human utilization in the study area is mainly through subsistence agriculture. Agriculture in the study area has been practiced mainly through shifting cultivation, although there is a growing tendency toward permanent agricultural settlements. When permanent, agricultural areas expand to the neighboring available land mainly through complete clearance. In contrast, shifting cultivation is commonly practiced in fields with substantial tree density (Fig. 3), and thus have a high potential for regeneration when abandoned. In addition, shifting cultivation with long-term fallow facilitates protection of seedlings and saplings from fire and thus their development into adult trees (Laris 2008). Therefore, although the study sites have been subjected to different levels of human utilization over time, they still host diverse plant communities. Together with agriculture, harvesting of tree species that are suitable for commercial timber products and domestic uses, charcoal production and extraction of fuel wood, are commonly practiced across the study area. In general, the majority of livelihood activities depend entirely on these woodlands but the intensity of human utilization vary across space.

Fig. 3. Illustration of the different extents of tree clearance in the shifting cultivation practice. Photos: B. Tarimo.

4.2. Datasets

This study utilizes both satellite-based and ground-based datasets. Satellite datasets comprise Landsat satellite images and the Moderate Resolution Imaging Spectroradiometer (MODIS) detected active fires. Ground-based datasets comprise woody species community properties and disturbances observed from different socioecological zones, as outlined below. Further details are provided in each paper (Paper I – III).

4.2.1. Satellite datasets

The Landsat satellite series provides the longest and most consistent satellite data available for earth’s surface monitoring. The datasets, which are available in the public domain, consist of multispectral acquisitions since 1972 at a 16-day repeat cycle. Simultaneous operation of more than one Landsat satellite, e.g. Landsat 7 and Landsat 8 may provide a shorter period between successive acquisitions. Although availability of Landsat dataset is constrained by image quality, particularly percent cloud cover, available dataset provide the most detailed historical record of the surface features. In this study, Landsat datasets consisted of imagery from the Multispectral Scanner (MSS), Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) sensors at 30 and 60 m spatial resolutions.

The MODIS fire record consists of the MOD14/MYD14 dataset provided as the location of a point centered at a 1 x 1 km ground pixel that had at least one fire actively burning at the time of satellite overpass. MOD14/MYD14 dataset is available since November 2000. The MODIS sensor records at least four observations each day at every location on earth providing a more complete spatio-temporal pattern of fire activity. Active fires are detected based on thermal anomalies. Consequently, the sizes of active fires detected by MODIS vary with vegetation type, which influence the temperature released by a fire, the satellite view angle and presence of obstructions, such as smoke and clouds. In general, an active fire covering ~1000 m^2 is detected by MODIS sensor but the size may be as small as and 100 m^2 when the fire temperature is high (Giglio et al. 2003; Maier et al. 2013). However, most of the surface fires in African savanna are not detected by MODIS, partly due to their sizes and the associated low temperatures (Giglio et al. 2003; Laris 2005). Nevertheless, MODIS provides an unprecedented record of fire activity.

Combining the Landsat and MODIS datasets facilitate a step toward meeting the pertinent demand for a better detection of the small, fragmented and low-temperature savanna fires (Randerson et al. 2012; Boschetti et al. 2015).

4.2.2. Vegetation sampling

Sampling of plant communities was conducted between August and December 2012. Two sampling strategies were employed, utilizing quadrats (Paper II) and distance based methods (Paper III). Further details on the sampling designs are provided in the methods sections of Paper II and Paper III.

4.2.3. Measures of disturbances

The dynamics and heterogeneity in savannas are largely a result of the differences in human and wildlife utilizations and the control by climate and the landscape vegetation pattern. Thus, the presence and quantity, where applicable, of agricultural activities, harvesting intensity, and livestock and wildlife herbivory were determined to account for the influence of these uses on the distribution, diversity and composition of woody species in Paper II and III.

4.2.3.1. Long–term agricultural expansion

The shifting agriculture practice usually involves small-scale farms, less than one hectare in size (McNicol et al. 2015). These may not be recognizable in satellite images when they are few and scattered within vegetated areas, and their detection may vary with seasons. Therefore, agricultural areas were recorded both on the ground (Paper II and III) and from satellite images (Paper III) in an attempt to compile a complete record of areas utilized for agriculture. On the ground, areas that were recently cleared for agricultural use and those that were abandoned or under fallow, identified based on physical signs such as terraces and abandoned temporary homesteads, were recorded.

The expansion of agricultural areas was quantified from satellite images, for the period 1972 – 2011. This was done by employing the Rapid Land Cover Mapper (RLCM) tool (USGS EROS 2015). RLCM is a dot grid image classification method (Fig. 4) that relies on a visual image interpretation technique. Visual interpretation was facilitated by high-resolution satellite images on Google Earth and the image analyst's field experience for the recent satellite images. Then changes were tracked in past images by visual analysis with the help of information on topographical maps, available aerial photographs, and historical satellite images on Google Earth.

4.2.3.2. Harvesting intensity

Harvesting intensity was measured by the number of tree stumps. The approximate time of harvest was determined by visual inspection of the stumps, which were categorized as fresh or decaying. The threshold for distinguishing fresh from decaying stumps was based on the dryness of the stumps.

4.2.3.3. Herbivory intensity

Livestock keeping forms one of the common livelihood activities in the study area. Herds vary in size but can comprise as many as a few thousand individuals. This necessitates nomadic pastoralism following seasonal availability of pastures. Livestock herbivory is therefore one of the common form of utilization, in addition to herbivory by wildlife populations. The intensity of utilization for livestock and wildlife herbivory was measured by the presence of their droppings and footsteps.

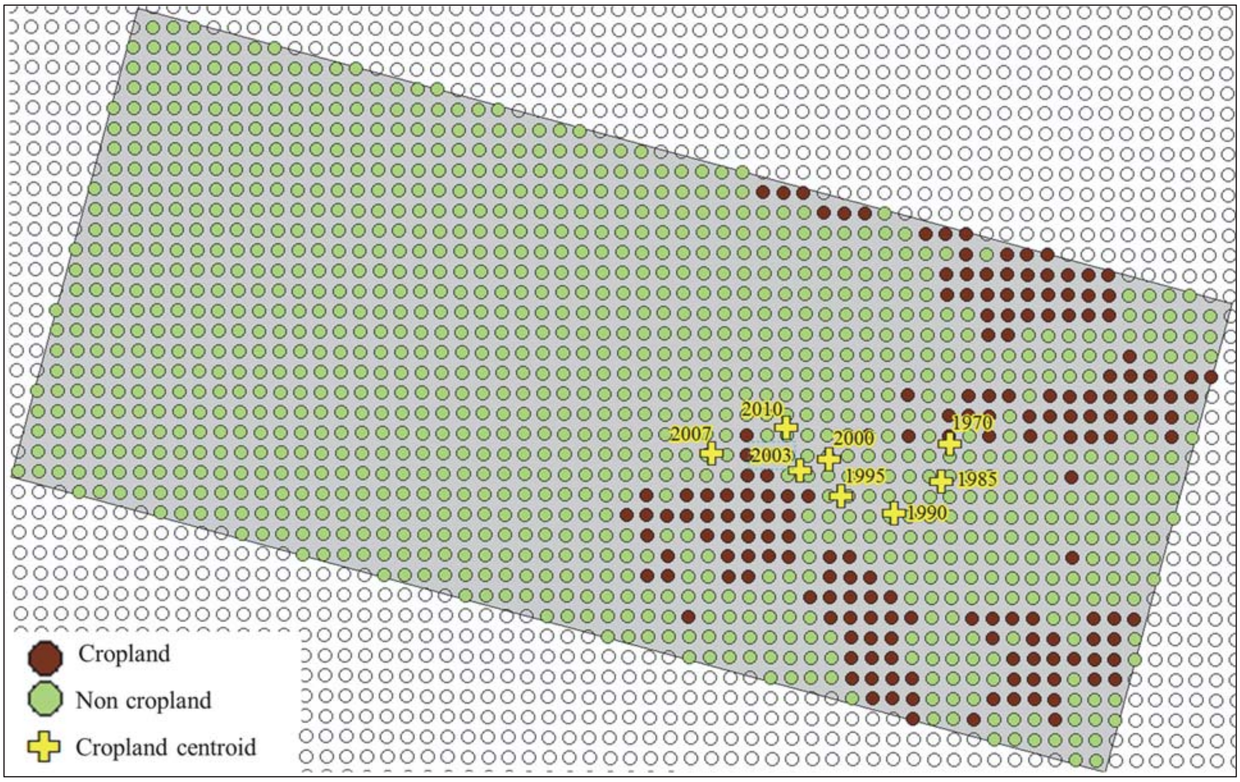

Fig. 4. Illustration of the Rapid Land Cover Mapper (RLCM) dot grid classification method for the extended area at Inyonga 1 (Fig. 1 in Paper III). The cropland and non–cropland areas are from the 1985 time interval. Centroids of the cropland areas are shown for all time intervals. The linear distance between these centroids was employed as an explanatory variable to account for the shifting nature of agricultural practices (see the methods section of Paper III).

4.3. Data analyses

The objectives and associated datasets required different analysis strategies, documented below as a supplement to information already contained in each paper (see Paper I – III).

4.3.1. Potential spectral indices for burned area mapping in savanna woodlands

One effective way of discriminating areas affected by fire from unaffected areas is to analyze post-fire against pre-fire characteristics of affected vegetation, as captured by satellite images. Burned and unburned pixels exhibit distinct spectral reflectance properties in the reflective and thermal wavelengths of the electromagnetic spectrum (Pereira 2003) that facilitate their discrimination. Spectral indices, which combine two or more spectral bands, enhance this discrimination by revealing patterns that are not evident in individual bands. However, the differences in spectral reflectance between pre-fire and post-fire satellite images can also result from other sources of change independent of fire. Therefore, the use of spectral discrimination requires wavelengths that are more sensitive to fire induced changes (Trigg et al. 2001). Spectral indices that comprise infrared wavelengths provide a better discrimination than other indices (Barbosa et al. 1999; Trigg et al. 2001; Chuvieco et al. 2002).

Eleven spectral indices (Table 1, Fig. 5) with potential for discriminating burned from unburned areas in savanna woodlands were identified through a literature review. These indices were quantified from a set of representative scenes to assess their performance in this discrimination. Representative scenes were selected to cover the spatial and temporal extents of the study and to represent characteristics of surface features. These included areas that were burned, not burned, cloud free, partially cloud covered, with topographic and cloud shadows, and other surface features namely vegetation, bare soil, water, scattered temporary settlements and peri–urban centers. The range of values in each spectral index for which burned pixels were well separated from other cover types was determined (Fig. 6). This range varied between satellite image scenes within the same cover type because of small seasonal differences in spectral reflectance from the cover types and across space. Therefore, the range from individual scenes and the differences among scenes formed the base for selection of spectral indices through logistic regression and for fuzzy sets definition.

Selection of spectral indices for burned area mapping

Penalized logistic regression was employed to analyze the performance of each spectral index in discriminating burned from unburned pixels. Elastic net penalties (Friedman et al. 2010) were preferred as they address the correlation structure of spectral indices while at the same time selecting desirable indices by constraining coefficients of others to zero. The λ penalty values were determined through cross validation of sampled pixels, each scene at a time, while values of α penalty were in the range $0.9 \leq \alpha < 1$. Indices were ranked based on how often they were selected or shrunk to zero. This ranking conformed to previous results; MIRBI (see Table 1) which ranked highest is reported to reduce confusion between burned and sparsely vegetated areas (Stroppiana et al. 2012). Conversely, NBR_L (Table 1) which ranked lowest has poor performance in savannas and is sensitive to soil type (Smith et al. 2005; Lentile et al. 2006; Smith et al. 2010). An analysis combining sampled pixels from all scenes was also done to investigate how well results at scene level could be generalized.

Table 1. Spectral Indices tested for the discrimination of burned from unburned areas. B represents the Blue, SSWIR/LSWIR the short/long Short–wave Infrared, R the Red and NIR the Near Infrared wavelengths of electromagnetic spectrum.

Index	Formulation	References
Burned Area Index (BAI)	$BAI = \frac{1}{(\rho c_3 - \rho_3)^2 + (\rho c_4 - \rho_4)^2};\ \rho c_3 = 0.1, \rho c_4 = 0.06$	Chuvieco et al. 2002
MODIS Burned Area Index – SSWIR (BAIM)	$BAIM = \frac{1}{(\rho c_4 - \rho_4)^2 + (\rho c_5 - \rho_5)^2};\ \rho c_4 = 0.05, \rho c_5 = 0.2$	Martín et al. 2005
MODIS Burned Area Index – LSWIR (BAIM$_L$)	$BAIM_L = \frac{1}{(\rho c_4 - \rho_4)^2 + (\rho c_7 - \rho_7)^2};\ \rho c_4 = 0.05, \rho c_7 = 0.2$	Bastarrika et al. 2011
Global Environment Monitoring Index (GEMI)	$GEMI = \eta(1 - 0.25\eta) - \frac{\rho_3 - 0.125}{1 - \rho_3};\ \eta = \frac{2(\rho_4^2 - \rho_3^2) + 1.5\rho_4 + 0.5\rho_3}{\rho_4 + \rho_3 + 0.5}$	Pinty & Verstraete 1992
Mid-Infrared Burn Index (MIRBI)	$MIRBI = 10\rho_7 - 9.8\rho_5 + 2$	Trigg & Flasse 2001
Normalized Burn Ratio – SSWIR (NBR$_S$)	$NBR_S = \frac{\rho_4 - \rho_5}{\rho_4 + \rho_5}$	Bastarrika et al. 2011
Normalized Burn Ratio – LSWIR (NBR$_L$)	$NBR_L = \frac{\rho_4 - \rho_7}{\rho_4 + \rho_7}$	Key & Benson 1999
Normalized Burn Ratio – SSWIR & LSWIR (NBR$_2$)	$NBR_2 = \frac{\rho_5 - \rho_7}{\rho_5 + \rho_7}$	Stroppiana et al. 2012)
Normalized Difference Vegetation Index (NDVI)	$NDVI = \frac{\rho_4 - \rho_3}{\rho_4 + \rho_3}$	Rouse et al. 1974
Soil and Atmospherically Resistant Vegetation Index (SARVI)	$SARVI = \frac{2.5(\rho_4 - \rho_3)}{1 + \rho_4 + 6\rho_3 - 7.5\rho_1}$	Huete et al. 1997
Soil Adjusted Vegetation Index (SAVI)	$SAVI = \frac{\rho_4 - \rho_3}{\rho_4 - \rho_3 + L}(1 + L); L = 0.5$	Huete 1988

ρ_1 (i.e. B), ρ_5 (i.e. SSWIR) and ρ_7 (i.e. LSWIR) represent Band 1, Band 5 and Band 7, respectively, of the TM and ETM+ sensors. ρ_3 (i.e. R) and ρ_4 (i.e. NIR) represent Band 5 and Band 7 of the MSS sensor onboard Landsat 1 – 3, Band 2 and Band 4 of the MSS sensor onboard Landsat 4 – 5, and Band 3 and Band 4 of the TM and ETM+ sensors, respectively. $\rho c_{3-5,7}$ are convergence values, which represent the radiative characteristics of recently burned areas in these spectral bands and L is a soil adjustment factor.

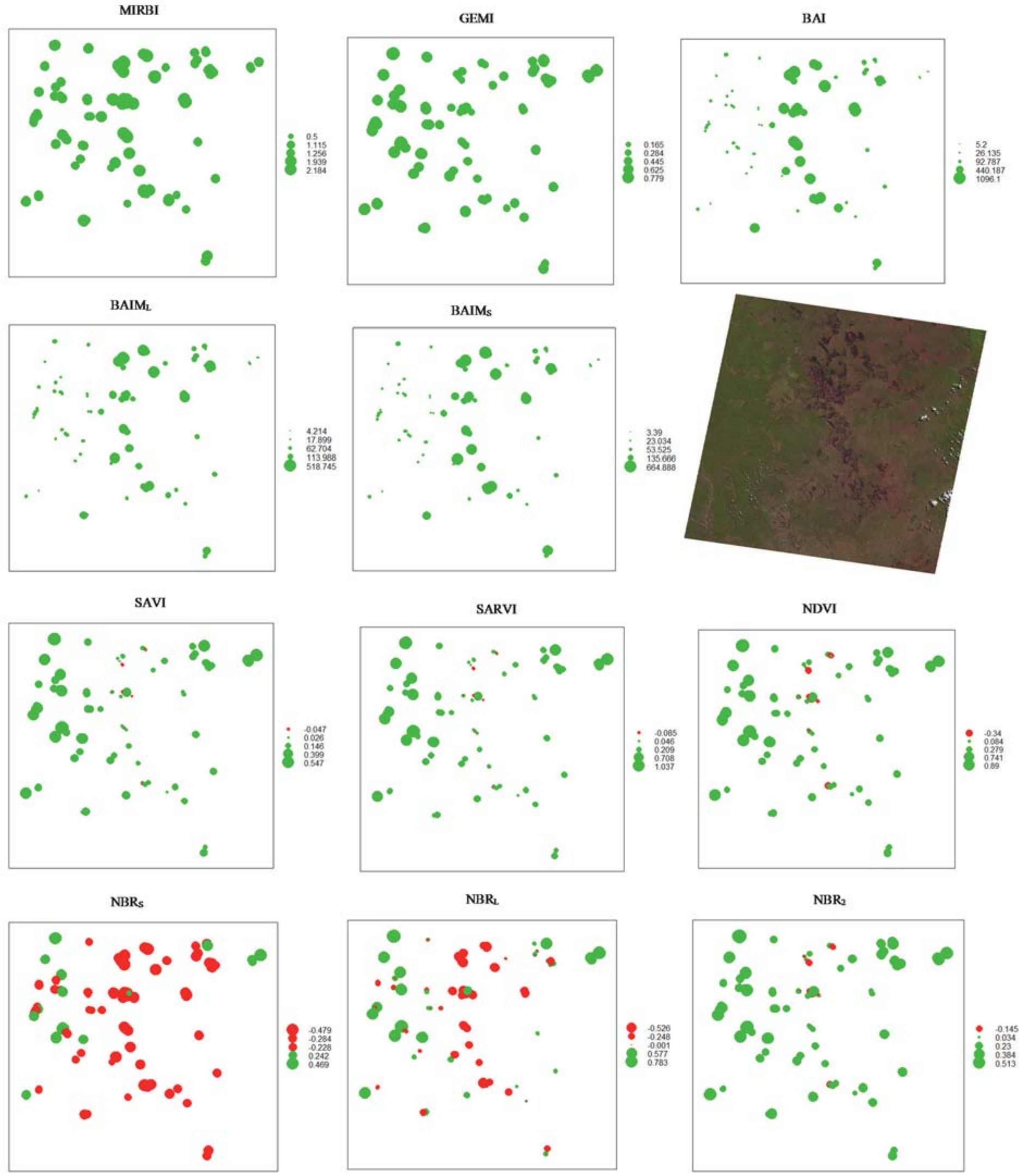

Fig. 5. Differences between the eleven spectral indices in their discrimination of burned and unburned cover types illustrated for a sample of pixels. The unclassified satellite scene from which these indices were quantified, displayed in RGB = 543 color composites, shows vegetation in green patterns, burned areas in dark colored patterns and exposed soils in the remaining light colored patterns.

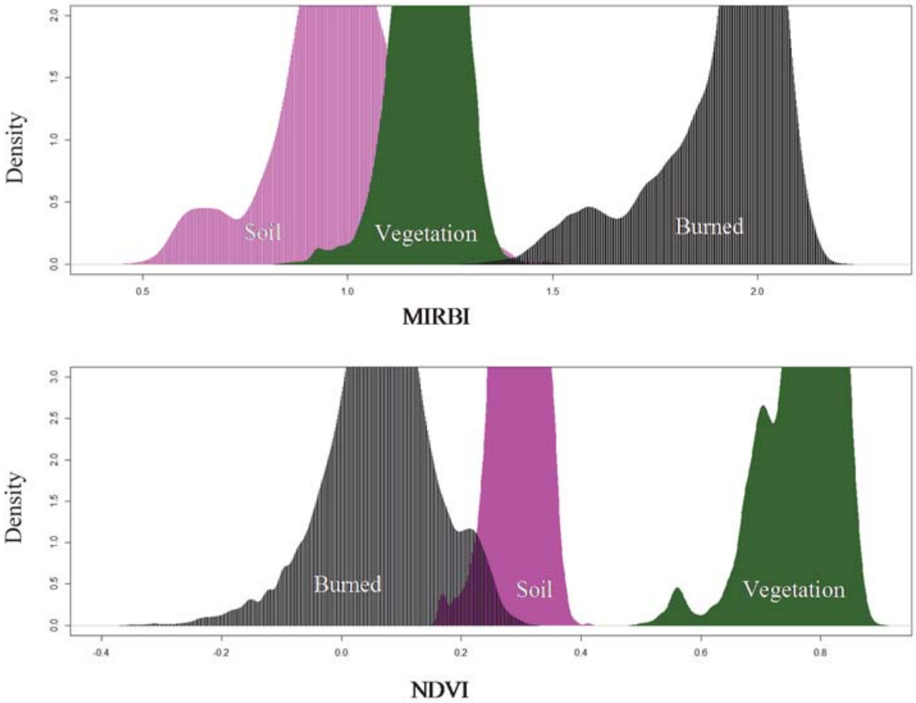

Fig. 6. Illustration of the range of values of spectral indices for burned areas, exposed soil and vegetation for two selected spectral indices: MIRBI that performed best relative to the other indices and NDVI that is widely used for vegetation analyses. Overlaps (spectral mixing) between the cover types commonly occur for most of the indices (see also Fig. 5). Thus, the potential of an index for burned area discrimination depends on the cover types that are spectrally mixed and if the range with higher density of burned areas is well separated from the other cover classes. Figures are truncated along the y–axis to emphasize the spectral indices.

Fuzzy classification

The spectral signature of burned areas in savannas varies at different post fire stages and often overlaps spectrally with other low reflecting surfaces, particularly water, dark soils and areas under shadows (Mitri & Gitas 2004; Smith et al. 2007). The use of thresholds on individual spectral indices may fail to distinguish different post burn stages from unburned areas. The discrimination is improved by integrating multiple indices and allowing for a gradual rather than sharp separating boundary between burned and unburned pixels (e.g. in Pereira et al. 1999). A gradual boundary provides an emergent distinction from evidently burned to evidently unburned pixels and allows other pixels to belong partly to both classes depending on how similar or distinct they are to each class. This is achieved by defining degrees of membership of each pixel to each class (Zadeh 1965; Jasiewicz 2011). A definite member is assigned a membership value of 1, a definite non-member a membership value of 0, while non-definite members are assigned a membership value in the range (0, 1). The grey area that lacks a definite distinction accommodates burned pixels at different post fire conditions and effectively separates them from neighboring unburned pixels by their membership grades.

Frequency-size statistics

Analyses of long-term fire characteristics have indicated that fire regimes portray a power-law probability distribution in that there is a high dominance of either small than large fires or large than small fires (Minnich 1983; Malamud et al. 1998). Frequency-size statistics are therefore widely utilized to define a fire regime and inform management strategies (Holmes et al. 2004; Malamud et al. 2005; Cui & Perera 2008). This study utilized frequency-size statistics to characterize the fire regime in the savanna woodlands of Tanzania. This analysis involved a regression in the log-log space such that the slope coefficient (β) provided the scaling of the fire sizes i.e. the ratio of the number of large to small fires. When $\beta = 0$, the fire regime is characterized by the same number of small and big fires, whereas as β increases small fires are more prominent than big ones (Malamud et al. 2005).

4.3.2. Association between spatial variation in woody species composition and fire

The woody plant community

Sites in Kilwa and Kilosa districts occur in miombo and Zanzibar-inhambane woodlands. The species composition of these sites draw individuals from these two formations. Initial analyses indicated that the sites differed substantially in their species pools (Table 2; Fig. 7). Sampled plots were more compositionally similar between sites in the same disturbance level, which were also the sites that were geographically closer to each other (Table 1 in Paper II and Fig. 1 in Paper II). This difference in the species pools likely influence the spatial variation in species composition (Karger et al. 2015), independent of the fire and disturbance history. Consequently, each site was analyzed separately as detailed in the methods section in Paper II.

Table 2. Comparison of species richness among sites and disturbance levels in Kilwa and Kilosa districts Tanzania.

Disturbance	Site	Species richness		
Low	Ihombwe	49	49	165
Intermediate	Mkarango	78	114	
	Kikole	66		
High	Kiduhi	31	44	
	Kimamba	33		

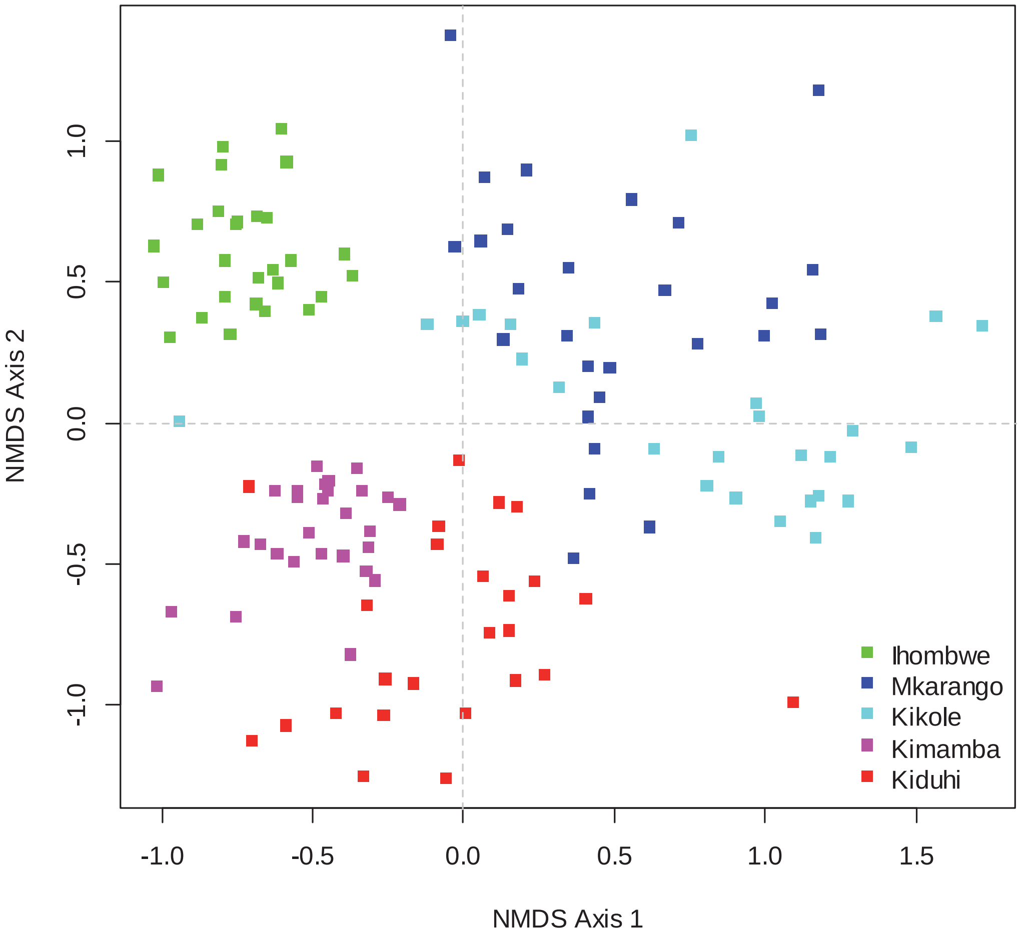

Fig. 7. The species compositional space occupied by each site illustrating the differences in species pools between sites. This difference led to the analysis of each site separately (see methods section in Paper II).

Definition of spatial variables

Spatial patterns commonly occur in the distribution of individuals in plant communities (Callaway 1995). Spatial patterns may result from biotic interactions, spatial variation in environmental conditions and historical disturbances (Borcard & Legendre 1994; Fortin & Dale 2005; Legendre & Legendre 2012). In savanna woodlands, these patterns are associated with the influence of fire (Skarpe 1991; Nangendo et al. 2005; Bacelar et al. 2014; Moustakas 2015). The presence of spatial patterns weakens the efficacy of statistical analyses, requiring analysis techniques that are capable of handling spatial patterns explicitly (Legendre & Fortin 1989; Dormann et al. 2007).

Powerful spatial analysis techniques are increasingly made available (Borcard & Legendre 2002; Dray et al. 2006). Recent advancement has advocated the use of spatial patterns as a source of information, rather than correcting for the presence of spatial patterns, in statistical analyses (Dray et al. 2012). Then, these patterns are modelled as spatial variables that may be related to available environmental conditions to identify the spatial scales at which the environmental conditions influence the plant community. Spatial variables may also represent unavailable environmental conditions, thus facilitating a better understanding of the processes and their spatial scales of influence on a plant community (Borcard & Legendre 1994; McIntire & Fajardo 2009; Dray et al. 2012). This study employed the Moran's eigenvector maps to accomplish such an analysis (Dray et al. 2006; Borcard et al. 2011; Dray et al. 2012).

The Moran's eigenvector maps (MEMs) is a generalization of the principal coordinates of neighbor matrices (PCNM) spatial modelling approach (Borcard & Legendre 2002). PCNM, and MEMs, allow definition of spatial variables sequentially across the spatial scales within the extent of the observed sites, thus analyses can be performed at variable spatial scales (Dray et al. 2006; Borcard et al. 2011). Both methods utilize the spatial arrangement of observed sites and a spatial weighting matrix (SWM) to define a set of spatial variables. As a generalization, the MEMs approach is flexible in the types of SWMs that can be used and provides spatial variables that are directly related to the spatial correlations between observed sites (Dray et al. 2006; Borcard et al. 2011). Each spatial variable (i.e. eigenvector) is extracted through an eigenfuction decomposition of the spatial locations of the sites, and represents a scale specific spatial pattern in the dataset (Borcard et al. 2011; Legendre & Legendre 2012). Therefore, analyzing compositional variation against the spatial variables (MEMs) reveal the scale at which important environmental conditions operate to influence the plant community composition. The variance explained by each MEM was determined by scalogram analyses (Dray et al. 2012; Legendre & Legendre 2012).

4.3.3. Association between temporal changes in woody plant community properties and fire

The description and analysis of the woody plant community properties in Katavi and Rukwa regions is detailed in Paper III. Site in these regions are spread across a wide spatial extent. The differences in the environmental conditions across this extent is shown in Fig. 8.

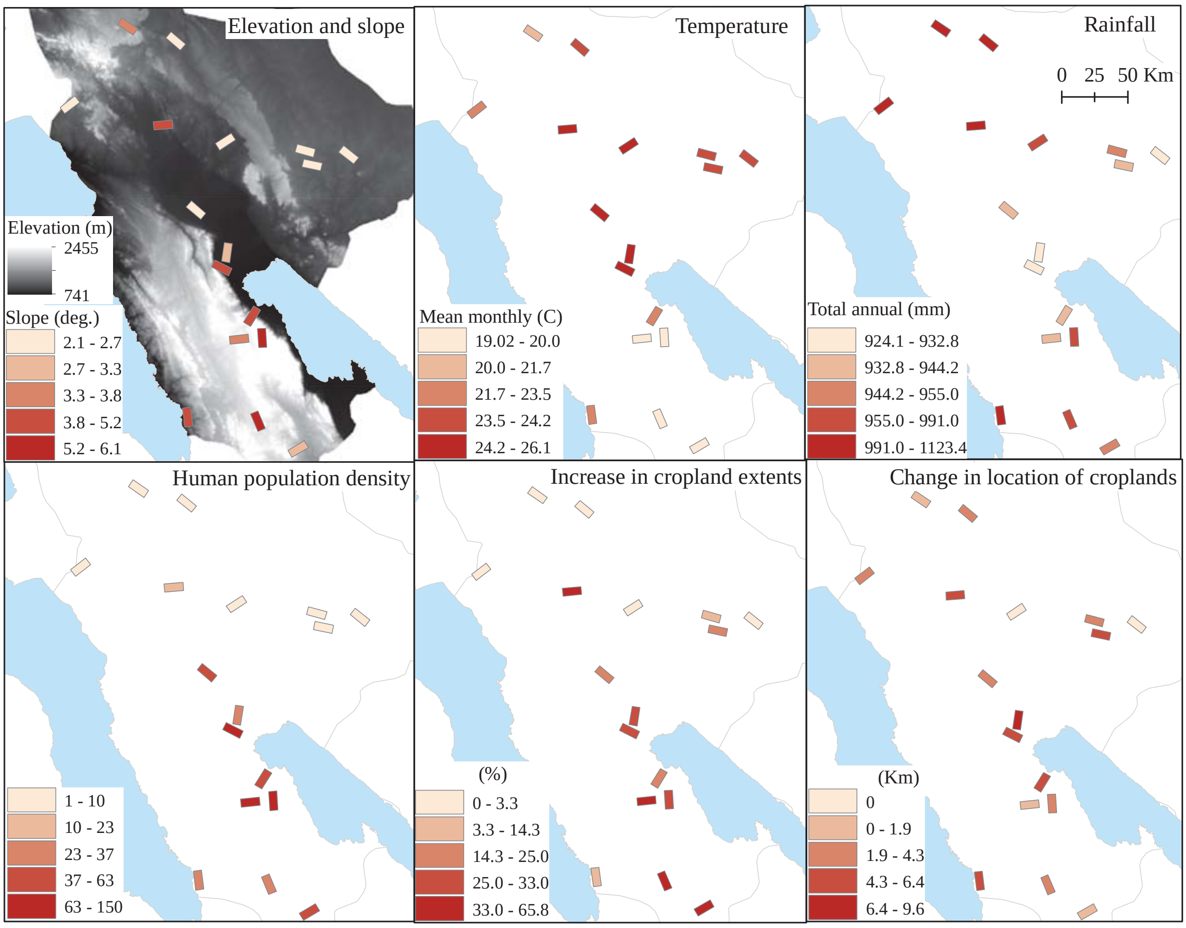

Fig. 8. Spatial heterogeneity between sites in abiotic conditions and utilization for agricultural activities. Each rectangle represent the extended area in each site (Fig. 1 in Paper III).

5. Results and discussions

This study highlights the fire regime (Paper I) in the savanna woodlands of Tanzania and its relationship with the spatial differences (Paper II and III) and temporal changes (Paper III) in woody plant community properties. Detailed results and discussions are presented in the separate papers. A summary of results and additional information is presented here.

5.1. The fire regime

Spatial and temporal patterns of fire activity extracted from satellite data between 1972 and 2013 provided the basis for the characterization of the fire regime (Paper I). Burned patch sizes were determined from Landsat satellite images during 1972 – 2011. Small fires are a common occurrence across both spatial and temporal scales, with an annual median of burned patch size in the range of 0.8 – 1.4 ha. The scaling of the frequency-size distribution, which indicates the ratio of the number of large to small fires, was 2.16 ± 0.04, thus a higher contribution by small fires than big ones to the total area burned. Fire return intervals were determined for different spatial extents, because of the difference in the characteristics of MODIS and Landsat datasets. Between 2001 and 2013 (MODIS dataset), the fire return interval was 2.7 years for an area of 314 ha, while between 1972 and 2011 (Landsat dataset) the return interval was 2.1 years for an area of 2500 ha. This similarity in return intervals, despite the limitations in availability of Landsat datasets, suggest that frequent fires have been part of these savannas throughout the study period. The fire season extends for the duration of the dry season, with very few fires also occurring during the wet season. Therefore, the fire regime comprises frequent and fragmented small-sized fires that progressively spread to cover large spatial extents each year. This regime is similar to that observed in other savanna woodlands in Africa and Australia (Russell-Smith et al. 1997; Laris 2002).

The fire regime is consistent over time, which is similar to previous studies from across African savanna woodlands, suggesting a low inter-annual variability in fire activity (Giglio et al. 2010; Laris et al. 2015). Fire occurs within approximately the same spatial extent every year. The timing of burning during the dry season is characterized by a spatial transition from west early in the dry season towards east later in the dry season. A similar pattern as found here also occurred from a global analysis of a lower resolution dataset (Dwyer et al. 2000). Similarly, consistency in the spatial extent and timing of burning occur in west African savannas (Laris et al. 2015). In that study, Laris et al. (2015) attributed this consistency to a control by the vegetation pattern and human burning practices over the occurrence of fire. Land use plays a key role in determining burning practices and may fragment the vegetation pattern. Particularly, fragmentation of the landscape for agriculture (Fig. 9; Grégoire et al. 2013; Andela & van der Werf 2014) and the economic value associated with land uses e.g. planted crops (Laris 2013) influence the location, timing and density of ignitions and spread of fires. There is an indication of a decreasing trend in fire activity in the recent past, observed both in this thesis and in previous studies across Africa (Archibald et al. 2009; Grégoire et al. 2013; Laris 2013).

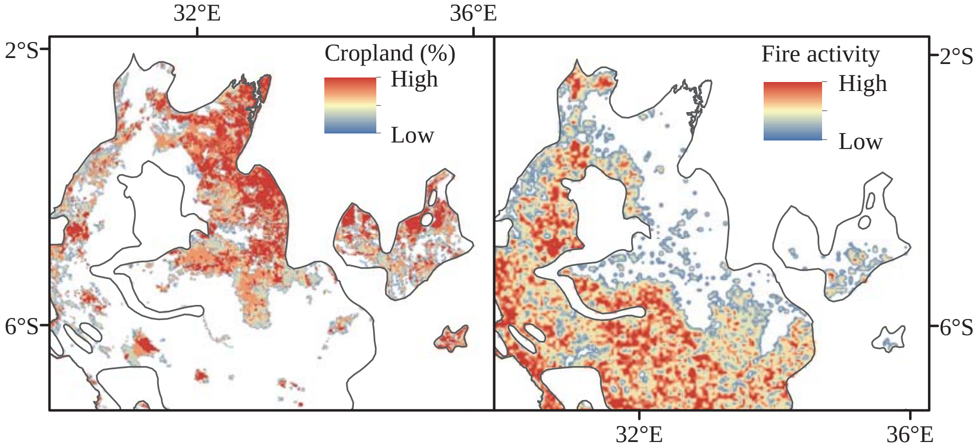

Fig. 9. Illustration of the decrease in fire activity with increasing extent of agricultural areas. Fire activity is compiled from 2013 MODIS data (Paper I) while croplands were obtained from GLC-SHARE Database (Latham et al. 2014).

5.2. Association between the fire regime and the spatial variation in woody species composition

Fire appears to be an important driver of the spatial differences in species diversity and composition. This spatial difference was significantly related to fire frequency at one intermediately disturbed and one highly disturbed sites in Kilwa and Kilosa districts, for the seedlings and adult trees size classes, respectively (see results in Paper II). On the other hand, spatial gains or losses in species in Katavi and Rukwa regions was significantly related to the frequency of historical fires and density of recent fires (see results in Paper III). Similarly, spatial differences in the change in species composition between 1977 and 2012 increased with fire frequency. Findings from both Paper II and Paper III suggest that the influence of fire on the spatial variation in woody species diversity and composition in these savanna woodlands is amplified by other disturbances. Similarly, the interplay between fire and land uses has caused changes in species composition across plant communities (Lawrence et al. 2005; Devineau et al. 2010; Vellend et al. 2013).

The species richness of each site indicated that sites with a high level of disturbance in Kilwa and Kilosa districts, determined based on agricultural activities, livestock herbivory and proximity to roads and settlements, had fewer species compared to less disturbed sites (Table 3). Land use is associated with the use of fire, thus it is likely that fire and land use interact to influence species distribution. On the other hand, beta diversity differed among the size classes within each site in Kilwa and Kilosa districts (Fig. 10). Sites at intermediate level of disturbances were more compositionally heterogeneous relative to sites at low and high levels of disturbances (Table 3 in Paper II). This is similar to the sites in Katavi and Rukwa regions, where sites with little influence from agricultural activities were more compositionally similar than sites utilized for agricultural activities (Fig. 6 in Paper III). These results suggest that disturbances facilitate compositional heterogeneity in these savanna woodlands while also exposing some species to the influence of fire.

In general, spatial differences in woody species composition were prominent across all study sites (Paper II and III). These differences varied spatially, at spatial scales ranging between 0.29 km and 5.87 km in Kilwa and Kilosa districts and between ~12 km and ~337 km in Katavi and Rukwa regions. Woody species in Kilwa and Kilosa districts portrayed significant spatial patterns, mainly at large spatial scale within the spatial extent of the sites (see results in Paper II). Furthermore, compositional similarity increased with spatial scale, suggesting species homogenization at large spatial scale in Kilwa and Kilosa districts (Table 3 in Paper II). Although this scale-explicit assessment was not performed for woody species in Rukwa and Katavi regions, it was clear that sites were more compositionally similar at large spatial scales (Fig. 2 in Paper III).

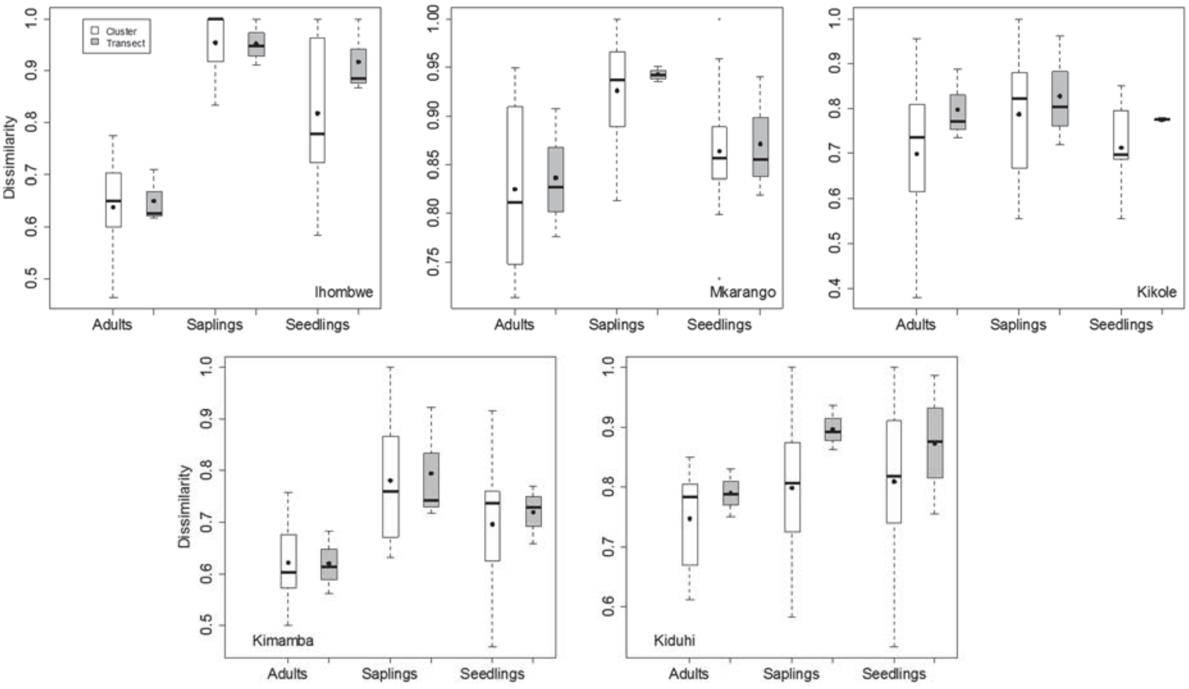

Fig. 10. Comparison of the Jaccard dissimilarities between small (cluster) and large (transect) spatial scales for each size class. The dots represent the mean dissimilarities among clusters/transects approximating the beta diversity at this scale.

5.3. Association between the fire regime and temporal change in woody plant community properties

Fire is a key driver of temporal changes in species diversity and composition. Species richness increased with historical fire frequency during 1977 – 2012 (see results in Paper III). Similarly, an increase in woody species richness with fire frequency has occurred in tallgrass prairies in the US and savannas of Brazil (Bowles & Jones 2013; Silva et al. 2013). In this thesis, the increase in species richness converged the species composition across sites. Furthermore, high frequency of historical fires and high density of recent fires were important in determining the species compositional space in 2012. The among-sites differences in the extent of temporal species replacement increased with historical fire frequency. The magnitude of change in species composition during 1977 – 2012, i.e. the displacement of sites in the compositional space, increased with decreasing frequency of historical fires. Overall, compositional similarity increased at large spatial scale resulting into taxonomic homogenization during 1977 – 2012.

6. Synthesis and application

In this thesis, I show that the fire regime in the savanna woodlands of Tanzania resembles that in other African savannas – frequent, small-sized fires with an annual spatial progression throughout the dry season. This fire regime influences woody plant diversity and composition across spatial and temporal scales where the magnitude of this influence depends on severity of historical uses. In general, the interplay between fire and land uses cause an increase in compositional similarities, i.e. taxonomic homogenization, at large spatial scale. These results will contribute to a better understanding of the dynamics between vegetation, fire, climate and human utilization in savanna woodlands at local and broader spatial scales.

6.1. The woody plant community properties and the fire regime in the savanna woodlands in Tanzania

A recent analysis of the MODIS 500 m burned area product during 2000 – 2011 for the whole of Tanzania (FAO 2013), suggest similar fire activity for the whole country as observed in this thesis for miombo woodlands. Similarly previous studies, although with limited fire records, have suggested the influence of fire on woody species composition in this savanna woodland (Backéus et al. 2006; Banda et al. 2006). Fire management practices are not consistent across the country. The majority of fire ignitions are associated with land uses whereas only a few of these ignitions are associated with forest management. Land resources are increasingly scarce limiting the traditional practices in shifting cultivation and nomadic pastoralism. This has already resulted into a change in burning practices in some parts of Tanzania (Butz 2009). Fire activity tend to decrease (Tarimo et al. 2015) partly due to increasing landscape fragmentation (Fig. 9). Future changes in human demography and climate, and adaptation of international policy frameworks such as the REDD+ are likely to further influence the fire regime and thus relationship with woody plant communities. The methodology employed in this thesis and the results will contribute to inform future analyses and monitoring initiatives.

6.2. African savanna context

Savanna woodlands across Africa experience similar fire regimes (van Wilgen et al. 2000; Archibald et al. 2010; Laris et al. 2015). Long-term experimental fires suggest that the composition of woody species in African savannas has responded little to the long-term fire regime (Furley et al. 2008). This lack of influence may be partly explained by the fact that other land uses are generally excluded in such long-term experimental studies. Results from Paper II and III in this thesis suggest that the severity of the influence of fire on woody species increases with the severity of other uses. Furthermore, the woody plant communities in savanna woodlands exhibit clustered spatial patterns, which have been associated with the fire history (Paper II in this thesis; Nangendo et al. 2005; Bacelar et al. 2014; Moustakas 2015). These clusters of individuals facilitate protection from fire and regeneration of woody species, which may further explain the persistence of woody species under recurrent fires.

The occurrence of fire in African savannas is closely linked with land use activities and thus human drivers overrides the control by climate over fire regimes (Archibald et al. 2010). Changes in fire regimes have been associated with a change in land uses (Grégoire et al. 2013; Andela & van der Werf 2014; Tarimo et al. 2015). The future of savanna fire regimes, therefore, depends on the factors influencing the choice of human burning practices. These may include livelihood needs, and fire management strategies aiming at mitigating global changes. In general, managing African savanna fire regimes require incorporating human burning practices (Laris 2011, 2013).

6.3. Tropical savannas and global context

Fire regimes with a higher occurrence of small fires have been observed in other regions across the globe, whereas a higher dominance of large fires persist, mostly in North America and Asia (Hantson et al. 2015). In their study, which comprised the global extent, Hantson et al. (2015) quantified the scaling of frequency-size distribution of fires in the range $0.68 \leq \beta \leq 3.61$. In this thesis, the scaling was in the range $1.71 \leq \beta \leq 2.57$ when analyses were performed for different spatial and temporal extents. In the United States, the scaling was in the range $1.30 \leq \beta \leq 1.81$ for different ecoregions in an analysis spanning 30 years from 1970 (Malamud et al. 2005). Similarly, the scaling was in the range $1.54 \leq \beta \leq 1.99$ during 1988 – 2007 in Spain (Moreno et al. 2011). These findings suggest that a greater contribution by small than big fires in the total area burned commonly occur across these regions, although the relative sizes of small and big fires in these regions may vary. Moreover, the fire regime characterized in this thesis has an even greater contribution of small fires, which is characteristic of savanna woodlands.

The relationship between these fire regimes and vegetation differ among regions and across spatial scales (Lehmann et al. 2014). This may include increases and decreases in species diversity, a change in species composition, species homogenization and habitat degradation (Turner 2010; McCune & Vellend 2013; Li & Waller 2015).

6.4. Application

Woody species play a key role in the carbon dynamics of tropical savannas (Grace et al. 2006). Carbon storage and sequestration potential in savannas depends on both the extent of tree cover and the composition of woody species (Grace et al. 2006; Ribeiro et al. 2013). Therefore, maintenance and enhancement of carbon stocks requires preservation of biodiversity (Kirby & Potvin 2007; Paoli et al. 2010; Hinsley et al. 2015). Managing fire regimes in African savannas for reduced deforestation and forest degradation, reduced biomass burning emissions and maintenance and enhancement of carbon stocks requires an understanding of the fire regime and the influence of fire on woody species composition, which are assessed in Paper I - III. Moreover, precise estimation of biomass-burning emissions relies on the accurate quantification of burned extents (Boschetti et al. 2004), thus results from Paper I may facilitate an understanding of the contribution of savanna biomass burning to the global carbon budget.

The findings from this thesis will contribute to strategic fire management planning when combined with results from previous studies documenting the influence of fire on vegetation. Fire management is desirable but priorities differ among habitats e.g. frequent fires to suppress woody encroachment or fire protection to safeguard woody cover and thus carbon stocks. Thus, management practices will vary at local scales. However, small patchy fires administered progressively from the beginning and throughout the dry season may regulate the intensity and thus severity of fires to plants (Laris 2011; Ryan & Williams 2011).

7. Conclusion

This thesis highlights the fire regime in the savanna woodlands of Tanzania and the relationship between fire and woody plant community properties. The key findings are:

i. Savanna woodlands in Tanzania have a consistent fire regime across spatial and temporal scales that is similar to fire regimes in other tropical savannas where traditional burning dominates over contemporary burning practices. The fire regime suggest a trend towards decreasing fire activity in the recent past.

ii. Woody species are persisting under the observed fire regime, which is consistent with results from long-term experimental fires. However, the influence of fire on the spatial variation in woody species diversity and composition depends on the interaction between fire and other land uses. Thus, the severity of historical land uses modify the relationship between fire and woody species and may lead into a change in species diversity and composition across spatial scales. Fire is relatively more important than land uses in determining the spatial differences in species richness and spatial species replacement.

iii. Historical fires drive long-term changes in species diversity and composition in this savanna woodland. Fire facilitates an increase in species richness but suppress regeneration of some species, particularly in selectively harvested sites. This leads to taxonomic homogenization over time. Temporal increases in species richness occurs in association with high intensity of human utilization whereas species replacement is associated with low human utilization. Fire is relatively more important than land uses in determining the temporal increase in species richness and temporal species replacement and thus species homogenization.

Abiotic conditions modify these fire–woody species–land uses relationships across spatial and temporal scales. The among-site spatial and temporal differences in species diversity and composition depend on the average monthly temperature, total annual rainfall, elevation and slope.

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Paper I

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RESEARCH

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Spatial distribution of temporal dynamics in anthropogenic fires in miombo savanna woodlands of Tanzania

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Abstract

Background: Anthropogenic uses of fire play a key role in regulating fire regimes in African savannas. These fires contribute the highest proportion of the globally burned area, substantial biomass burning emissions and threaten maintenance and enhancement of carbon stocks. An understanding of fire regimes at local scales is required for the estimation and prediction of the contribution of these fires to the global carbon cycle and for fire management. We assessed the spatio-temporal distribution of fires in miombo woodlands of Tanzania, utilizing the MODIS active fire product and Landsat satellite images for the past ~40 years.

Results: Our results show that up to 50.6% of the woodland area is affected by fire each year. An early and a late dry season peak in wetter and drier miombo, respectively, characterize the annual fire season. Wetter miombo areas have higher fire activity within a shorter annual fire season and have shorter return intervals. The fire regime is characterized by small-sized fires, with a higher ratio of small than large burned areas in the frequency-size distribution ($\beta = 2.16 \pm 0.04$). Large-sized fires are rare, and occur more frequently in drier than in wetter miombo. Both fire prevalence and burned extents have decreased in the past decade. At a large scale, more than half of the woodland area has less than 2 years of fire return intervals, which prevent the occurrence of large intense fires.

Conclusion: The sizes of fires, season of burning and spatial extent of occurrence are generally consistent across time, at the scale of the current analysis. Where traditional use of fire is restricted, a reassessment of fire management strategies may be required, if sustainability of tree cover is a priority. In such cases, there is a need to combine traditional and contemporary fire management practices.

Keywords: Burned area, Carbon stocks, Fire history, Frequency-size distribution, Landsat, Miombo woodland, MODIS, Surface fires

Background

Anthropogenic fires are historically an integral component of African savannas. They strongly influence the composition, structure and distribution of mesic savannas in particular, where tree cover is not constrained by climatic conditions [1–4]. Fire regimes in African savannas, including the frequency and season of burning, are mainly human regulated [5]. The variability of fire regimes in African savannas is more dependent on human drivers than on climate and thus human drivers may regulate the future of savanna fire regimes under changing climate conditions [6–9]. Human activities associated with fire ignitions and fragmentation of the landscape play a key role in determining the occurrence of fire and resulting spatial extents of burned areas [10–14]. Tropical savannas, predominantly in Africa, contributes the highest proportion of the global burned area [15], and their contribution to biomass burning emissions is substantial [16, 17]. The role of these fires as a management tool or as a threat to woody cover, and in the global carbon cycle, vary within savannas and is dependent on the fire regime. Efforts to change fire regimes in favor of

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management priorities, such as carbon sequestration, are being challenged in the light of traditional fire regimes that are more suited for the sustainability of savannas [10, 18–21]. Viable fire management plans aiming at maintenance of stored carbon requires an understanding of historical fire regimes at local scales, which is generally lacking for many parts of African savannas. This understanding is required for precise estimates of the contribution of savanna fires in the global carbon dynamics. Characterization of current fire regimes at local scales is required in order to set references against which assessment of changes in burning practices and their contribution to the carbon cycle will be made [22]. This is of particular importance in fire-adapted ecosystems, such as miombo woodlands, that also support a wide range of human subsistence activities.

Fire is regarded essential to the structure and stability of miombo woodlands [23, 24]. Intense fires suppress tree biomass when their frequency is higher than the rate of tree regeneration and growth [23, 25, 26]. Frequent and intense fires threatens the maintenance of stored carbon stocks, and consequently undermines the potential benefits of activities that comprise the reducing emissions from deforestation and forest degradation (REDD+) policy instrument [27]. Fire contributes to long-term degradation that, although significant, has proven difficult to quantify and monitor, and thus receive less attention in REDD+ negotiations compared to deforestation [28–30]. In addition, they impede the enhancement of carbon stocks for REDD+ payments and sustainability of tree cover at large. Tree recruitment and succession are constrained by recurrent fires [23, 31], which instead facilitates grass encroachment and colonization that may fuel more intense and frequent fires [32, 33]. Exclusion of fire on the other hand facilitates tree dominance of the ecosystem [34], which limits the growth of light demanding grasses and consequently fuel loading. The timing of burning further regulates fire effects, such that late dry season fires have adverse effects on both vegetation and soils, whereas prescribed early dry season fires may be a beneficial management tool [23, 26]. Fire management is of crucial importance for successful forest management [23]. However, it is impaired by the limited understanding on which controlled burning treatments are beneficial for respective components of woodland savannas, coupled with the socio-economic dependency from their surroundings, which play a major role in shaping fire regimes. Characterization of the long-term fire regime will contribute to the ongoing efforts to quantify carbon stocks and fluxes for the purposes of monitoring and verification in the context of REDD+ policy framework and for better fire management practices in general.

A key challenge to both the estimation of carbon fluxes from fires and fire management efforts in African savannas is lack of complete and consistent fire records. In Tanzania, the vast majority of fire events stem from anthropogenic ignitions for different purposes, including farm preparation, pasture management, hunting, honey harvesting, charcoal production, arsons, and for security around settlements and roads [35]. Fire records are limited to a few isolated areas that implement fire management plans. In the absence of long term systematic ground fire records, satellite data forms a unique source of the recent fire history [e.g. 36, 37]. Since tropical savanna fires are fueled mainly by grasses and litter, they sweep the ground surface and leave tree crowns and soil sub-surface unaffected. The resulting burned scars persist for a few weeks only [38–41]. Therefore, frequent observations are required to capture most of the area burned in the course of a fire season. Monthly composites of observation of fire events may be representative of the spatial and temporal distribution of African savanna fires [42–44]. Although the use of different satellite systems provides multiple acquisitions every month, data availability is constrained by cloud cover and other limitations.

Datasets on active fires and burned areas derived from along track scanning radiometer (ATSR), SPOT-VEGETATION and moderate resolution imaging spectroradiometer (MODIS), among other satellite sensors, are available in the public domain. They provide fire patterns at a coarse spatial resolution and at very short temporal coverages. However, comparisons of burned areas derived from coarse resolution (1 km) with those derived from finer resolutions (e.g. 30 m) satellites, show that the majority (up to 90%) of small burned areas characteristic of fragmented fires in tropical savannas, are not detected by coarse resolution burned area products [41, 42, 44, 45]. The low detectability of small-burned areas by coarse spatial resolution products limit the efficacy of these products at smaller spatial scales when detailed information is required. There is thus a need to quantify spatial and temporal fire patterns and resulting burned extents at finer resolutions than those available in the public domain.

The availability of Landsat satellite images in the public domain provides the opportunity to extract burned area records since the early 1970s. Methods are being developed for (semi)automatic burned area mapping at finer spatial resolution e.g. [46, 47], which facilitate frequent and complete mapping at local and regional scales. However, few studies have employed the utility of these methods in African savannas. Thus, burned area records are still missing despite the availability of satellite images. We aim at assessing the fire history during the past ~40 years and respective spatial patterns from satellite based data.

Burned areas are mapped by fuzzy classification using spectral indices that include infrared wavelengths, since they are more sensitive to fire induced changes than other spectral combinations [48–50]. We discuss the derived fire return intervals, seasonality and burned extents in Tanzanian miombo relative to those from other African savannas, and the observed frequency-size statistics relative to those reported from other ecosystems. We highlight the consistency in the fire regime across spatial and temporal scales and point out priority areas requiring further analyses and reassessment of management practices.

Results

Validation of detected burned areas

Table 1 summarizes classification accuracy analysis of detected burned areas. Omissions of burned pixels are mainly in the partially burned areas, which are not included in Table 1.

Based on an independent validation, the overall performance of the fuzzy classification when including partially burned areas was 57%, which is not as good as that of the completely burned areas (Table 1). It should however be noted that the definition of fuzzy membership scores to distinguish burned from partially burned areas (see "Validation of detected burned areas" in the "Methods" section) on one hand, and the subjective element of the result of the visual interpretation on the other hand, might have had an impact on the quantification of the performance of the fuzzy classification.

Spatial and temporal patterns of burned areas

Burned patch sizes

For each particular year, the majority (up to the third quartile) of burned patches are less than five hectares in size (Fig. 1). The annual median of burned patch size ranged from 0.8 to 1.4 ha. Small burned patches are more common in wet miombo than in dry miombo areas, with annual median ranging from 0.8 to 1.4 ha and 0.7 to 1.8 ha, respectively. Relatively few and very occasional big fires may reach sizes of up to ~60,000 ha. These account for a large proportion of the total area burned but they tend to decrease in frequency during the 1972–2011 period, relative to other size classes. Overall, small-burned patches, which are a common occurrence over spatial and temporal scales, account for more of the total area burned than large burned patches.

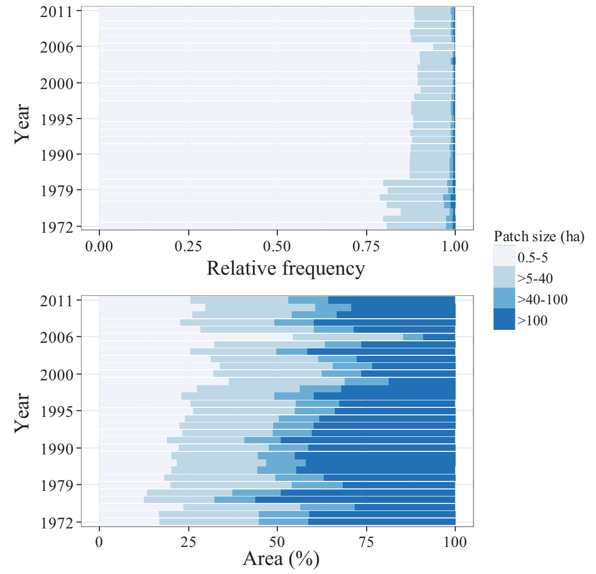

Fig. 1 Burned patch sizes in miombo woodlands in Tanzania based on Landsat satellite images. The relative frequency of patch sizes and their corresponding percent contribution to the total area burned during 1972–2011.

Table 1 Omission and commission errors of burned pixels

Class	Samples		Errors	
	Correctly classified	Incorrectly classified	Omission (%)	Commission (%)
Burned	1,022	365	26.3	0.7
Not burned	7,826	7	0.1	4.5

Kappa coefficient = 0.82.

Frequency-size distribution of burned patches

Frequency-size statistics of burned areas suggest a fire regime dominated by small-sized fires with scaling, $\beta = 2.16 \pm 0.04$, with $r^2 = 0.99$ for the whole woodland during 1972–2011. Wet miombo has a slightly smaller scaling, $\beta = 2.13 \pm 0.03$, with $r^2 = 0.99$ relative to dry miombo where scaling, $\beta = 2.15 \pm 0.04$, with $r^2 = 0.99$. Given the high number of annual burned patches, it was deemed relevant to analyze the annual frequency-size distributions. Annual analyses resulted in scaling ranging from $\beta = 1.89 \pm 0.04$ to $\beta = 2.53 \pm 0.15$, with $r^2 > 0.98$ for the whole miombo woodland. Similarly, wet miombo has a slightly smaller scaling than dry miombo from annual analyses, ranging from $\beta = 1.71 \pm 0.17$ to $\beta = 2.50 \pm 0.19$, with $r^2 > 0.95$ and from $\beta = 1.82 \pm 0.05$ to $\beta = 2.57 \pm 0.43$, with $r^2 > 0.94$, respectively.

Burned extents

Figure 2 presents patterns of burned areas detected from Landsat images, summarized at a 5 × 5 km grid. At this scale, fire incidences appear to be consistently within the same spatial extents. Temporal differences in the extent burned per window show an irregular spatial trend. Annually, up to 13.7% and 12.6% of the total area with available

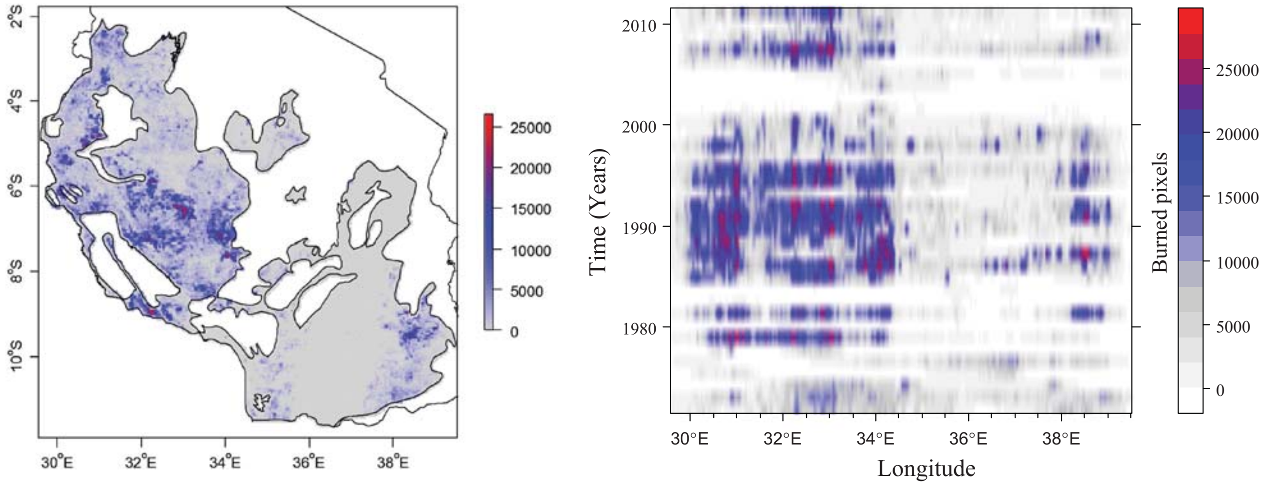

Fig. 2 Spatio-temporal patterns of annual burned areas in miombo woodlands in Tanzania. Burned areas from Landsat imagery are summarized at 5 × 5 km resolution, to show the spatial extent for a selected year (1995) on the *left* and spatial–temporal patterns (1972–2011) on the *right*. For the hovmoller diagram on the *right hand side*, *white spaces* represent missing data and areas outside miombo woodland extent while *zero* represents areas not burned.

imagery was detected as burned in wet and dry miombo, respectively. When combined with partially burned areas, up to 65.8% and 42.1% of wet and dry miombo, respectively, was detected as burned annually. For the whole miombo woodland in Tanzania up to 11.3% is burned annually, while when combined with partially burned areas, up to 50.6% of the woodland is affected by fire annually. Table 2 provides a decadal summary of the contribution of wet and dry miombo areas to the total area burned for the whole woodland. In this table, comparisons are more reliable between dry and wet miombo for the same duration than between durations due to differences in the number of years with available data for each location.

Spatial and temporal patterns of active fires

Early and late dry season burning

A west-to-east transition of fire events from early to late burning is observed in Fig. 3. The sudden drop of

Table 2 Burned area characteristics in (a) dry and (b) wet miombo areas in Tanzania during 1972–2011

Duration	P (ha)	A (%)	M [Dry] (%)	RI	Scaling (β)	A_P
(a) Dry miombo						
1972–1979	930–53,300	3.6–12.6	5.2 [2.9]–11.3 [9.8]	1.6	1.82–2.11	NA
1980–1989	5.4–27,270	3.7–6.5	4.5 [2.2]–8.6 [3.6]	1.8	1.97–2.57	14.3–26.9
1990–1999	1,649–64,650	0.6–8.0	0.8 [0.4]–10.0 [5.1]	2.4	2.00–2.15	10.0–34.1
2000–2011	676.4–21,090	0.7–6.1	1.0 [0.5]–6.6 [4.3]	2.8/3.0[a]	1.93–2.29	4.3–23.6
Duration	**P (ha)**	**A (%)**	**M [Wet] (%)**	**RI**	**Scaling (β)**	**A_P**
(b) Wet miombo						
1972–1979	1,199–29,050	6.7–11.0	7.6 [2.2]–5.2 [2.3]	1.4	1.83–2.12	NA
1980–1989	8.2–15,760	5.9–11.2	4.5 [2.3]–8.6 [5.0]	1.6	2.04–2.50	16.3–31.3
1990–1999	1,166–36,530	1.6–13.7	0.8 [0.4]–10.0 [4.9]	1.4	2.02–2.14	13.3–52.1
2000–2011	9.1–15,160	0.2–7.7	0.8 [0.1]–6.6 [2.3]	2.0/2.1[a]	1.71–2.26	1.2–25.3

Values in square brackets represents the percent contribution of dry/wet miombo to *M*.

P the range of largest annual burned patches detected, may have aggregated with time during the fire season, *A* the range of the total area burned in dry/wet miombo as a percentage of the dry/wet miombo area with data, A_P the total area partially burned in dry/wet miombo as percentage of the total dry/wet miombo area with data, *M* the total area burned in miombo at the same time when *A* was recorded, as percentage of miombo area with data, *RI* Fire return interval observed for every 2,500 ha from Landsat satellite images.

[a] Based on MODIS detected fires for every 314 ha for the period 2001–2013.

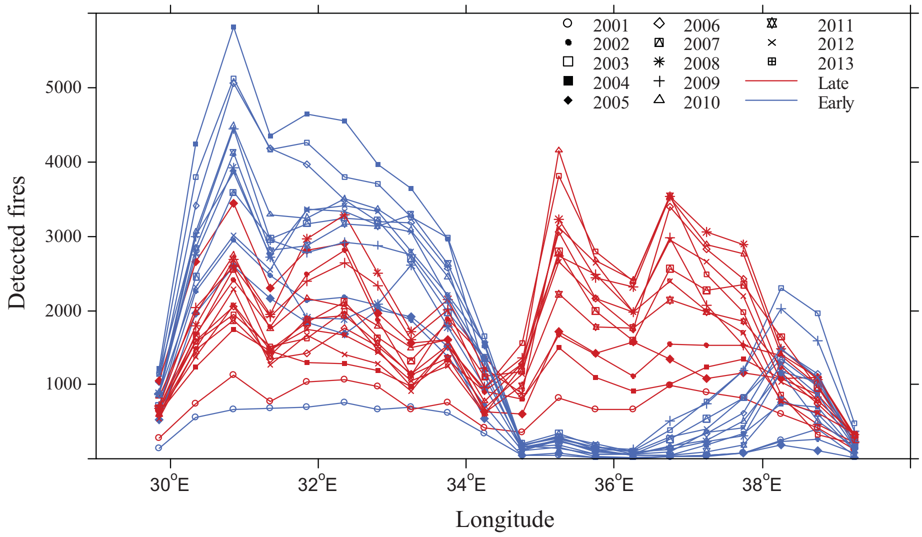

Fig. 3 Spatial distribution of MODIS detected fires in miombo woodlands in Tanzania. July was defined to mark the end of early dry season burning for the entire woodland; local variations are likely to occur.

incidences at ~35.75°E is partly explained by the extent of miombo woodland areas (see Fig. 4) and it marks a distinction between an early dry season burning dominated west to a late dry season burning dominated east.

Based on the number of detected fires each month the fire season peaks during the first part of the dry season in July (Fig. 5). To investigate the effect of early dry season burning on late dry season fires, fire radiative power (FRP) values of late dry season fires were compared for those fires which were either close (within 1 km; i.e. approximately within the same fire pixel) or far (>1 km) from early dry season fires during the same fire season. There is no significant reduction, at 95% confidence level, of FRP values in the late dry season fires, which were close to early dry season burned areas than those far from them.

Fire activity

The combined characteristics of detected active fires provide a composite estimate of fire activity given in Fig. 6. Fire activity is consistently high in the western part of the woodland with the exception of areas along its northeastern border. An increasing systematic westward reduction in fire activity is observed along this border during 2001–2013 (Fig. 6). This reduction is associated with the expansion of croplands when interpreted in the context of the GLC-Share land cover types [51]. On the other hand, there is a shift from high to low fire activity between years on the central, south and eastern parts of the woodland.

Fire return interval

The mean fire return interval for a circular area of ~314 ha, centered at the location of MODIS detected fires was 2.7 years (range 1–13 years) between 2001 and 2013. When the analysis was performed for every 2,500 ha during 1972–2011, based on burned areas detected from Landsat images, the interval was reduced to 2.1 years.

Discussion

Historical fire regimes are best reconstructed from long-term consistent ground records, charcoal deposition in soils or fire scars on trees with annual growth rings [52–55]. In the absence of these, fire history in miombo woodlands of Tanzania was documented from Landsat satellite images and MODIS detected active fires for the past ~40 years. Both fire prevalence and burned extents have recently decreased (Table 2). This decrease is likely an outcome of a number of contributing factors, including a reduction in miombo woodland coverage through e.g. conversion of the woodland into permanent cultivated fields and fire management practices in some parts of the woodland. Burned areas and detected active fire events are consistently within the same spatial coverage (Figs. 2, 6), at the scale of the current analysis. The lack of an independent burned area perimeter for validation restricted our analysis to burned pixels with the highest confidence, which underestimate the total area burned. When thoroughly validated, an analysis including partially burned areas might increase fire activity and shorten fire return intervals in some parts of the woodland. This however, will not affect the general patterns presented in this study.

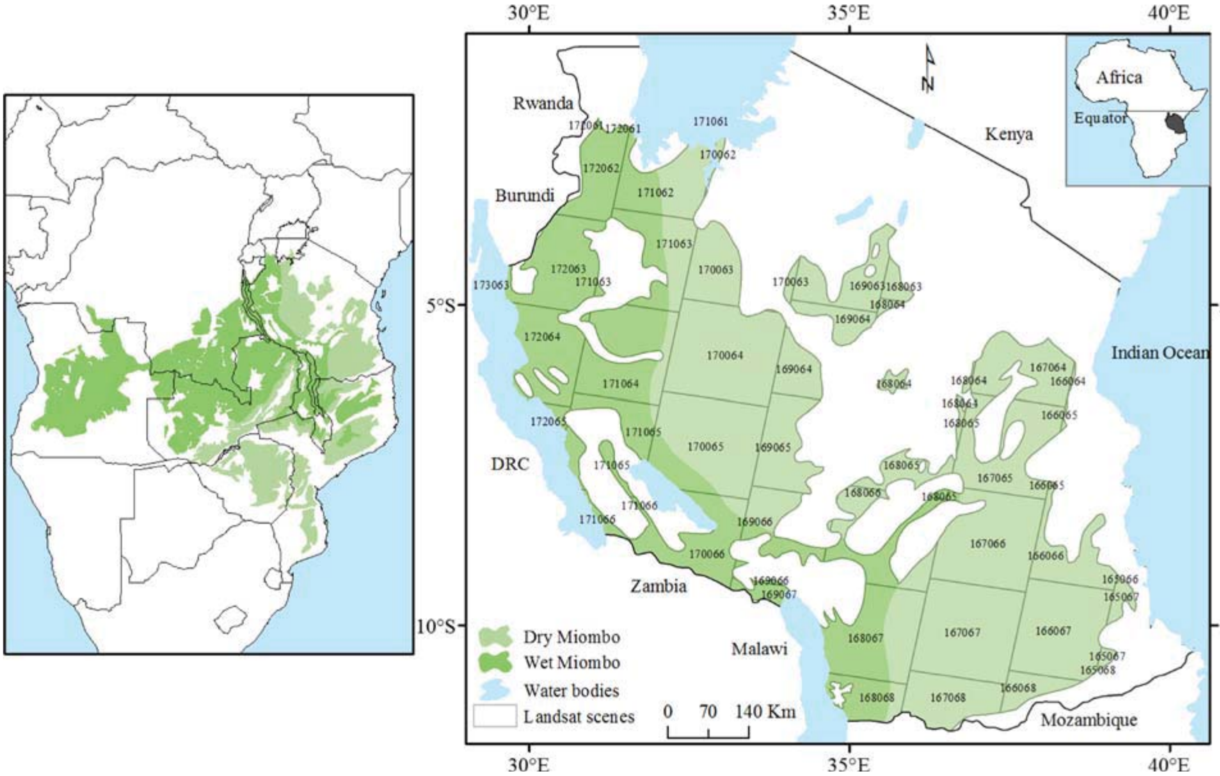

Fig. 4 Distribution and classification of miombo woodlands in Tanzania. The map is based on White's vegetation map of Africa [74]. *Numbers* show the identification (path and row numbers) and extents of Landsat TM/ETM+ scenes.

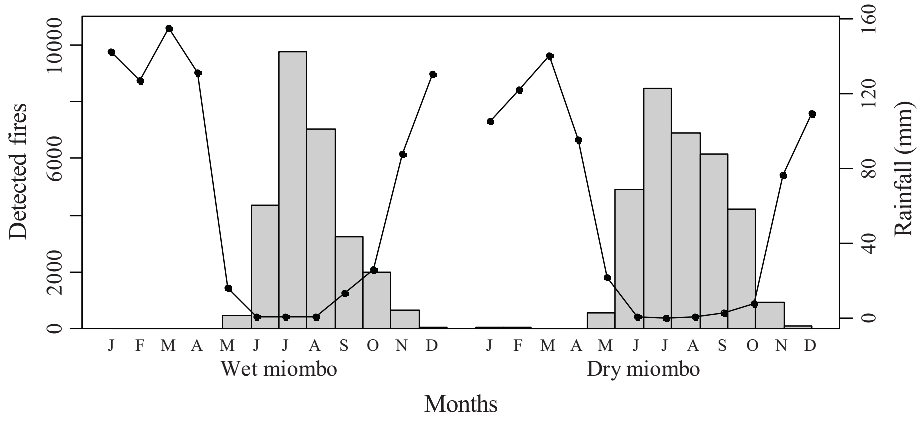

Fig. 5 The fire season in wet and dry miombo areas in Tanzania. *Bars* show mean monthly-detected fires for the period 2001–2013 based on MODIS active fires dataset (see "Data sets and preprocessing" section), and *lines* mean monthly rainfall climatology for 1983–2012 period. Rainfall data is sourced from TARCAT [96].

Fire prevalence

About 46% of the woodland area had a mean fire return interval of <2 years for every 314 ha during 2001–2013 period. Field observations in a dry miombo site have shown a mean fire return interval of 1.6 years in Zambia [23], while a return interval of 3 years on a regional scale was observed based on satellite data [24]. In a global study, the fire return interval for African savannas and grasslands has been reduced, from 4.8 years early in 1900 to 3.6 years towards 2000 [15]. Fire return interval

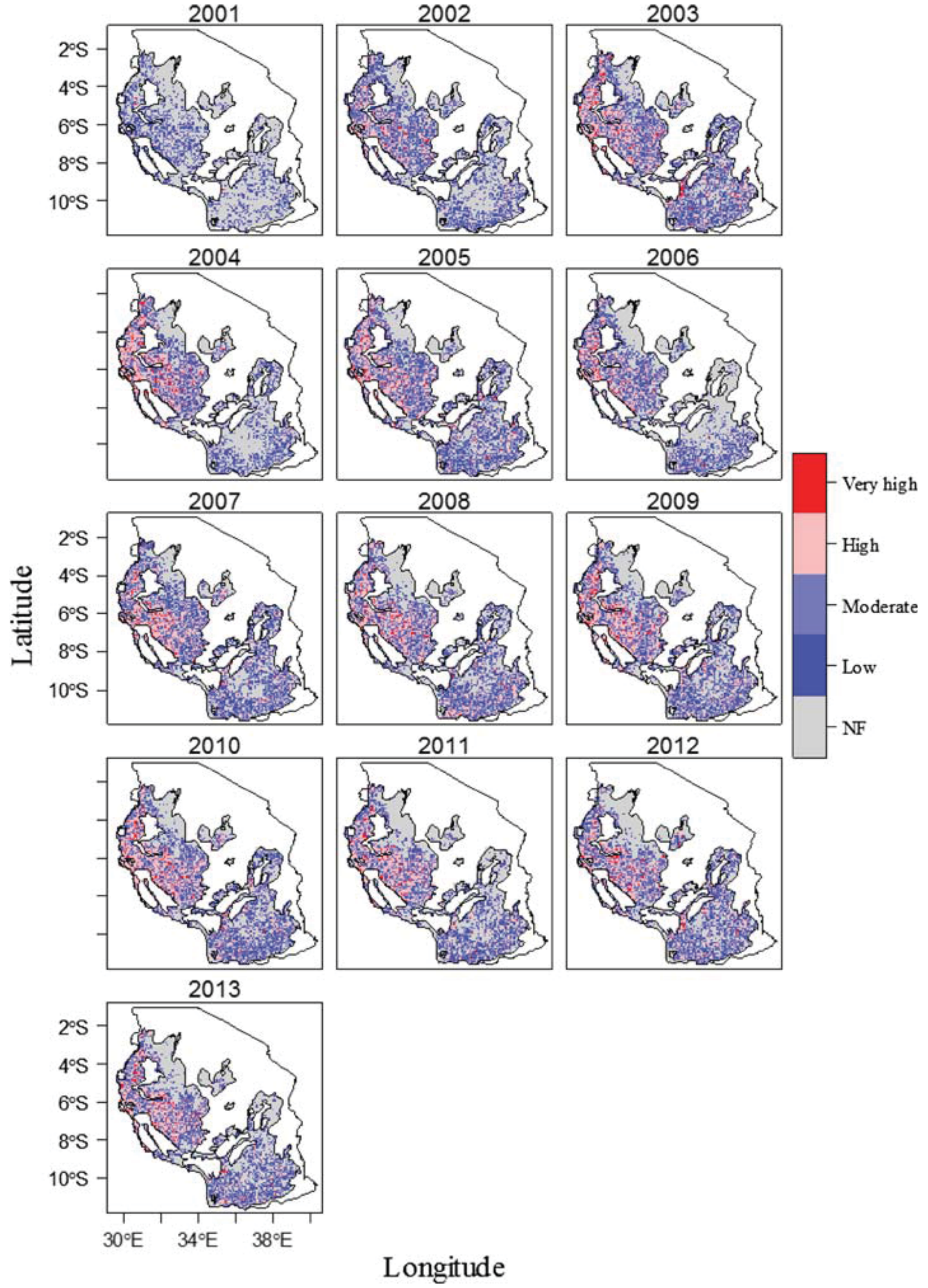

Fig. 6 Fire activity in miombo woodlands in Tanzania. Fire activity based on density, proximity and fire radiative power of MODIS detected fire events, and annual length of the fire season, at a 5 × 5 km resolution. *NF* represents areas with no fire activity.

and burning seasonality have selective effects on different components of the woodland, as they influence the intensity of fires and extents burned. Results from a study that combined field observations and modelling, from miombo sites in Zimbabwe and Mozambique, show that at least 2 years are required between successive low intensity burns to allow tree establishment and development [25]. Although spatial variation is expected within the scale at which fire activity and return intervals are estimated in the present study, our results indicate that almost half of the woodland is ignited at a return interval that threaten the longer-term sustainability of the tree cover. However, the resulting burned patterns (see "Burned extents" section) indicates an offset, to some extent, of the effect of recurrent fires. About 74% of the woodland area had a mean return interval of <2 years for every 2,500 ha between 1972 and 2011. Therefore, frequent fires have been part of some portions of the woodland for the past ~40 years, when satellite data is available. It is important to note that there is a seasonal and inter-annual variation of burned patches within each of the 2,500 ha and thus the return interval varies at smaller scales. Shorter fire return intervals are observed in wet miombo (Table 2), which are the same areas where annual fire activity is consistently high (Fig. 6). Within dry miombo, shorter return intervals persist in western- as compared to eastern- dry miombo areas. The mean fire return interval was 2.5 and 3.8 years for western- and eastern- dry miombo areas, respectively, for the period 2001–2013. On wider spatial and temporal extents, western- and eastern- dry miombo areas have 1.8 and 2.9 years of fire return intervals, respectively, for the period 1972–2011. Western parts of the woodland, including both dry and wet miombo areas, have higher fire prevalence than eastern parts of the woodland, which consist mainly of dry miombo areas. The higher fire prevalence is mainly a result of the interacting effects of rainfall patterns that influence fuel availability, and ignition sources. In southern African savannas, shorter return intervals occurred in higher rainfall areas but interacted with soil properties and herbivory, over a time period encompassing fire suppression, natural fires and controlled fires [55]. Similarly, in western African savannas, higher fire prevalence occurred in relation to increasing rainfall but interacted with both vegetation type and choices by herders and farmers to burn at different times during the fire season [11]. Rainfall influences productivity of grasses that make up the fuel load, but the fire prevalence is ultimately dependent on human influences on ignitions, fire season and extents burned [6, 7, 11, 56].

The west to east dominance of early and late dry season burning, respectively (Fig. 3), might be explained by differences in the length of the dry season. Parts of the western side of the study area receives light rains during September, from north and extending southward. These light rains continues through the main rainy season, thus reducing the length of the fire season. Central and eastern parts have a unimodal rainfall pattern and thus remain relatively dry until the beginning of another season in November/December, facilitating conditions favorable for late dry season fires.

The observed reduction in fire activity from north towards west (Fig. 6) is associated with expansion of croplands. The expansion of croplands in this area is likely a response to growing mining activities and respectively settlements in the Geita and Kahama districts, north of the study area. Expansion of croplands has had similar effect in northern hemisphere African savannas, where decreasing annual burned area occurred with increasing croplands [57]. As with fire activity, croplands had smaller burned extents when compared to vegetated cover types in the GLC-Share Database [51] for the extent of the study area. Based on GLC-Share cover types, our results show that up to 1.6% of the croplands are burned annually compared to 4.3% of grasslands, 2.6% of tree covered areas, 3.9% of shrubs covered areas and 10% of herbaceous vegetation, aquatic or regularly flooded. The datasets used to compile GLC-Share database for Tanzania is from 2001. Therefore, the values presented above are within a decadal range; from 1995 to 2005.

Burned extents

Burned patch sizes

Small-burned patches, less than five hectares in size, are the most prevalent across spatial and temporal scales. Smaller burned patches are a common occurrence across tropical savannas and are mainly associated with traditional fire management practices [18, 21, 58, 59]. Burned patches with similar sizes were associated with farm preparation in a neighboring Mozambican savanna [60]. Similarly, small fires within African savannas have been associated with agricultural activities and fragmentation of the landscape as a result of high population densities [14, 61]. These fires, burning small patches at a time progressively during the dry season, are generally a desirable management tool and are less damaging to savanna woodlands [18, 62, 63], unless they escape to burn unintended areas. Most of the cases of escaped fires are associated with clearing of new farms as opposed to burning agricultural residues in established agricultural areas. As discussed in the "Fire prevalence" section, our results show that burned extents were smaller in croplands than in other cover types. We could not quantify the effect of other sources of fire on burned patch sizes. However, Butz [21] has observed an increase is large accidental fires and a decrease in small fragmented fires, within a pastoral community in the savannas of northeastern Tanzania. In this area, a decline in nomadic pastoralism has occurred with a trend towards sedentarization and diversified livelihoods [64, 65]. Butz identified changes in rainfall patterns, population growth and fire suppression policies as the drivers of the change in the fire regime. Similar drivers of change in fire regimes persist in western African savannas [8]. In general, competition over land areas increases with a growing population, leading to changes in socioeconomic practices [64] and increasing land fragmentation. Consequently, fire regimes including the frequency, season and sizes of burned areas vary with localized adaptation to these changes in the context of the landscape pattern, and may be influenced by public policies and rainfall patterns [8, 14, 61, 66]. Fires with a higher threat are those ignited within woodland areas where tenure accessibility and private uses are restricted. This threat is associated with increasing homogeneity and buildup of fuels with decreasing human activities [61]. In such cases, the prevailing weather regulates the spread of a fire when ignited [7], as opposed to the human control that fragments the landscape with small fires. In a recent analysis of MODIS burned area product (at 500 m resolution) for the whole of Tanzania between 2000 and 2011, up to 77% of the annual burned area in the country was detected on gazetted land [67]. Although the causes of these fires were not evaluated, it is less likely that they all stem from control burning for fire management purposes. Similarly, protected areas in the southern hemisphere African savannas had relatively larger burned areas than outside protected areas [13]. In the Llanos savannas of Columbia, relatively larger burned areas associated with hunting were observed in a national park compared to indigenous reserves and ranches [68]. In western African savannas, higher densities of fire events occurred in protected areas of Burkina Faso and lower populated areas of Mali [12, 69]. At a smaller scale, the highest tree mortality associated with fire in central Zambia occurred within an encroached part of a national park [70]. This highlights priority fire causes and affected areas that need further detailed analyses and probably a reassessment of management practices. Combining traditional and contemporary fire management practices may achieve reduction in burned extents and consequently biomass burning emissions [71].

We observed a larger scaling of frequency-size distribution, indicating a higher ratio of small relative to large fires, in this study as compared to other ecosystems, e.g. in the United States and Spain [53, 72]. In a global study of fire size distribution, Hantson et al. [14] have also observed a dominance of small fires in our study area, with a similar range of the scaling parameter, β (see "Frequency-size distribution of burned patches" section, Table 2). Small fires are recurrent in both dry and wet miombo areas but dry miombo areas experiences both smaller and larger fires than wet miombo areas (Table 2). The difference in size classes of burned patches in wet and dry miombo contributes to the slightly smaller scaling of frequency-size distribution in wet miombo, which implies large burned patches contribute slightly more to the total area burned in wet than in dry miombo. These large burned patches are partly a result of aggregation of smaller fires during the fire season. Generally, large fires are rare but small fires accumulate to cover extended areas in the course of a fire season each year. Archibald et al. [13] found similar contribution of small fires to the annual burned area in southern hemisphere Africa savannas. Small recurrent fires reduce the risk of occasional large fires, which have recently occurred in areas where fire suppression strategies are enforced.

Partially burned areas

Partially burned areas were defined to include intermixed pixels groups that are burned, partially burned and those with a diminishing char signature. They cover relatively wider extents than completely burned areas each year, ranging between 3.2 and 40.6% and 0.8–11.3%, respectively, for the whole woodland. Table 2 provides a decadal summary for wet and dry miombo areas. Between 9 and 14% of Tanzania's area was detected as burned annually during 2000–2011 from a lower (500 m) resolution burned area product [67]. Of this burned area, 69% occurred in the woodland. Miombo woodland areas covers approximately 90% of the forested areas in Tanzania, implying that much of the burned areas in the country are not detected at the lower resolution. Lower detection rates are possibly higher in the mixed burned–unburned pixels. Similar to completely burned areas, western parts of the woodland have relatively larger extents of partially burned areas, predominantly in wet miombo, than eastern parts of the woodland. Rigorous validation was not performed for partially burned areas, thus they were not further analyzed. However, they provide crucial information for understanding vegetation dynamics, which requires the season and severity of fires at specific areas.

Conclusions

We have documented the recent fire regime, for the past ~40 years, of the miombo woodland areas of Tanzania at spatial and temporal resolutions that have not been recorded before, to the best of our knowledge. The observed fire patterns for the past 40 years show that the majority of fire events occur in the western parts of miombo woodlands, consisting of wet miombo and western dry miombo areas. Fire events on the western parts of the woodland occur mainly during the first part of the dry season. Thus, an early dry season fire peak characterizes the west while a late dry season fire peak characterizes the east. Almost half of the woodland area has fire return intervals of <2 years. Return intervals are shorter in wet than in dry miombo areas. Short return intervals limit fuel loading and therefore prevents large intense fires. Human activities play a major role in shaping fire regimes. Mainly small sized fires characterize the regime across spatial and temporal scales. Occasional large fires are more frequently detected in dry than in wet miombo areas. Management strategies need to address spatially specific needs of wet and dry miombo areas, in the light of their fire regimes and socio-economic context.

Methods

Study area

The study area is miombo woodlands in Tanzania (Fig. 4). Miombo woodlands are disturbance driven moist savannas that are shaped by natural and anthropogenic disturbances, to a larger extent, than by nutrient and water availability [1, 73]. They occur on nutrient poor soils and generally experience a warm-to-hot climate with a dry cold season [24]. The average annual rainfall ranges between 600 and 1,500 mm and falls during 5–6 months [23], followed by an extended dry period. Wet miombo areas, which receives more than 1,000 mm of average annual rainfall, are distinguished from dry miombo areas receiving less than 1,000 mm of average annual rainfall [74]. The woodland is characterized by wooded canopy species and an understory consisting of shrubs and light demanding grass species [24]. The annual production of these flammable, 0.5–2 m tall, grasses every rain season followed by accumulation of litter from the deciduous trees, makes miombo woodland highly susceptible to annual fires.

The fire season extends from the onset of the dry season to its end (Fig. 5), although isolated burning events may occur throughout the year at different localities. During the fire season, individual fires burn small patches at a time with the exception of very occasional big fires in areas where fuel load is accumulated and continuous. Towards the end of the fire season, a mosaic of burned and unburned patches occur.

Data sets and preprocessing

Landsat Level 1 Terrain (L1T) corrected product satellite images and MODIS collection 5 Level 2 MOD14/MYD14 active fire product form the major data source for this study. We derive fire patterns from the two datasets independently and compare results. Similar patterns will indicate that the datasets are representative of the fire patterns in the study area. This is important because although Landsat provides a finer spatial resolution its temporal resolution (16 days), and further limitation by cloud cover, may limit detection of savanna fires. On the other hand, MODIS detected active fires provide a more complete coverage at high temporal resolution but its temporal coverage is relatively short (since 2000) compared to that of Landsat (since 1972). In addition, MODIS can detect small active fires that are not captured by coarse resolution burned area products [45]. Thus, combining the two datasets benefits from their complementary availability, spatial and temporal characteristics [41].

All available Landsat images were downloaded from the USGS Global Visualization Viewer [75], to cover the study extent (Fig. 4) and for the period 1972–2011. Availability was constrained by image quality, predominantly percentage cloud cover within the study extent. Thus, a complete spatio-temporal dataset was difficult to achieve. For each year, processing and analysis was performed for areas where at least one image was available during the fire season. A total of 1,835 scenes, among them 234 MSS, 1,284 TM and 317 ETM+ SLC-On, were processed. Landsat TM imagery was preferred over MSS imagery for the period when both were available. Each image was converted to at-surface reflectance using the Dark Object Subtraction (DOS) method [76–78].

MODIS active fire data for the whole country were downloaded from the Fire Information for Resource Management System (FIRMS) [79], for the period between November 2000 and December 2013. MOD14/MYD14 provides, among others, coordinates of detected fires (the center of fire pixels at 1 km resolution), their acquisition date and time and respective FRP. Fire locations within miombo were retrieved and categorized as early dry season burning (January–July) or late dry season burning (August–December). Isolated fire events during the wet season were included in respective dry season burning based on the month of their detection. July was chosen to mark the end of early dry season burning for the entire woodland area, consistent with prescribed early burning between May and July in some parts of Tanzania [80–82]. This distinction was made to capture patterns of fire during the dry season, since the timing of burning influences the intensity and spread of a fire and thus its effects, such that fire management through prescribed burning is recommended during early dry season [23].

Spatial and temporal patterns of burned areas and active fires

Burned areas were detected by means of fuzzy classification of spectral indices derived from Landsat satellite images while spatial patterns of active fires were analyzed based on MODIS dataset. We limited our analysis to prevalence, burned extents and spatial patterns of active fires and burned patches. The general processing flow is summarized in Fig. 7. Analyses were performed in GRASS GIS [83] and R version 3.1.0 [84].

Training and testing of the fuzzy classification

A total of 523,092 pixels were sampled by visual interpretation from representative scenes for training and testing purposes. Burned areas were identified based on color composites with SWIR, NIR and VIS bands in RGB display, an approach that has been employed to extract image based training, and testing samples [46, 47, 85]. Active fires captured by Landsat satellite images and the analyst's field experience were utilized in line with the color composites. These formed the basis for selection of spectral indices.

Spectral Indices used for fuzzy classification

Spectral indices commonly used for burned area mapping were identified based on literature review. Eleven

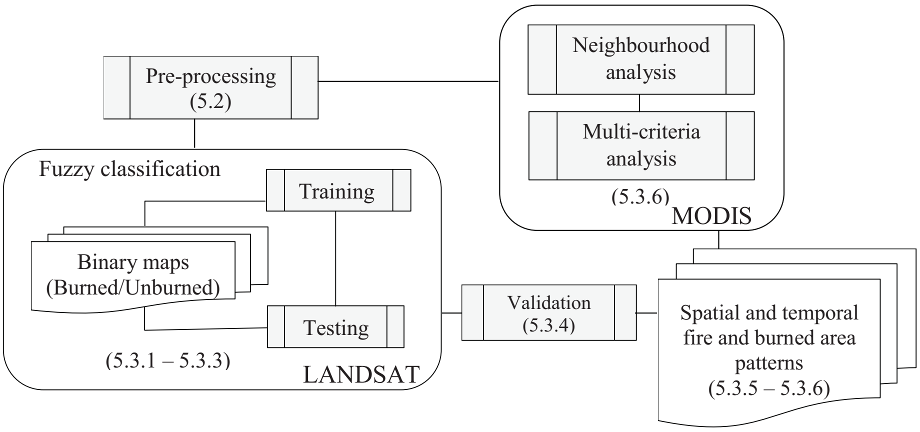

Fig. 7 General processing flow with respective detailed sections in *parentheses*.

indices with a potential for discriminating burned areas in sparsely vegetated areas were selected and tested. These included BAI [49], BAIM [86], $\mathrm{BAIM_L}$ [46], GEMI [87], MIRBI [50], $\mathrm{NBR_S}$ [46], $\mathrm{NBR_L}$ [88], $\mathrm{NBR_2}$ [47], NDVI, SARVI [89] and SAVI [90]. The range of values from individual scenes and the differences among scenes, for which burned pixels were well separated from other cover types, was determined for each index to form the base for fuzzy sets definition (see "Fuzzy membership rules" section). Penalized logistic regression was then employed to analyze the discrimination performance of burned from unburned pixels for each spectral index. An analysis combining sampled pixels from all scenes was also done to investigate how well results at scene level could be generalized.

Table 3 Spectral indices used in fuzzy classification

Indices	Use
$\mathrm{BAIM_L}$ and MIRBI	Detect burned areas at different post-fire conditions
$\mathrm{BAIM_L}$ and threshold	Mask bare soil, water[a], topographic and cloud shadows
$\mathrm{NBR_L}$ and threshold	Distinguish active fires from other features
BAI	Detect burned areas on MSS imagery

$BAI = 1/(\rho_{c2} - \rho_2)^2 + (\rho_{c4} - \rho_4)^2$; $\rho_{c2} = 0.1, \rho_{c4} = 0.06$.

$BAIM_L = 1/(\rho_{c4} - \rho_4)^2 + (\rho_{c7} - \rho_7)^2$; $\rho_{c4} = 0.05, \rho_{c7} = 0.2$.

$MIRBI = 10 \times \rho_7 - 9.8 \times \rho_5 + 2$.

$NBR = (\rho_4 - \rho_7)/(\rho_4 + \rho_7)$.

$\rho_2 =$ Band 2 of MSS on Landsat 4-5 and Band 5 of MSS on Landsat 1-3.

$\rho_4 =$ Band 4 of MSS on Landsat 4-5, Band 7 of MSS on Landsat 1-3 and Band 4 of TM/ETM+ .

$\rho_7 =$ Band 7 of TM/ETM+ .

[a] Permanent water bodies were manually masked out from fuzzy classification results.

Fuzzy membership rules

Fuzzy discrimination employs membership rules that are defined in terms of fuzzy sets [91], whose elements differentiate definite members from definite non-members and those with some level of uncertainty as to whether they are members or not. Fuzzy classification was experimented for each index individually and for different combinations of indices. Indices and combinations thereof were selected (Table 3) for fuzzy set definition based on how well they distinguished burned from unburned areas. Selected indices conformed to regression results (see "Spectral Indices used for fuzzy classification" section).

Validation of detected burned areas

Due to the lack of an independent burned area perimeter for validation, completely burned areas were distinguished from partially burned and unburned areas, based on their membership scores, for the purpose of restricting further analysis to definite burned areas. Partially burned areas consisted of intermixed pixel groups of burned, partially burned and those with a diminishing char signature (Fig. 8). These areas were not included in subsequent analyses but they indicate the spatial and temporal extents of areas affected by fire each year. Validation of completely burned areas, which are referred to as burned areas, was performed based on visual interpretation of randomly selected samples, from another set of representative scenes different from those used for training and testing fuzzy classification. To validate the performance of the fuzzy classification when including also the partially burned areas, we employed visual analysis and unsupervised clustering. This approach, combining visual interpretation and unsupervised clustering, is suitable for discriminating burned areas in African savannas [42].

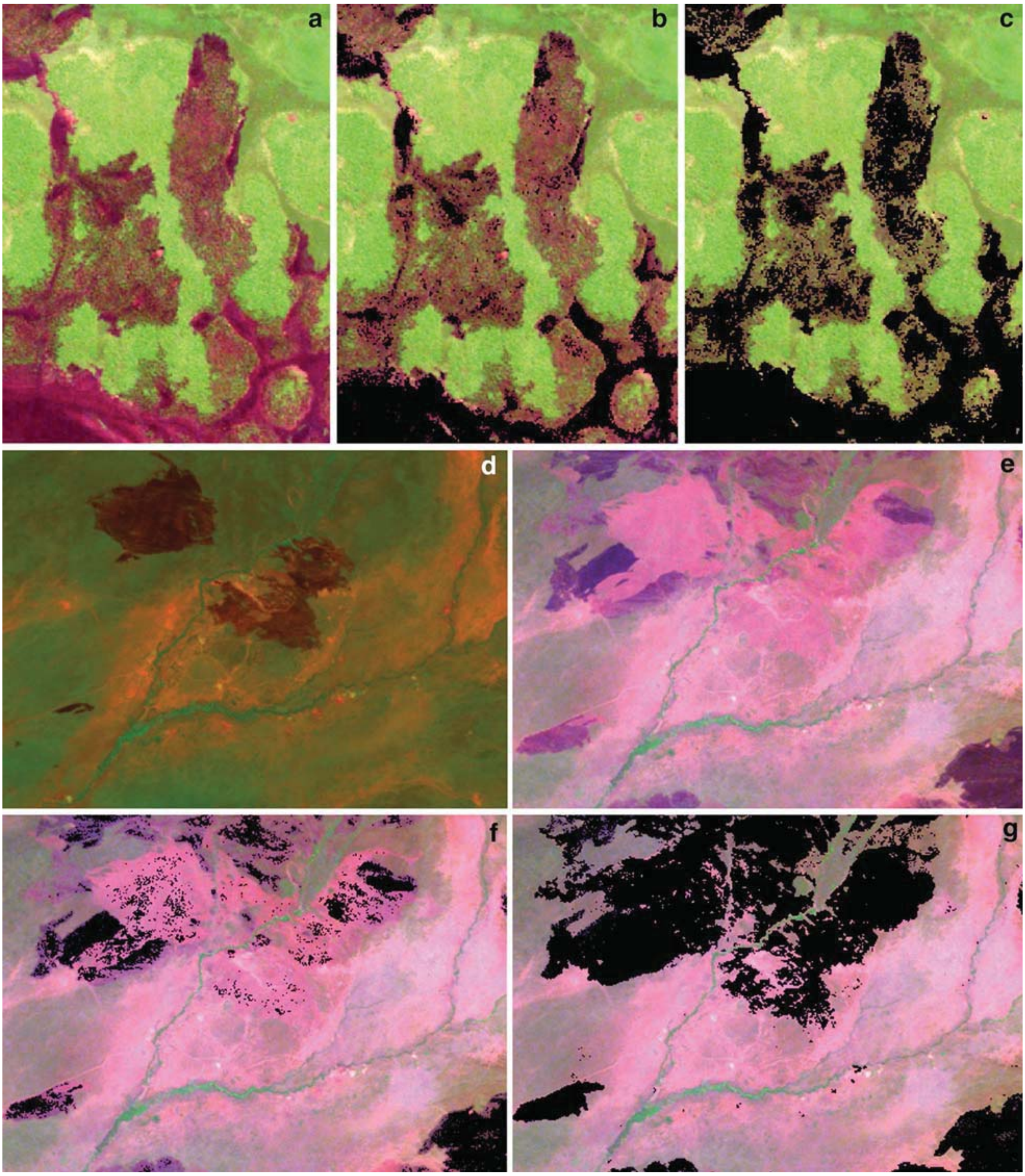

Fig. 8 Illustration of areas defined as partially burned. The *top panel* shows an area with mixed burned and unburned pixels (**a**). The *middle panel* shows burned patches at the beginning of the fire season (**d**) and the same area later (**e**) during the fire season. Burned areas (**b**) and (**f**), consist of contiguous groups of burned pixels with a definite fire scar. A mix of burned and unburned pixels and those with a diminishing fire scar were defined as partially burned, shown in (**c**) and (**g**) when combined with burned areas. Detection of burned areas with a diminishing fire scar is desirable when an image from an earlier date during the fire season is not available.

We adapted the approach described in [47] where three 1,000 × 1,000 pixels image subsets were visually interpreted to delineate burned/partially burned area perimeters. An independent image analyst examined these visually interpreted burned areas with support of false color composites (bands 432 and 741 as RGB) in combination with clustering of the bands 741 data subset, utilizing ERDAS Imagine 2014. The results were then used to validate the combined burned and partially burned area.

Burned patch sizes and spatio-temporal variation in burned extents

The sizes of burned patches were calculated based on contiguous burned pixels at scene level, while burned extents from annual mosaics after accounting for multiple detections between acquisitions. The fire return interval based on detected burned areas was determined by overlaying a 5 × 5 km grid on annual burned area maps, thus a return interval for every 2,500 ha. Grid cells containing burned patches >0.5 ha were considered affected by fire in respective years and provided a crude estimate of fire return interval for each cell. We use this estimate for consistency across the spatial and temporal extents with different Landsat data availability and for comparison with MODIS data (see "Occurrence and spatial patterns of active fires" section). The 0.5 ha threshold was selected based on reported burned patch sizes from anthropogenic fire sources in neighboring Mozambican savannas [60]. Frequency-size distributions of burned patches >0.1 and >0.4 ha for TM/ETM+ and MSS imagery, respectively, were examined for the period 1972–2011. Frequency densities of patch size classes were analyzed in log–log space, where the slope coefficient, β, provided the scaling of burned patch sizes i.e. the ratio of the number of large to small fires [53].

Occurrence and spatial patterns of active fires

The spatial association of detected fires was examined by Ripley K function for inhomogeneous spatial patterns [92]. Annual fire activity was derived at a 5 × 5 km resolution as a composite measure of active fire characteristics, including density and proximity of fires, annual duration of the fire season and range of FRP values. These combined characteristics of active fires provides a classification of the fire activity that is related to the fire regime [93]. The FRP values, for instance, are associated with the type of vegetation burned [94] and the density of fires is a good predictor of burned areas [13]. The grid resolution was based on both an optimal choice for spatial aggregation when comparing datasets with different resolution as applied in [44, 95] and for practical handling purposes. Fire return interval based on detected active fires was examined by a neighborhood analysis within a 1-km distance from each detected fire. Thus, a return interval for an area of ~314 ha, which is the area of a circle of 1 km radius, centered at the location of detected active fires. This distance was selected to reflect the ground size of detected fire pixels. Results for each year provided fire return interval given locations of detected fires for that year and their average provided mean return interval for all years.

Abbreviations

BAI: Burned Area Index; BAIM: MODIS Burned Area Index; FIRMS: Fire Information for Resource Management System; FRP: Fire Radiative Power; GEMI: Global Environment Monitoring Index; MIRBI: Mid-Infrared Burn Index; MODIS: Moderate Resolution Imaging Spectroradiometer; NBR: Normalized Burn Ratio; NDVI: Normalized Difference Vegetation Index; SARVI: Soil and Atmospherically Resistant Vegetation Index; SAVI: Soil Adjusted Vegetation Index.

Authors' contributions

BT planned and implemented the study and prepared the manuscript. ØBD performed an independent visual analysis. TG planned some of the methods and prepared the manuscript. ØT prepared the manuscript. All authors contributed in revising the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical guidelines

Competing interests

The authors declare that they have no competing interests.

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Paper II

Relationships between woody plant species composition and recent fire history across spatial scales in Tanzanian savanna woodlands

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Abstract

Question: Does recent historical fires (~40 years) influence the composition of woody species in savanna woodlands across spatial scales and along disturbance gradients?

Location: Kilosa and Kilwa districts in Tanzania.

Methods: We sampled the properties of the different growth stages (seedlings, saplings, adults) of woody species across spatial scales at each of five sites. We allocated sites into three disturbance levels based on the presence of farms, proximity to settlements and roads, and grazing pressure. We recorded recent fire events onsite and retrieved historical fire events from satellite-based datasets. We analyzed species compositional patterns by gradient analyses and spatial patterns by Morans Eigenvector Maps and scalogram analyses.

Results: The composition of woody species was spatially variable for all site-growth stage combinations. The ability of fire alone in explaining this spatial variation was lower than the synergistic influence of fire and other disturbances. The relationship between fire and woody species composition was site specific, with no generalizable patterns across spatial scales or along the disturbance gradients. However, there is an indication that fire contributes to increased species homogenization for the adult growth stage at large spatial scales.

Conclusions: Our results suggest that historical fires contribute in determining the spatial occurrence of woody species and interact with the type and severity of historical disturbances to influence the composition and abundance of woody species at all growth stages. A strong association of fire and woody species was not apparent for the duration of our fire record, most likely because the current species composition has been shaped by fire conditions that have persisted for a longer period than our historical fire records.

Keywords: Anthropogenic fires; Disturbances; Fire history; Moran's Eigenvector Maps; Spatial patterns; Taxonomic homogenization

Running head: Fire influence on woody species composition

Introduction

Disturbances play a fundamental role in shaping plant communities (Sousa 1984; Dornelas 2010) and are often classified as either natural or anthropogenic, although the distinction is not always obvious (Bowman et al. 2011; Magurran & McGill 2011). For example, forest fires can be a natural or a human initiated disturbance. In general, human modification of natural disturbance regimes is a major driver of biodiversity change and loss (Moorcroft & Levin 2009). At a global scale, the most significant human modification of natural disturbance regimes has been through changes in the frequency of fires (Moorcroft & Levin 2009; Bowman et al. 2011). In African savannas, the recurrence of fire is evident from fossil records for over millions of years (Scott 2000; Bond 2015), and human use of fires has been widespread (Bird & Cali 1998; Archibald et al. 2012). Currently, almost all fires in African savannas originate from anthropogenic ignitions (Archibald et al. 2012; Andela & van der Werf 2014). Thus fire regimes, including their frequency, intensity, timing and extent, depend on human burning practices. The influence of different fire regimes on the structural composition of African savannas is widely documented. Frequent and intense fires progressively suppress the cover of woody vegetation and cause a dominance of fire-tolerant species (Laris & Wardell 2006; Furley et al. 2008; Smit et al. 2010; Ryan & Williams 2011). A long-term suppression of fires on the other hand, causes an increase in woody cover, particularly by fire-sensitive species (Chidumayo 1997; Hoffmann & Moreira 2002; Bond et al. 2003; Bond et al. 2005). Fire can also interact with other drivers of vegetation change, such as herbivory, to influence woody species at different growth stages (Zida et al. 2007; Mapaure & Moe 2009; Staver et al. 2009; Midgley et al. 2010). Despite the widely documented influences of fire on the structural composition of savanna vegetation, the influence of different fire regimes on woody species composition is less understood (Anderson et al. 2015). Results from long-term experimental fires suggest that the composition of woody species in African savannas is resilient to different fire treatments (Enslin et al. 2000; Furley et al. 2008; Scott et al. 2012; Pellegrini et al. 2014). However, the fixed return intervals of experimental fires and their limited replication and spatial coverage is not always representative of the variability in abiotic conditions, human burning practices, and other disturbances interacting with fire under natural conditions (Laris & Wardell 2006; Holdo 2007; Furley et al. 2008). Moreover, woody species portray differences in their immediate and long-term responses to fire regimes (Hoffmann & Moreira 2002). These responses may also interact with other disturbances. For example, Nangendo et al. (2005) and Ribeiro et al. (2008) predicted an imminent homogeneity of woody species composition under the influence of frequent fires and herbivory by elephants.

Fire can facilitate homogeneity or heterogeneity of species composition, depending on the fire regime (Hudak et al. 2004; Sheuyange et al. 2005; Turner 2010; Smit et al. 2013; Myers et al. 2015). In savannas, the occurrence of fire and its influence on woody species vary with spatial scale (Skarpe 1992; Romme 2005; Sheuyange et al. 2005; Lookingbill et al. 2011; Levick et al. 2012). At the landscape scale, savannas are naturally heterogeneous and human burning practices in savannas result into small fragments of burned areas that progressively accumulate to cover large areas during the fire season (Russell-Smith et al. 1997; Laris 2002; Hudak et al. 2004; Baldeck et al. 2014). At a large scale, the timing and intensity of burning vary spatially during each fire season, whereas at a small scale the frequency, intensity, and season of burning are likely similar both in spatial and temporal extents (Smit et al. 2013). At both small and large scales, fire is a top-down influence that acts on the existing composition and abundances of species (Gillson 2004; Bond 2008; Sankaran et al. 2008). Moreover, the surface fires that are typical of African savannas are generally detrimental to juveniles, as opposed to crown fires that may cause complete mortality of all individuals. Thus, the influence of fire on woody species is likely dependent on how individual trees of each species, at the existing composition and abundances, are resilient to fires over the longer term. In addition, other historical events interacting with fire, such as rainfall and land use practices, are likely to influence community properties at different spatial scales (Borcard & Legendre 1994; Fortin & Dale 2005; Levick et al. 2015). Consequently, compositional responses of woody species to fire are likely to vary with spatial scale, depending on existing species composition and other disturbances.

Human ignited fires have extended the fire season in African savannas from the beginning of the wet season, when the main ignition cause was lighting, to include the whole duration of the dry season. Fire-return intervals are also significantly shortened, with up to annual fires in some areas (Frost & Robertson 1987; Van Wilgen et al. 2000). Recurrent fires maintain seedlings and saplings in the juvenile growth stage, and therefore, they require protection from fire to reach heights and stem diameters that make them less affected by fire (Chidumayo 1997; Higgins et al. 2000; Zida et al. 2007; Ryan & Williams 2011). Thus, changes in species composition caused by fire are likely dependent on the relative abundance of different growth stages and the species' resilience to both fire and other disturbances (e.g. Ben-Shahar 1998; Moncrieff et al. 2008; Helm et al. 2011; Helm & Witkowski 2013; Levick et al. 2015).

Our primary aim was to examine the relationship between fire and the composition of woody species in savanna woodlands and if this relationship vary across spatial scales. We predicted that woody species composition varies with the frequency of historical fires and across spatial scales, and that this variation is altered by the severity of other disturbances. We also examine if the influence of fire leads to a taxonomic homogenization of woody species and if this homogenization, if it occurs, varies across spatial scales and with the species' degree of tolerance to fire. We predicted that the magnitude of homogenization decreases with increasing spatial scale because of increasing heterogeneity in both fire characteristics and underlying abiotic conditions at larger spatial scales.

Materials and methods

Selection of study sites

We studied the relationship between the composition of woody species across spatial scales and fire occurrences in the recent history in five sites distributed within two districts in eastern Tanzania (Fig. 1, Table 1). The districts were selected for a broader research theme that encompasses the current study, across cultural and socioeconomic practices and with anthropogenic uses of fire. Sites in both districts occur in woodland savannas areas, classified by White (1983) as Zanzibar-inhambane and drier miombo woodlands. We considered the whole extent of the woodland areas in each district as candidates for sampling, because there was no clear indication of spatial or temporal patterns in the occurrence of fires prior to sampling. To select sample sites within the two districts, we divided each district into grid cells, each covering 100 km^2. In each district, we randomly selected half of the grid cells as potential sampling sites. We then utilized Landsat satellite images, Google Earth and standard topographical maps at 1:50 000 scale to categorize the selected grid cells into three levels of anthropogenic disturbance: high, intermediate and low (Table 1). The disturbance level was determined based on utilization pressure indicated by the presence of farms, historical livestock grazing intensity determined with the help of resident forest officers and proximity to settlements and roads. The patchy distribution of woodland areas limited the availability of contiguous grid cells for each disturbance level at different locations within the districts. Thus, in each district we selected two or three grid cells that were most representative of each disturbance level, depending on availability. We then verified the characteristics of these selected cells in the field with the assistance of resident forest practitioners. We carried out sampling for five verified grid cells (Table 1, Fig. 1): two in each of the high and intermediate disturbance levels and one in the relatively undisturbed (low) level.

Topographical maps of each site, dating between 1967 and 1971, show the presence of human settlements in all sites. However, population density, anthropogenic utilization and accessibility to the outside world have differed for each site throughout the past 40 years. Sampled sites (Table 1, Fig. 1) included (i) Kimamba, a peri-urban center whose neighborhood has been managed for animal husbandry and plantations and is served by a railway line through Kilosa district center. Roads and tracks to the nearby Kilosa (~19 km away) and other towns and peri-urban centers are currently operational throughout the year and some plantations are still productive. The site is located ~13 km from Kimamba center and occurs partly within an area previously managed as a ranch. The location of (ii) Kiduhi village center has changed over time, but is currently permanent with separate areas set aside for farmers and herders and it is accessible by seasonal tracks. The site is located within an area with a long history of both small-scale agriculture and livestock grazing. It borders the Mikumi national park and is ~48 km from Mikumi town center. (iii) Mkarango is a small village that practices small-scale shifting cultivation and has very limited road accessibility. The site is located ~55 km from Kikanda center and ~104 km from Kilwa district center. (iv) Kikole village also practices small-scale shifting cultivation and is accessible by seasonal tracks. The site is located ~49 km from Kilwa district center. Kikole village enforces forest management plans through village level natural resource committees. (v) Ihombwe village also has a village level environmental committee that enforces forest management plans. It is accessible by roads and tracks from nearby towns and peri-urban centers. The site is located ~12 km from Ihombwe village center and ~22 km from Mikumi town center.

Sampling of vegetation data

We carried out sampling between September and December 2012. In each site (Fig. 1), three radial transects were randomly established from the center of the site, with 120^o angle between transects. One rectangular plot (20 m x 50 m) was placed at the center of the site and three plots were located at each of 1, 2 and 3 km from the center of the site along each transect (Fig. 1). At each of these distances, one plot was placed on the transect line and one plot 300 m on each side, perpendicular to the transect line. Thus, each transect had nine plots, giving 28 plots per site including the plot at the center of the site. At Kiduhi, we sampled 25 plots since three plots occurred within Mikumi national park, where we could not secure entrance permit. Transect lines and plot locations were pre-determined in LISCAD v.6.2 software and tracked on the ground by their pre-determined UTM coordinates using hand held GPS receivers.

We subdivided each plot into ten 10 m x 10 m sub-plots. We recorded the diameter at breast height (dbh at 1.3 m) for all trees with dbh > 4 cm (adults) in all subplots. We measured the dbh of each stem of multi-stemmed trees individually. At five alternating sub-plots, we also recorded dbh for all trees with dbh between 2 cm and 4 cm (saplings). In the same sub-plots, we counted all individuals with dbh < 2 cm (seedlings). We identified tree species by vernacular names onsite and collected voucher specimens of all species for identification at the herbarium of the University of Dar es Salaam, Tanzania. Because we conducted fieldwork during the fire season (dry season) and because most species are deciduous, we did not find specimens (i.e. mature leaves, flowers or fruits) for all species. For the species which we did not find specimens, we utilized botanical names with the same vernacular names from the species list of the Ministry of Natural Resources and Tourism in Tanzania (NAFORMA 2010). We also checked for species nomenclature against the Plant List Database (The Plant List 2013).

Fire incidences

We determined recent fire incidences based on fire scars recorded in the same sampling plots as the vegetation data. In each sub-plot, we recorded the presence of char, white ash, and soot on trees and on the ground. Not all of these signs of recent fires were present at each site and therefore we categorized recent fire incidences as present or absent (based on the presence of any of the signs) for further analyses.

Historical fire incidences (i.e. for the last four decades) were determined from Landsat satellite images and from MODIS active fire product (MOD14/MYD14). We did not achieve a complete spatio-temporal coverage over the study sites since Landsat image availability was constrained by image quality, predominantly the extent of cloud cover. The MODIS active fire product provides a more complete coverage of detected active fires, observed twice daily since November 2000. Long periods with missing data were more prevalent during the 1970s and 1980s, similar to Hudak et al. (2004) in southern Africa savannas. The longest interval with missing data was 10 years, which is within the range of fire return intervals of 1 to 13 years that was derived from MODIS active fire data (Tarimo et al. 2015). Based on the spatial and temporal patterns of occurrence of fire from the combined MODIS active fires and Landsat datasets, we believe that our record is representative of the fire regime and the relative differences in the fire history among plots within each site and among sites. Burned areas were delineated from all available Landsat satellite images between 1972 and 2011, as documented in Tarimo et al. (2015). We determined the number of years each plot was affected by fire from this dataset. During 2001 – 2012, we scored each plot that was within locations of MODIS detected active fires as burned. The total number of years that each plot was burned formed the historical fire record. For the duration of the study, datasets were available for 21 years for the Kimamba, Kiduhi and Ihombwe, and for 24 years for the Mkarango and Kikole study sites. Due to this incomplete temporal coverage of satellite images, a complete time-series analysis was not feasible. Thus, we weighted the fire record based on the time since recorded fire events occurred. Weights ranged between 1 – 4, with 4 for fire events detected in the 1970s, 3 for fire events detected in the 1980s, 2 for fire events detected in the 1990s and 1 for the recent fire events detected since 2000. Historical fire variables thus consisted of the total number of weighted fire counts for each plot.

Measurement of environmental variables

To control for potential edaphic influences on the spatial variation in woody species composition, we collected a composite of soil samples from nine alternating corners (Fig. 1) among the eighteen corners of the sub-plots. Samples were collected from the top 20 cm soil layer. Laboratory analyses of the soil samples were conducted at Seliani Agricultural Research Institute, Arusha, Tanzania, to determine soil properties of each plot. These included soil pH (in a 1:2.5 soil:water suspension), organic carbon (Walkley-Black method; %) (Walkley & Black 1934), available phosphorus (Olsen method; parts per million) (Olsen et al. 1954), electrical conductivity (1:2.5 soil:water ratio; millimho), and exchangeable bases: calcium, magnesium, potassium and sodium (ammonium acetate extraction method; milliequivalents of charge per 100 g soil). Soil samples for fifteen of the 138 plots were lost before laboratory analysis, and these plots were not included in some of the statistical analyses (see below). To account for anthropogenic disturbances other than fire, we counted all stumps in each sub-plot and categorized their state as fresh or old based on visual inspection. We also counted subplots with animal droppings and/or footsteps, thus a value ranging from 0 – 10 at plot level. These were categorized as domestic or wild for further analyses, with the help of the local members of the field team.

Statistical analyses

We expected spatial variation, both in the fire variables and in underlying abiotic influences. It was therefore necessary to explicitly take into account the presence of spatial patterns in the statistical analyses (Dormann et al. 2007). One approach to achieve this is to define the spatial arrangement of observed sites as a set of spatial explanatory variables, and use them in statistical analyses to gain an understanding of the likely processes generating the spatial patterns (Borcard & Legendre 1994; McIntire & Fajardo 2009; Peres-Neto & Legendre 2010). Among the methods for extracting spatial variables from observed sites, Moran's eigenvector maps (MEMs) are probably the most advantageous as they provide both the spatial patterns and the scales at which these patterns are more prominent, within the scales of the study design (Dray et al. 2006; Dray et al. 2012). Each of the eigenvectors represents a scale-specific spatial pattern in the dataset (Legendre & Legendre 2012). Therefore, analyzing species compositional variation against MEMs reveal the scale at which important explanatory variables influence the composition.

Definition of spatial variables

Spatial variables consisted of Moran's eigenvector maps (MEMs) defined from UTM coordinates of plots within each site. We computed MEMs based on a spatial weighting matrix (SWM). The SWM consisted of a connectivity matrix (links connecting plots) based on a connection scheme and a distance-based weighting function representing the strength of the spatial interaction through each link (Dray et al. 2006; Borcard et al. 2011). In general, we expected closer plots to have experienced more similar fire characteristics than distant plots. However, the distance separating plots in the sense of their similarity in fire characteristics is likely to vary within a site, depending on the size and intensity of recurrent fires relative to the location of each plot. Thus, we followed a data driven selection of the SWM (Dray et al. 2006) to accommodate variation in the spatial interrelationships among plots within each site. In this approach, the selected SWM provides a multivariate spatial model with the lowest Akaike information criterion that is bias-corrected for small sample size (AICc). We tested combinations of connection schemes and distance-based weighting functions (Dray et al. 2006; Borcard et al. 2011) to identify the best SWM. The connection schemes consisted of Delaunay triangulation, Gabriel graph, relative neighborhood graph and variogram analysis of distances between plots, and the weighting functions consisted of $f_1 = 1 - (D/D_{max})^y$ and $f_2 = 1/D^z$. For each weighting function, D is the length of the link connecting any two plots, and D_{max} is the length of the longest link in the connection scheme within a site. We tested integer values between 1 and 10 for the parameters y and z. A principal coordinate analysis (PCoA) of the selected spatial weighting matrix provided the MEMs. We retained MEMs with both positive and negative eigenvalues for further analyses. We utilize these MEMs to investigate both large and small scales in compositional patterns within each site that may have resulted from the influence of fire.

Analysis of variation in species composition

Initial analyses utilizing nonmetric multidimensional scaling and pooling species abundances from all sites indicated substantial differences in species pools among the sites, i.e. many species occurred only in one or a few sites. Pooling the species from all sites resulted in a heavily zero-inflated dataset, and we therefore analyzed each site independently.

In order to summarize the compositional gradients of each of the tree adults, seedlings and saplings size classes; we employed unconstrained redundancy analyses (i.e. principal component analysis on Hellinger transformed species abundances). We employed partial redundancy analyses to assess the proportion of the variation in species composition of each size class explained by fire variables (historical from satellite images and recent from the presence of ground scars), and controlling for the potential effect of other environmental variables (Appendix S1). We only included those variables that were not collinear in this analysis, as assessed by variance inflation factors (VIF) < 10. We carried out all analyses on Hellinger transformed community abundances (Legendre & Gallagher 2001). The Hellinger transformed data were detrended by multiple linear regression on sites' geographic location upon detection of a significant linear trend (Borcard et al. 2011; Legendre & Legendre 2012).

To quantify the independent contribution of fire and spatial variables, while controlling for the effect of other environmental variables in explaining the variation in community composition, we performed separate variance partitioning on redundancy analysis models for each size class and each site. We included the same environmental variables in this analysis as we did in the partial redundancy analyses. We conducted a forward selection on the spatial variables with significant ($p<0.05$) spatial correlation, identified by the Moran's I test for spatial correlation, in order to avoid overestimation of the explained variance (Blanchet et al. 2008; Borcard et al. 2011). We then categorized the selected spatial variables into large and small scales for variables with positive and negative spatial correlation, respectively. Variance partitioning was carried out on Hellinger transformed (but undetrended) community abundances.

The spatial patterns contained in the spatial variables represent processes that have shaped the community across both spatial and temporal scales (Dray et al. 2012). To test if fire variables contributed to the spatial patterns in species composition, we employed redundancy analyses of the detrended abundances on the spatial variables retained during forward selection. For each significant model, we tested the significance of the ordination axes and then regressed the significant axes on fire variables.

Analysis of spatial patterns

To test for the presence of spatial patterns in the variation of the community composition (unconstrained) and in the variation explained by fire variables, we analyzed scalograms (Legendre & Legendre 2012) for each size class and each site separately. We computed each scalogram by projecting site scores on the two axes of the redundancy analyses on all spatial variables (i.e. the MEMs) defined for each site. The partial variance explained by each spatial variable was determined and tested for significance based on partial redundancy analyses (Appendix S2 in Legendre & Gauthier 2014). The amount of variance explained by each spatial variable indicated the scale of the spatial patterns in the variation in community composition summarized by the two axes. We also projected the residuals of the partial redundancy analyses on the spatial variables and in each case partitioned the unexplained variations in the residuals into respective scales of the spatial variables (Dray et al. 2012).

Spatial variation in species composition

We tested for a change in species composition with increasing spatial scale through a multivariate test for homogeneity in dispersion, using the Jaccard dissimilarity measure to quantify compositional dissimilarity (Anderson et al. 2006). We tested the null hypothesis of no compositional difference among clusters and among transects based on permutation tests. Clusters consisted of the three closest plots along the transect line (Fig. 1). Thus, there were three clusters for each of the three transects in a site. The plot at the center of the site was not included in this analysis. For each analysis, we computed each group’s centroid based on principal coordinate analysis of the dissimilarities and then obtained an average dissimilarity of each plot to its group’s centroid.

All analyses were performed in R v. 3.1.2 using the packages packfor, vegan, and spacemakerR and following Borcard et al. (2011) and Dray et al. (2012). The partial variance of MEMs in scalogram analyses was computed by R code adapted from Legendre and Gauthier (2014). Plots of site scores were made using the sr.value.R function (Borcard et al. 2011) and those of scalograms using R code adapted from Dray et al. (2012).

Results

Spatial weighting matrices

The SWM that provided a spatial model with the lowest AICc differed among sites. At Kimamba and Ihombwe, the best model was based on un-weighted variogram analysis of distances between plots. The best model at Kiduhi and Kikole was based on weighted variogram analysis, by the f_2 weighting function with z = 2 and z = 1, respectively. At Mkarango, an un-weighted relative neighborhood graph provided the best model. Small and large spatial scales within each site range between 0.29 km and 5.87 km, which are the shortest and longest distances among plots within a site, respectively.

Spatial variation in woody species composition

Woody species composition varied spatially for all site-size class combinations. The scale of the spatial variation in species composition varied among size classes in each site. For the adult size class (Figs. 2 and 3, left panels) in the highly disturbed sites, spatial variation in species composition was prominent at a small-scale in Kimamba and at a large-scale in Kiduhi. Both the intermediately disturbed sites (Mkarango and Kikole), had a dominant large-scale spatial variation in the composition of adult trees, while the second axis at Mkarango (Appendices S3 and S4, left panels) had an additional small-scale variation. For the relatively undisturbed site (Ihombwe), spatial variation in the composition of adult trees was dominant at a large-scale along the first axis and at a small-scale along the second axis (Appendices S3 and S4, left panels). Similar spatial patterns exists for saplings and seedlings, such that the spatial variability in species composition was prominent at small, medium and large scales along the first and second axes of redundancy analyses (Appendices S3 and S4, left panels).

The influence of fire on the spatial variation in woody species composition

Based on the adjusted R^2 of the global partial redundancy analyses, fire explained a significant (p= 0.047) portion (9.8%) in the spatial variation of the species composition of adult trees at one of the highly disturbed sites (Kiduhi). Fire also explained variable proportions of the spatial variation in species composition for the other site-size class combinations (Fig. 2 and Appendix S3, middle panels and Appendix S2), although these proportions were not significant.

The significant proportion of variation in species composition of adult trees explained by fire variables at Kiduhi was prominent at a large spatial scale along the first axis (Fig. 3, middle panel), and at a medium spatial scale along the second axis (Appendix S4, middle panel). The role of fire in influencing species composition at this site varied from medium to large scales within the site. At the remaining sites, where the global redundancy analyses were not significant, the proportions of variation explained by fire had significant spatial variation at both large, medium and small scales (Fig. 3 and Appendix S4, middle panels and Appendix S2).

Figure 4 shows the composition of adult trees when pooling species abundances from all sites and emphasizing those with known response to fire. We could not identify any clear compositional patterns from this figure, partly because we do not have information about the degree of fire tolerance for the majority of species in our data set. However, there appeared to be a higher dominance of fire-tolerant species with increasing disturbance. At one of the highly disturbed sites (Kiduhi), the two most dominant species among adult trees, based on frequency of individuals, were *Lonchocarpus capassa* and *Acacia nigrescens* that are both fire tolerant. Other dominant species with known fire tolerance were *Piliostigma thonningii* and *Dalbergia melanoxylon*, which are semi-tolerant to fire. At one of the sites with intermediate disturbance (Mkarango), the most dominant species among the seedlings was *Commiphora africana*, which is also fire tolerant.

Independent and combined spatial and fire-related proportions of variation in species composition

Variance partitioning showed that of the total variation in the composition of adult trees at one of the highly disturbed sites (Kiduhi), 4.3% of the variation was explained by fire, independent of the spatial patterns (Table 2). Four spatial variables identified during forward selection explained a significant 22.7% of large-scale spatial variation independent of fire. At one of the intermediately disturbed sites (Mkarango), fire alone independent of spatial patterns significantly explained 3.3% of the variation in the composition of seedlings. An additional spatially structured portion (1.8%) of the variation was explained by fire, prominently at large spatial scale. Three spatial variables at this site, identified during forward selection, explained a significant 8.4% of large-scale spatial variation in the composition of seedlings that was unrelated to fire. Global analyses prior to forward selection of spatial variables for variation partitioning were not significant at the relatively undisturbed site (Ihombwe) for saplings. This was also the case at one of the intermediately disturbed site (Mkarango) for saplings, and at the relatively undisturbed site (Ihombwe) and one of the highly disturbed site (Kiduhi) for seedlings. For the other site-size class combinations, fire variables did not explain an independent significant proportion of the variation in species composition (Table 2). Spatial variables explained independent and significant large-scale proportions of the variation in species composition at all sites. They also explained significant small-scale proportions at one of the highly disturbed sites (Kimamba) and the relatively undisturbed site (Ihombwe) for adult trees, and at one of the intermediately disturbed sites (Kikole) for seedlings (Table 2).

Significant relationships among spatial variables and fire indicate that fire contributed in generating the spatial patterns in species composition. Large-scale spatial variables were marginally significantly related ($p = 0.058$) to historical fire records for the adult size class at one of the intermediately disturbed sites (Kikole). The large-scale spatial variables were also significantly related ($p = 0.005$) to recent fires (ground observed fire scars) for the saplings size class at one of the highly disturbed sites (Kiduhi). For other site-size class combinations, there was no significant relationship between spatial variables and fire variables.

Spatial patterns in the unexplained variation in species composition

The residuals of the redundancy analyses varied spatially for all site-size class combinations (Fig. 2 and Appendix S3, right panels). At one of the highly disturbed sites (Kiduhi), where fire variables had a significant relationship with the composition of adult trees, the unexplained variation was prominent at both a small and a medium spatial scale (Fig. 3 and Appendix S4, right panels). At one of the intermediately disturbed sites (Mkarango), the unexplained variation in the composition of seedlings was prominent at a small spatial scale. Similar spatial patterns existed for the other site-size class combinations (Figs. 2 and 3, and Appendices S3 and S4, right panels).

Spatial scale in the variation of species composition

Based on the test of homogeneity of multivariate dispersion (Table 3), changes in species composition with increasing scale varied among the disturbance levels and size classes. Sites with intermediate level of disturbance were more heterogeneous in species composition than highly disturbed and relatively undisturbed sites. Species composition differed significantly among transects for adult trees and seedlings but did not differ among clusters for the same size classes at one of the intermediately disturbed sites (Mkarango). This indicates an increase in compositional dissimilarity with spatial scale. For one of the highly disturbed sites (Kimamba), and the relatively undisturbed site (Ihombwe), the composition of seedlings differed significantly among clusters, but not among transects, indicating an increase in compositional similarity with spatial scale.

Discussion

Plant species composition generally vary along abiotic gradients and across contrasting spatial scales and is altered by disturbances, which also vary with spatial scale (Borcard & Legendre 1994; Fortin & Dale 2005). The composition of woody species in our study sites was spatially variable for all site-size class combinations with high spatial correlations at either large, medium or small scales (Figs. 2 and 3, and Appendices S3 and S4, left panels). Fire variables at each site were effective at explaining some of this spatial variation for most of the site-size class combinations (Figs. 2 and 3, and Appendices S3 and S4, middle panels). However, the magnitude and significance of the explained variation (Table 2 and Appendix S2) suggest that fire alone has a lesser influence than the combined influence of fire and other disturbances on the spatial variation in woody species. The influence of fire was more pronounced in the highly disturbed sites, although it was not clearly associated with disturbance severity. Spatial heterogeneity in woody species composition was higher at lower growth stages (seedlings and saplings) and decreased with spatial scale.

The influence of fire on woody species composition:

Contrary to our prediction, the variation in woody species composition was not strongly associated with fire history. Similar to our findings, there was no relationship between fire and the composition of woody species in savanna woodland areas of northeastern Tanzania, after 25 years of observation (Van De Vijver et al. 1999). Fires with frequencies ranging from 1 – 6 years were not related to species diversity in Zimbabwean woodland savannas (Gandiwa & Kativu 2009). Likewise, there was no relationship between fire and species diversity in southern African savannas (Trollope et al. 1998). Moreover, fire was not related to species composition in a fragmented open canopy forest in Australia (Etherington & Shapcott 2014). Similar to the above observational studies, fires have not influenced woody species composition after long-term experimental burning lasting for up to 58 years across tropical savanna localities (Brookman-Amissah et al. 1980; Enslin et al. 2000; Furley et al. 2008; Scott et al. 2012; Pellegrini et al. 2014). These findings indicate that the composition of woody species in savannas is resilient to variable fire regimes. In contrast, fire was related to woody species composition along a vegetation gradient spanning from a forest to a savanna (Nangendo et al. 2006) and in woodland areas (Lykke 1998; Nangendo et al. 2005). These contrasting results may be explained by the difference in the density of individuals in fire-affected, as compared to fire-unaffected, areas. Fire reduces woody cover in savannas, and Myers et al. (2015) have shown that the observed relationship between fire and woody species composition was a result of reduced density of individuals in fire affected relative to unaffected sites.

A reason for the lack of a strong association of fire and woody species composition in our study could be that the species assemblages have been trapped in a compositional state, shaped by a fire regime that has persisted for a longer period than our historical fire records. In fire-adapted ecosystems, a consistent fire regime for a long time, which is a characteristic feature of African savanna fires (Giglio et al. 2010), may result in consistent responses of the woody species to fire (Scholes & Archer 1997). Changes in woody species composition only occur after major changes in the fire regime when the altered fire characteristics are beyond the species’ resilience to fire (Dublin et al. 1990). The surface fires in African savannas are most detrimental to seedlings, scorching their shoots, but rarely affect their roots (Higgins et al. 2000; Furley et al. 2008; Hanan et al. 2008; Ryan & Williams 2011). The unaffected root system provides a resilient source of re-sprouting, often with a higher stem density and a rapid post burn growth that is persistent for a long time (Bond 2008; Chidumayo & Gumbo 2010; Ryan & Williams 2011). Persistence in re-sprouting and successful growth into adult size class facilitates resilience to fire in the woody species assemblage. Yet, although shoots of all species are equally susceptible to fire, the degree of subsequent persistence of seedlings and re-sprouts vary among species (Gignoux et al. 1997; Bond & Midgley 2001; Ryan & Williams 2011; Grady & Hoffmann 2012). Furthermore, the composition of seedling species germinated from seeds depends on the adult populations that have survived periodic fires. We observed significantly greater variation in species composition of seedlings and saplings than of adult trees (Table 3), indicating that some juveniles are suppressed from maturing into larger size classes. Similarly, woody species that were abundant as saplings occurred infrequently as adult trees in the savanna woodlands of Mozambique (Ryan & Williams 2011). This was also the case in savanna woodlands of northeastern Tanzania where the composition of juveniles differed from that of adult trees (Anderson et al. 2015). In their study, similarity in species composition among adult trees and juveniles increased with decreasing frequency of fires. Based on these and our results, we argue that changes in species composition caused by fire can occur over time depending on seedling establishment and successful growth of juveniles into adult size classes.

The main factors influencing variation in woody species composition in savanna woodlands are annual rainfall, soil properties, topography, herbivory and human disturbances (Frost 1996; Witkowski & O'connor 1996; Chidumayo 1997; Backéus et al. 2006; Ribeiro et al. 2008). We controlled for the potential effect of these important variables in our analyses. However, fire legacies may be coupled with temporal variability in abiotic conditions and with other anthropogenic disturbances associated with the use of fire. Therefore, it may be difficult to detect the separate effect of fire. The remaining spatial clustering in the residuals (Figs. 2 and 3, and Appendices S3 and S4, right panels) indicates that there are other factors that cause the spatial variation in woody species composition and that are not included in our analyses. The variation that was not explained by our models was prominent across all spatial scales for most site-size class combinations (Fig. 3 and Appendix S4, right panels). A uniform response was not expected, but the relationships between woody species composition, fire history and disturbance levels observed in this study suggest dynamic responses that are context specific, particularly to the site’s historical disturbances, as has also been observed in previous studies (Nyerges 1989; Chazdon et al. 2007; Vellend et al. 2013; Murphy & Romanuk 2014). Our study concur with previous studies that have found that fire alone is not strongly related to the composition of woody species (Hoffmann & Moreira 2002; Furley et al. 2008; e.g. Smit et al. 2010; Romme et al. 2011; Scholtz et al. 2014). Yet, although we did not find a strong relationship between fire and woody species composition, there are indications that fire contributes to the spatial variation in the composition of woody species.

Influence of fire at sites with differing levels of anthropogenic disturbance

Disturbances contributed to the relationship between fire and woody species composition but did not show a general trend across spatial scales. This relationship reflects the synergistic roles that fire and other drivers of vegetation change, mainly herbivory and human disturbances, play to influence woody species composition at different growth stages (Moncrieff et al. 2008; Midgley et al. 2010). Fire rarely affect adult trees (Higgins et al. 2000; Hanan et al. 2008), but herbivory and human disturbances exacerbate the degree of influence of fire by exposing adult individuals to fire (Nangendo et al. 2005; Holdo 2007; Midgley et al. 2010). Moreover, the influence of fire on regeneration is higher in disturbed sites. The dominance by fire tolerant species increased with increasing fire frequency at sites that were regenerating after clear felling (Chidumayo 2004). Lower fire frequency and intensity, however, did not affect the composition of woody species re-growing after clear felling (Chidumayo 2004). Similar to abandoned farms and clear felling, Mapaure et al. (2009) and Riberio et al. (2008) have shown that herbivory, largely by elephants, in fire affected sites resulted in a higher dominance of fire tolerant species. Similar to seedlings, adult trees produce a high density of coppices and root suckers after the main stem is destroyed, for instance by elephants (Bond & Midgley 2001; Chidumayo 2004; Luoga et al. 2004). However, sprouting density decreases with increasing fire frequency and the survival rate of sprouts in subsequent fires varies among species (Zolho 2005; Ryan & Williams 2011). In conclusion, recurrent fires combined with other disturbances likely causes an increase in the number of fire-tolerant species, as suggested by our results and those from previous studies (Holdo 2007; Midgley et al. 2010).

Spatial clustering in woody species

Spatial clustering of woody species at varying spatial scales was prominent for all site-size class combinations (Figs. 2 and 3, Appendices S3 and S4) and was not clearly associated with disturbance severity. Similarly, woody species were spatially clustered in fire-affected savanna woodland areas in Uganda (Nangendo et al. 2005). Spatial clustering of individuals may protect them from fire because their canopies reduces grass biomass and consequently limits the occurrence of fire (Hochberg et al. 1994; Bacelar et al. 2014). Thus, the effects of fire, including mortality of seedling and sapling shoots, decreases with increasing proximity to tree clusters (Holdo 2005; Bacelar et al. 2014). In this way, trees play facilitative roles by enhancing the establishment of other trees (Lawton 1978; Scholes & Archer 1997; Moustakas 2015). Moustakas (2015) found that spatial clustering of trees in south African savannas was higher at burned compared to unburned sites. In the burned sites, facilitative and competitive interactions among trees occurred at small and large scales, respectively. Our analyses on spatial patterns at the plot-level revealed positive (large-scale) and negative (small-scale) spatial correlations in species abundances (Fig. 3, Appendix S4), indicating facilitation and competition, respectively (Fortin & Dale 2005; Dray et al. 2006; Dray et al. 2012). At the scale of individual trees, Moustakas (2015) found positive spatial correlation (i.e. facilitation) among trees at a small scale, while our results suggest that positive correlation among species abundances occurs at large spatial scales, within the scales of the present study design (Fig. 1). Thus, the abundance of different species with different fire tolerances at large scales likely facilitates protection from fire, while at the individual tree level, proximity to other trees is more important for fire protection than the species identity. Among the species with known degree of fire tolerance, only the fire tolerant species occurred at all sites. Similarly, fire tolerant species not only predominated half of the sampled sites in woodland areas of western Tanzania, but also occurred at high densities across all sites (Kikula 1986). Areas with a high occurrence of these tolerant species, referred to as chipya, have been described as degraded miombo woodlands resulting from repeated burning (Stromgaard 1985). With facilitative roles among species, the presence of fire tolerant species facilitate the recruitment of semi-tolerant ones and later-arriving fire-sensitive species (Brookman-Amissah et al. 1980; Chidumayo 1997; Hoffmann & Moreira 2002; Geiger et al. 2011). However, sensitivity to fire and other disturbances limits the occupancy, spatial distribution and abundance of woody species.

Variation in species composition with scale

We expected an increase in compositional heterogeneity of woody species with increasing spatial scale because of increasing heterogeneity in fire characteristics and underlying abiotic factors at large spatial scale. However, the species composition was relatively homogeneous in the highly disturbed and the relatively undisturbed sites at both small and large scales (Table 3). Seedlings and saplings had, in general, a higher variability in composition at small (cluster) scale than adult trees. Similar patterns were observed in the scalogram analyses (Fig. 3 and Appendix S4, left panels), as indicated by the scales at which the spatial correlation was prominent. Homogeneity in species composition increases with increasing scale of the spatial correlation among species (Lookingbill et al. 2011). The analyses of scalograms show that, except for Kimamba, all sites had generally homogeneous species composition of adult trees, as indicated by the prominence of large-scale spatial correlation (Fig. 3, left panel). Variability in the composition of adult trees, as indicated by the small-scale spatial correlation, was also prevalent in the second ordination axis (Appendix S4, left panel). Similar patterns were also observed for seedlings and saplings (Appendix S4, left panel). In addition, a transition between similarity and variability in the species composition was also prevalent for some of the sites, as indicated by the medium scale spatial correlation (Appendix S4, left panel). The coexistence of both similarity and variability in species composition may indicate that woody species within each site are being gradually homogenized. In Ugandan savanna woodlands, Nangendo et al. (2005) found that sites with a similar fire regime became more compositionally similar after 46 years of observation. We found that fire contributed in explaining the spatial patterns in species composition, mostly at large and medium scales (Fig. 3 and Appendix S4, middle panels). This may indicate that fire contributes in homogenizing woody species composition at the large scales of our study.

Conclusion

We have assessed the relationship between fire and the variation in woody species composition across spatial scales in savanna woodland areas with different disturbance histories. Our results suggest that historical fires contribute in determining the spatial occurrence of woody species at all growth stages. Fire interacts with the type and severity of historical disturbances to limit the diversity and abundance of, particularly, fire and disturbance-sensitive woody species. We have not found a strong association between fire and woody species composition, most likely because historical fires have shaped the current composition for a longer period than our historical fire record. We have observed spatial clustering of abundances of existing species at large spatial scales. This clustering, and that of individual trees at small scales (Moustakas 2015), probably enhance protection of woody species from the influence of recurrent fires. There appeared to be a gradual and ongoing homogenization of woody species, most pronounced for larger size classes and at large spatial scales of our study design. Legacies left by fire alone and interactively with other disturbances may have been difficult to quantify and thus to account for in our statistical analyses. Our results suggest that there are other drivers of the variation in woody species composition not accounted for in our analyses. These may include both biotic, abiotic and disturbance drivers with spatial variation at both small and large scales (Dray et al. 2012; Biswas et al. 2015). Identification and inclusion of these drivers in spatially explicit statistical analyses may improve our understanding of the contributing influences of fire and other disturbance histories in determining the spatial patterns of biodiversity in savanna woodlands.

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Sporting Information

Appendix S1. List of environmental variables used.

Appendix S2. Summary of partial redundancy analyses.

Appendix S3. Figures showing site scores along the two axes of redundancy analyses for the site-size class combinations.

Appendix S4. Figures showing spatial scales in the variation of the site scores along the two axes of redundancy analyses for the site-size class combinations.

Table 1. Description of study sites in Kilosa and Kilwa districts in Tanzania (see Fig. 1). Temperature and rainfall were sourced from the WorldClim database (Hijmans et al. 2005). Population is at the ward administrative level with indicative values of population at the village level in parentheses. Population density is at the region administrative level. Environmental heterogeneity represents the average standardized Euclidean distance of the explanatory variables used in redundancy analyses (see analysis of variation in community composition)

Disturbance level	Site (Census Ward)	Annual Rainfall (mm)	Temperature Min-Max (ºC)	Elevation Min-Max (m)	Population 2012	Population density 2002/2012	Environmental heterogeneity
High	Kimamba (Rudewa)	920	19.5 – 30.8	394.1 – 457.4	18352 (3607)	25/31	5.74 ± 1.03
High	Kiduhi (Kilangali)	944	19.8 – 29.8	448.7 – 470.9	10679 (2864)	25/31	3.84 ± 1.11
Intermediate	Mkarango (Kipatimu)	1190	21.0 – 29.0	173.5 – 287.7	14606 (1577)	12/13	4.60 ± 1.41
Intermediate	Kikole (Kikole)	1148	22.4 – 30.3	37.9 – 98.3	4294 (1486)	12/13	4.90 ± 1.41
Low	Ihombwe (Mikumi)	1148	18.5 – 27.8	640.3 – 892.6	19977 (2141)	25/31	5.33 ± 1.26

Table 2. Summary of variance partitioning. Showing percentage adjusted R^2 values for proportions explained by fire and spatial variables. Some of the partitioned fractions and values < 0 are not shown, thus, the proportions shown do not sum up to 100. The letters in the superscript represent the small (S) and large (L) scales of the spatial component of the fire influence. Sites where global analyses prior to forward selection of the spatial variables were not significant are not included.

Size class	Disturbance level	Site	Fire	Fire and spatial scale	Large scale	Small scale	Residuals
Adults	High	Kimamba	0	1.3^{S}	41.3*	12.6*	51.1
	High	Kiduhi	4.3*	0	22.7*	…	73.3
	Intermediate	Mkarango	0	1.1^{L}	11.0*	…	88.0
	Intermediate	Kikole	0	5.2^{L}	18.6*	…	78.2
	Low	Ihombwe	0.9	$1.3^{S,L}$	12.5*	5.5*	86.5
Saplings	High	Kimamba	0.5	0	21.3*	…	79.2
	High	Kiduhi	0	3.1^{L}	2.2	…	95.0
	Intermediate	Kikole	3.4	4.8^{L}	14.9*	…	76.9
Seedlings	High	Kimamba	2.4	0	12.5*	…	85.9
	Intermediate	Mkarango	3.3*	1.8^{L}	8.4*	…	86.5
	Intermediate	Kikole	1.2	3.0^{L}, 0.7^{S}, $0.7^{L,S}$	22.8*	2.4*	71.4

*Significant proportions ($p < 0.05$) of the explained variation

Table 3. Spatial variation in woody species composition. The range in the multivariate dispersion, corresponding to variation in species composition, with respective p-values in parentheses. Clusters consist of the three closest plots (small scale) within each of the three radial transects (large scale) (Fig 1).

Disturbance level		High		Intermediate		Low
Site		Kimamba	Kiduhi	Mkarango	Kikole	Ihombwe
Clusters (n=9)*						
	Adults	0.29-0.44	0.35-0.49	0.36-0.55	0.23-0.55	0.27-0.45
		(0.548)	(0.075)	(0.096)	(**0.008**)	(0.095)
	Saplings	0.37-0.58	0.34-0.52	0.25-0.56	0-0.56	0-0.53
		(0.065)	(0.572)	(**0.001**)	(**0.001**)	(**0.014**)
	Seedlings	0.27-0.53	0.25-0.58	0.43-0.58	0.34-0.49	0-0.56
		(**0.006**)	(**0.001**)	(0.409)	(0.446)	(**0.001**)
Transects (n=3)						
	Adults	0.38-0.46	0.49-0.56	0.52-0.61	0.50-0.59	0.41-0.47
		(0.196)	(0.268)	(**0.043**)	(**0.01**)	(0.241)
	Saplings	0.50-0.62	0.54-0.59	0.58-0.63	0.44-0.61	0.59-0.63
		(**0.001**)	(0.536)	(0.342)	(**0.009**)	(0.583)
	Seedlings	0.44-0.51	0.51-0.64	0.55-0.63	0.52	0.58
		(0.231)	(**0.02**)	(**0.034**)	(0.987)	(0.991)

*n=8 at Kiduhi

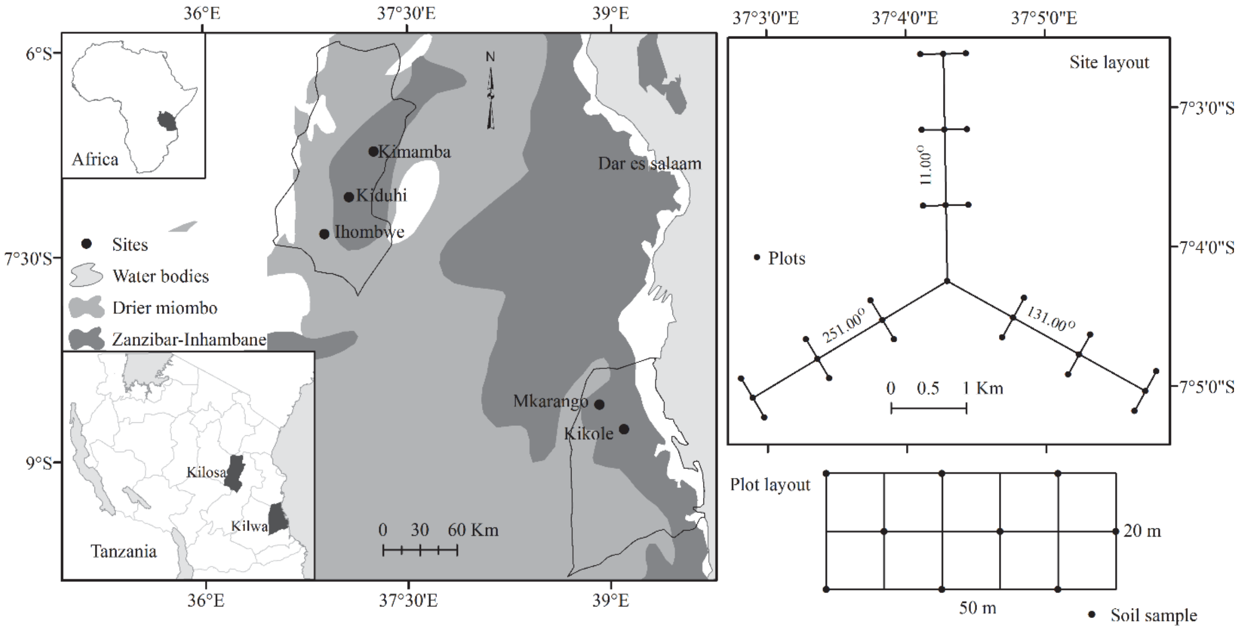


Fig. 1. Location of the five study sites in Tanzania and layout of the study design. At each site, three radial transects were established from the center of the site (top right). One rectangular plot (bottom right) was placed at the center of the site and three plots at each of 1, 2 and 3 km from the center of the site along each transect. At each of these distances, one plot was placed on the transect line and one plot 300 m on each side, perpendicular to the transect line. These three closest plots constituted a cluster. Vegetation types were obtained from White (1983).

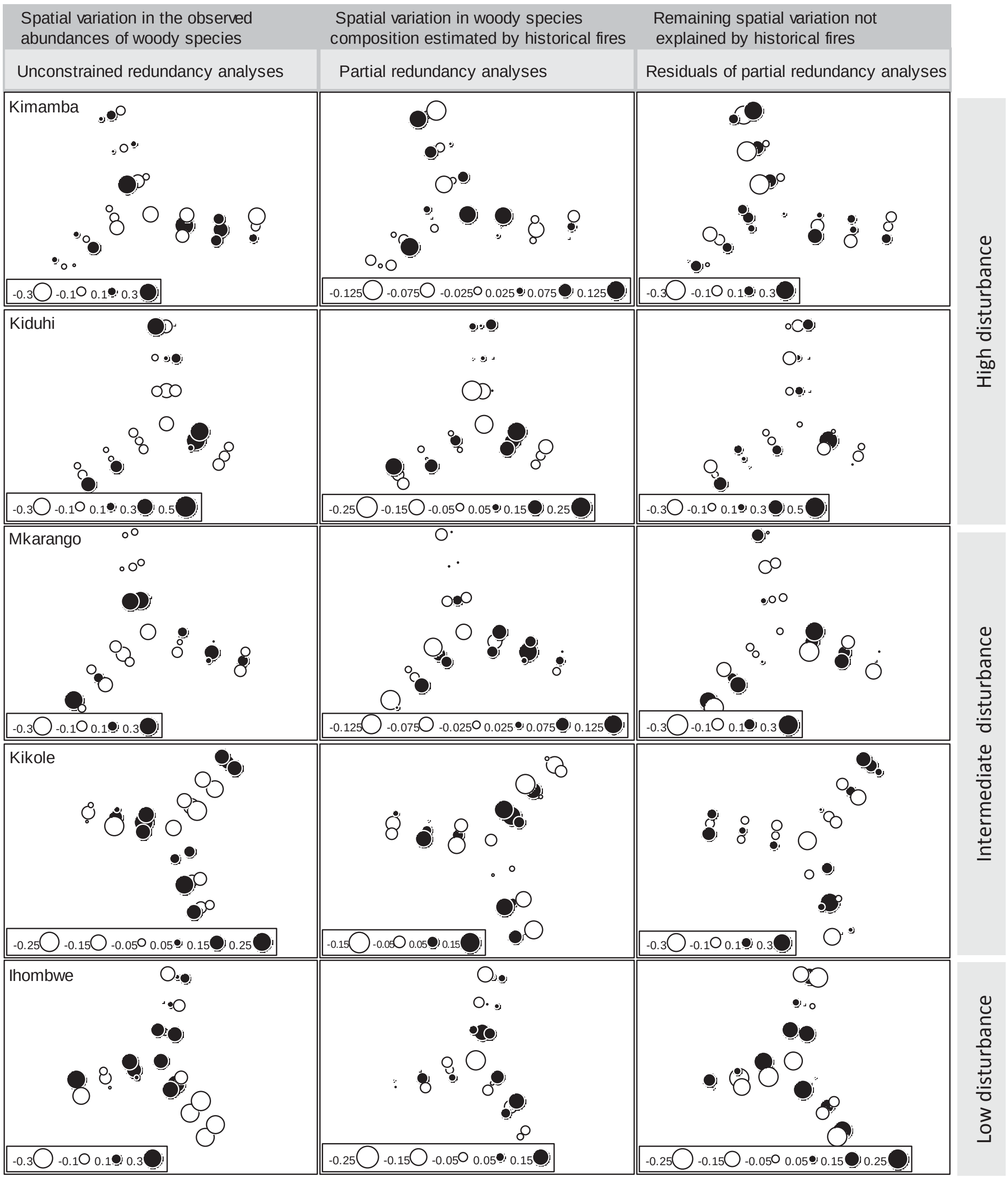


Fig. 2. Site scores along the first axis of redundancy analyses for the adult size class. Panels show the spatial patterns in the observed, fitted and unexplained variation in woody species composition. The partial redundancy analyses controlled for the potential influence of other environmental variables (Appendix S1). The size of the circles is proportional to the difference in species composition of each site from the composition of a mean site, with positive and negative representing values higher and lower, respectively, than the mean.

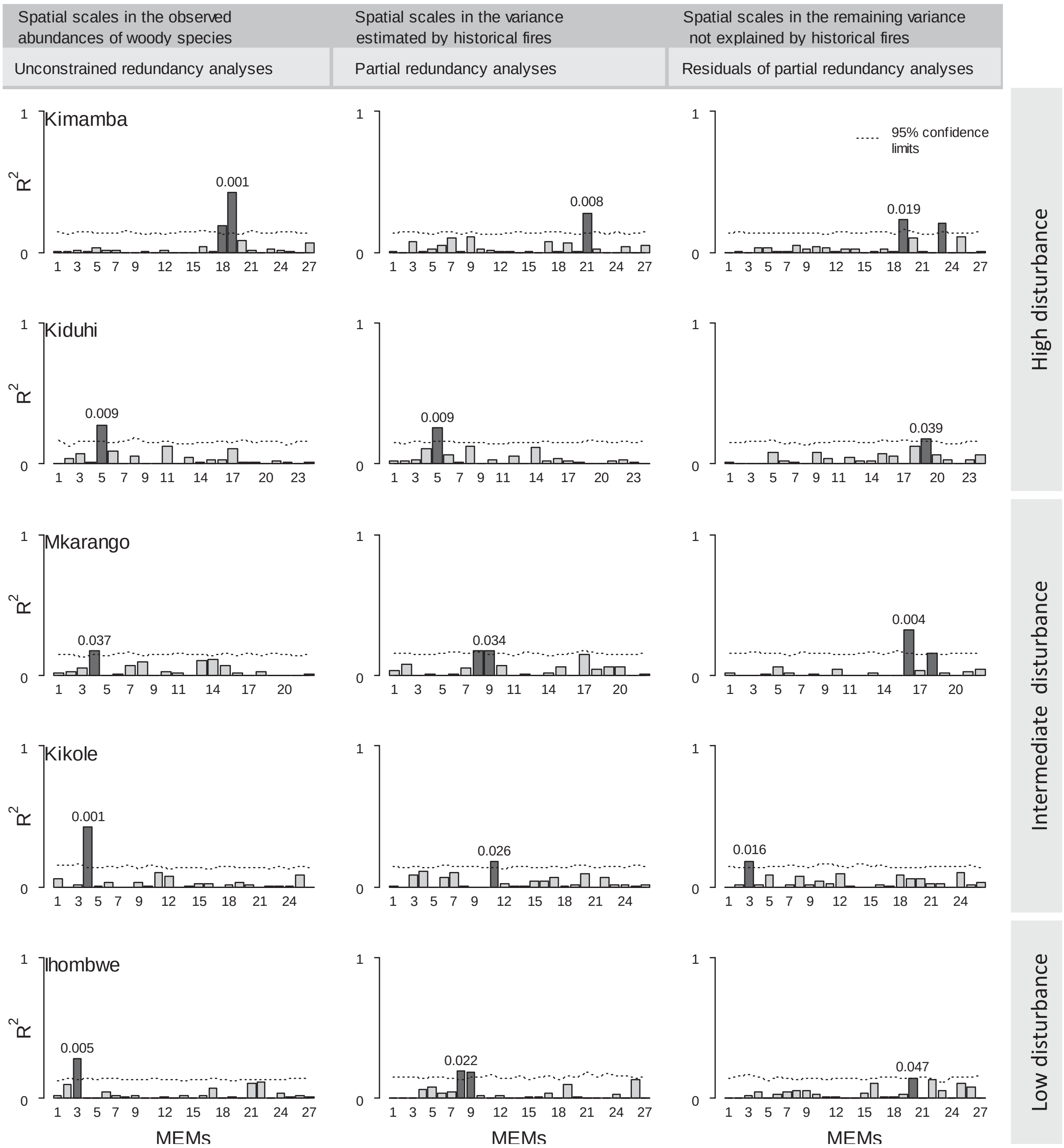


Fig. 3. Spatial scales of the site scores along the first axis of redundancy analyses for the adult size class shown in Fig. 2. Spatial scale decreases from the left (large) to the right (small) hand side. Darker bars shows significant spatial variables (MEMs), with p-values for only the highest R^2 explained by the spatial variables.

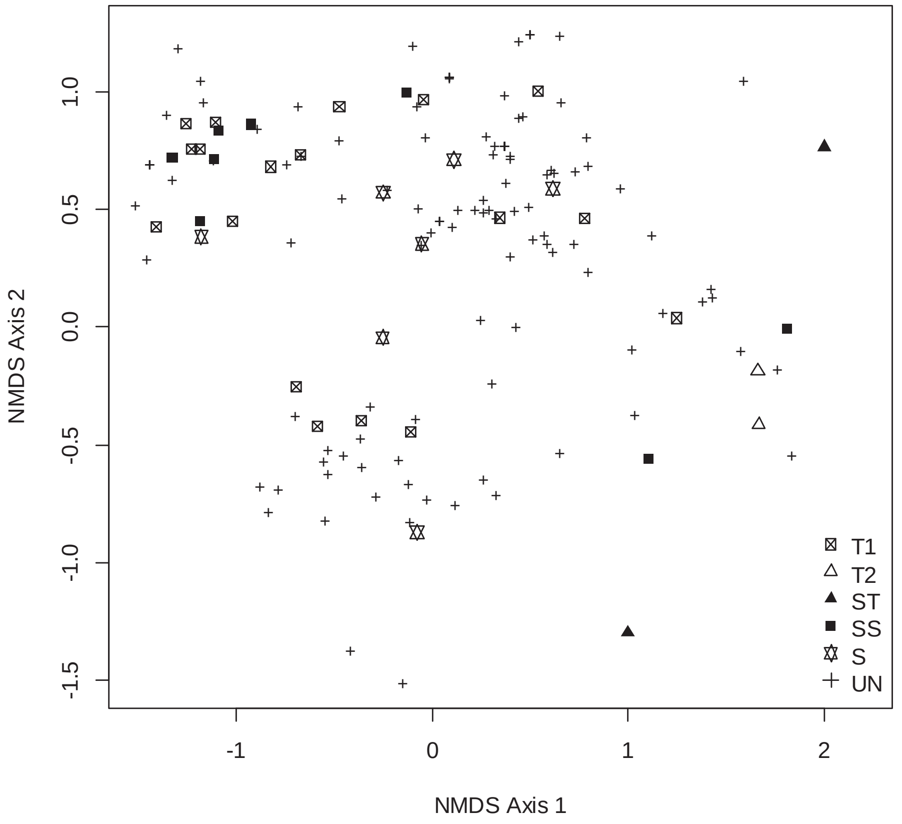


Fig. 4. Species composition of adult trees from all five sites emphasizing fire tolerance traits. T1 = Species tolerant to fire but intolerant to shade; T2 = Species tolerant to fire and shade; ST = Species semi-tolerant to fire; SS = Species semi-sensitive, they require protection from fire at juvenile growth stage; S = Fire sensitive species; UN = Species with unknown response to fire.

APPENDICES

Appendix S1. Environmental variables available for each of the sites in Kilosa and Kilwa districts in Tanzania (see Fig. 1 in the main text). Temperature variables are the first two principal components of monthly temperature at each site. Single and double symbols indicate variables that were not recorded and collinear, respectively, at each site.

Category	Variable	Type	Notes
Fire	Historical	Numeric	...
	Recent	Presence / Absence	ƚ
Disturbances	Domestic animals	Numeric	§, ¶
	Wild animals	Numeric	...
	Cultivation	Factor: three levels	ƚ, *
	Stumps condition	Factor: four levels	...
	Stumps count	Numeric	...
Distances	To roads	Numeric	ƚƚ, ǂǂ, ¶¶
	To Settlements	Numeric	ƚƚ, §§, ¶¶
Soil	pH	Numeric	...
	Electrical conductivity	Numeric	...
	Organic carbon	Numeric	...
	Phosphorus	Numeric	...
	Calcium	Numeric	§§
	Magnesium	Numeric	...
	Potassium	Numeric	§§
	Sodium	Numeric	¶¶, **
Weather	Rainfall	Numeric	§§, **
	Temperature 1	Numeric	ǂǂ
	Temperature 2	Numeric	ǂǂ, §, ¶, *
Topography	Elevation	Numeric	§§, ¶¶
	Slope	Numeric	...

ƚ = Kimamba; ǂ = Kiduhi; § = Mkarango; ¶ = Kikole; * = Ihombwe

Appendix S2. Summary of partial redundancy analyses. For each size class, sites where fire variables did not explain variation in species composition (global adjusted R2 ≈ 0) are not presented. Only the significant variation explained by MEMs based on scalogram analyses is shown. Values in parentheses are p-values for the variation explained by MEMs.

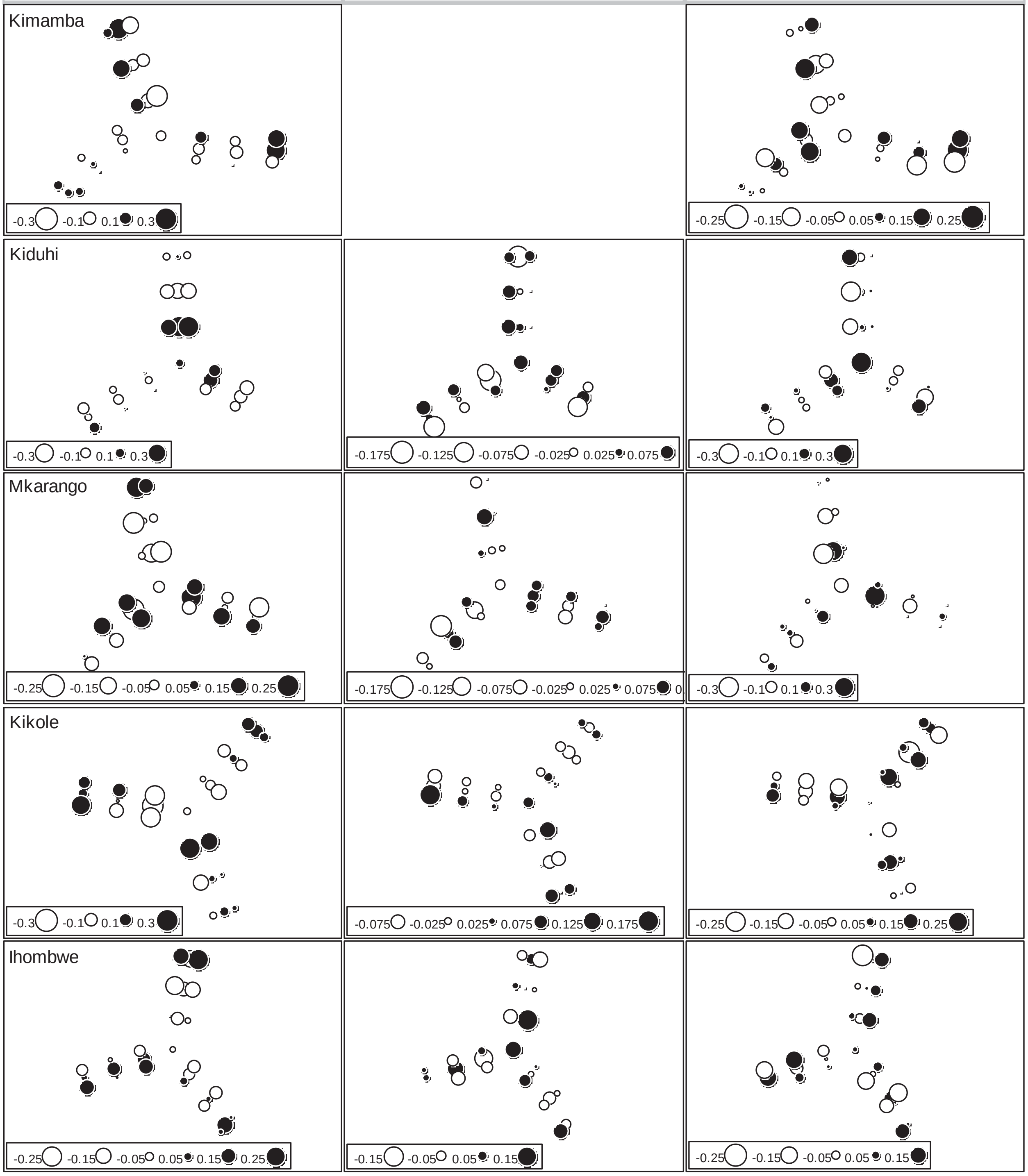
	Redundancy analysis				Scalogram analysis; partial R2 (%)					
		Constrained variance (%)			Large-scale		Medium scale		Small-scale	
	Global Adj. R2 (%)	Total (R2)	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Adults										
Kimamba (n=28)	0.4	4.1			…	…	…	…	27.99 (0.006)	…
Ihombwe (n=28)	3.3	9.1	53.29	46.71	19.69 (0.028) 18.33 (0.038)	…	…	16.98 (0.042)	…	22.14 (0.019)
Kiduhi (n=25)	9.8*	13.1*	70.91	29.09	25.40 (0.013)	…	…	16.64 (0.040)	…	…
Saplings										
Mkarango (n=22)	6.1	9.6	65.04	34.96	…	…	20.76 (0.040) 18.73 (0.041)	39.56 (0.006)	…	…
Kikole (n=24)	0.2	8.2	70.30	29.70	21.36 (0.019) 17.38 (0.048)	…	…	17.91 (0.030)	…	…
Seedlings										
Ihombwe (n=20)	2.3	10.0	74.87	25.13	21.71 (0.038) 20.70 (0.044)	27.24 (0.018)	…	…	…	…
Kiduhi (n=23)	7.3	10.7	74.50	25.50	25.11 (0.024) 17.44 (0.038)	…	…	46.25 (0.001)	…	…
Kikole (n=28)	5.4	9.4	70.73	29.27	…	…	27.50 (0.007)	20.59 (0.013) 16.17 (0.047)	14.10 (0.049)	…

* Significant proportion (p < 0.05) of the explained variation

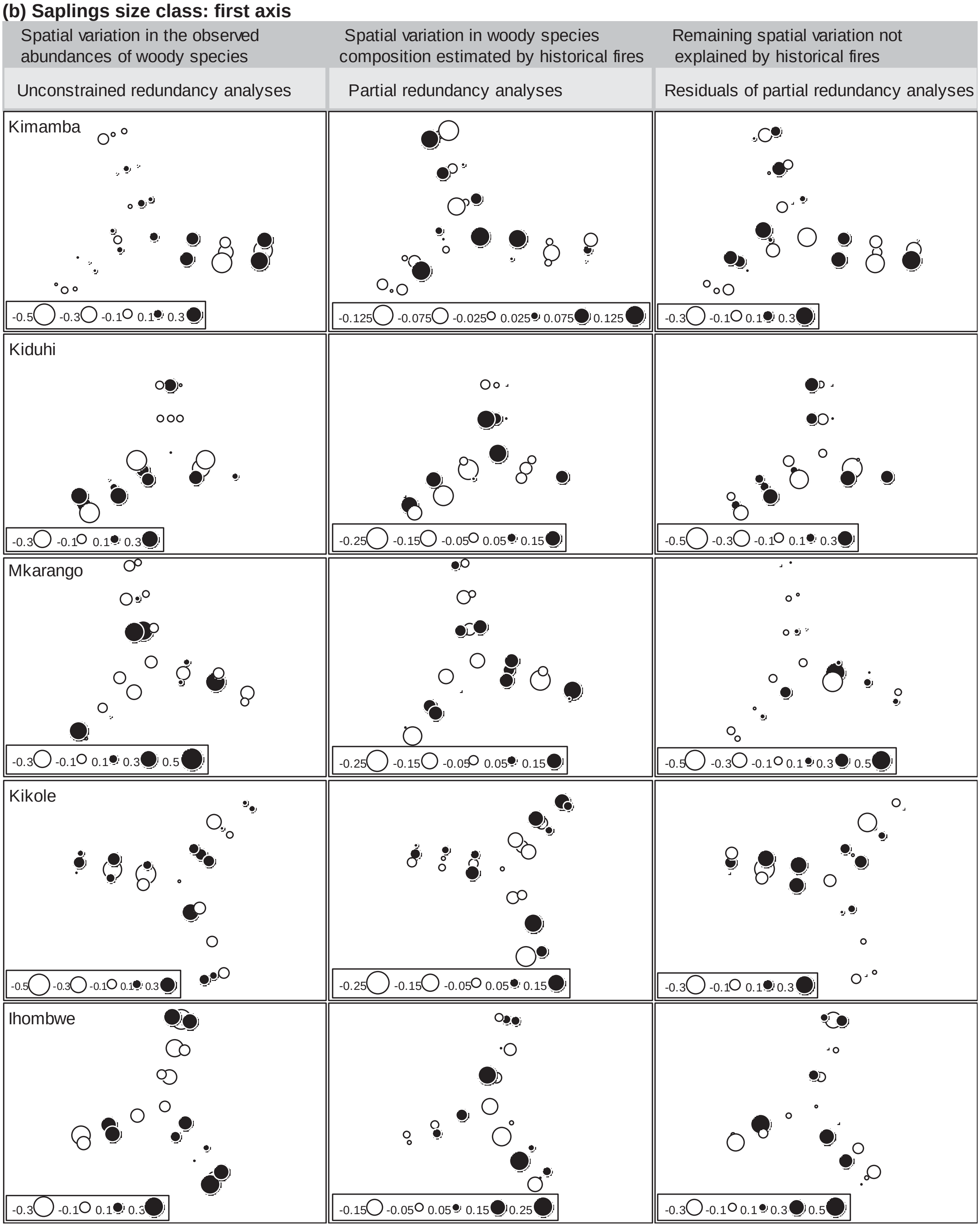
Appendix S3. Site scores of redundancy analyses along the second axis for the (a) adults size class and along the first and second axes for the (b) saplings and (c) seedlings size classes. Showing the spatial patterns in the observed, fitted and unexplained variation in woody species composition. The first axis for the adults size class is included in the main text. The partial redundancy analyses controlled for the potential influence of other environmental variables (Appendix S1).

(a) Adults size class: second axis

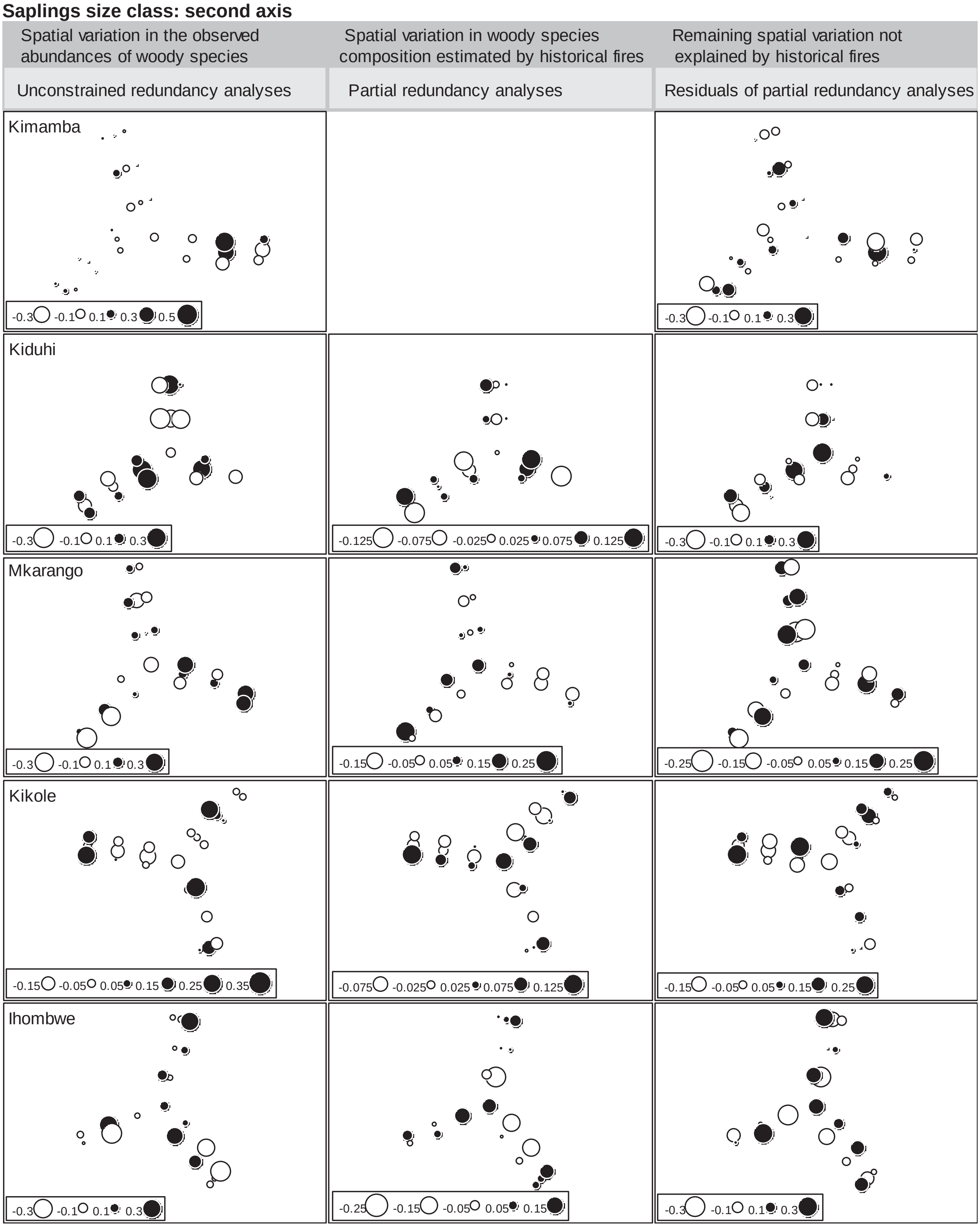
Spatial variation in the observed abundances of woody species	Spatial variation in woody species composition estimated by historical fires	Remaining spatial variation not explained by historical fires
Unconstrained redundancy analyses	Partial redundancy analyses	Residuals of partial redundancy analyses



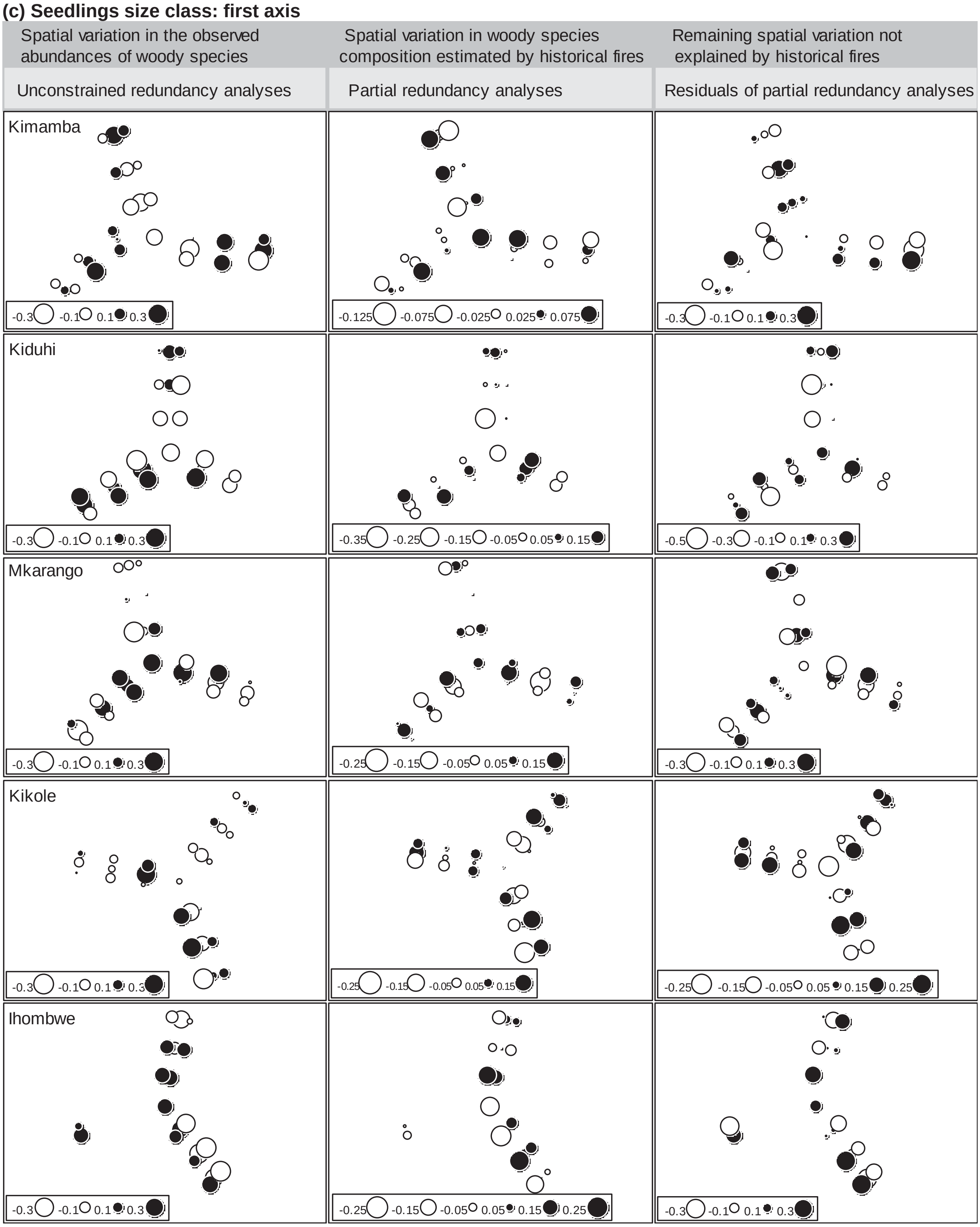
(b) Saplings size class: first axis



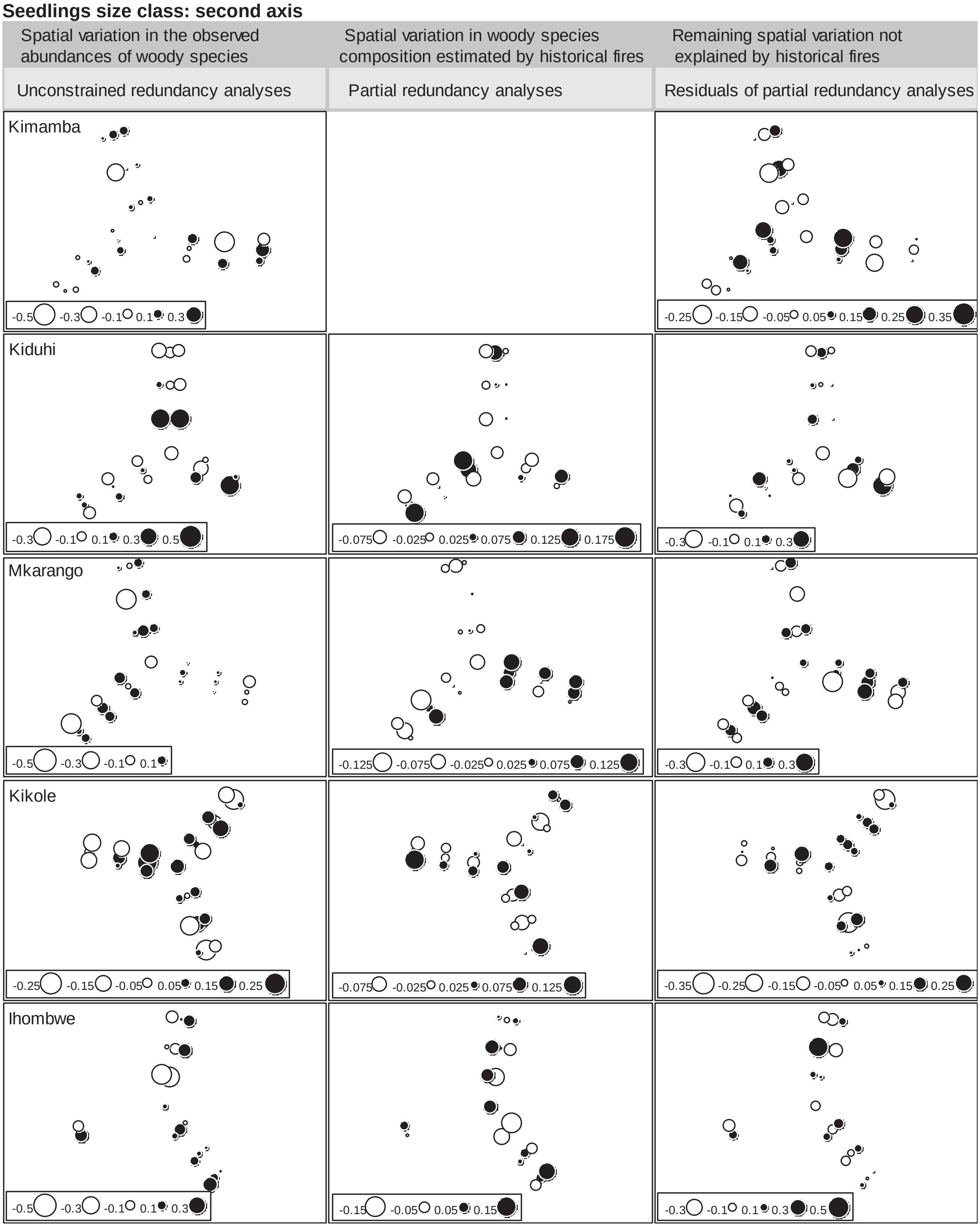
Saplings size class: second axis



(c) Seedlings size class: first axis



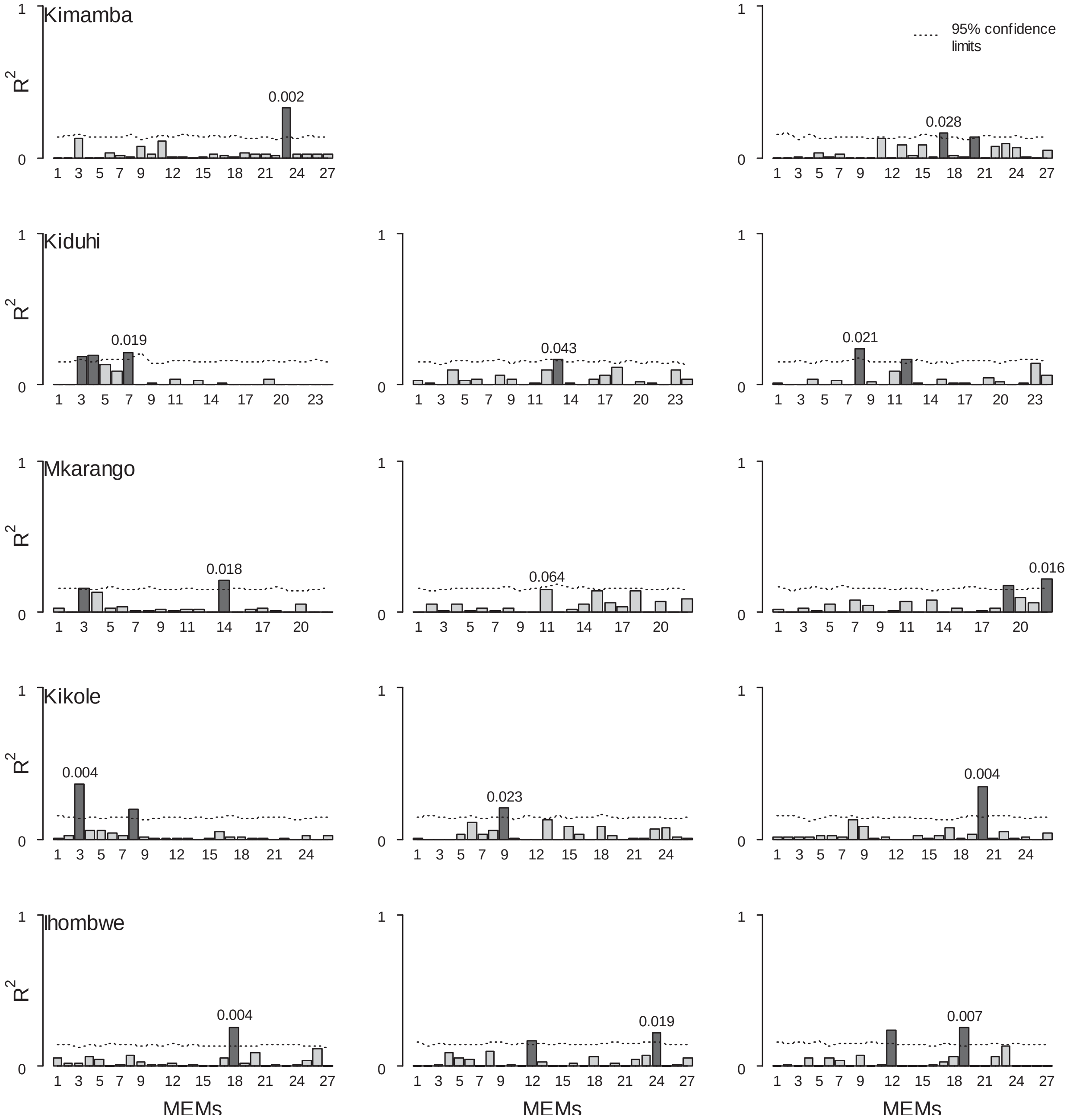
Seedlings size class: second axis



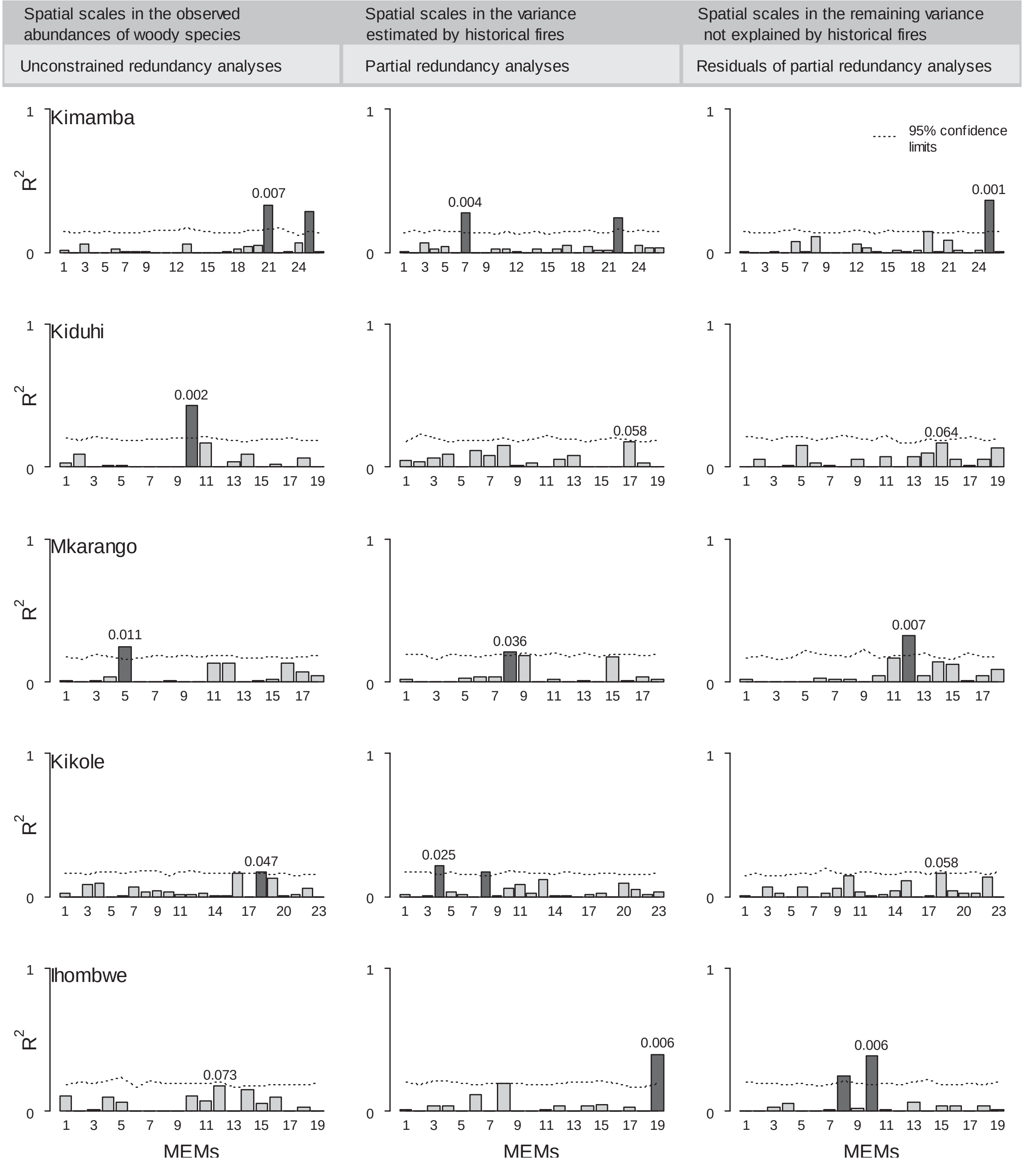
Appendix S4. Spatial scales of the site scores along the the second axis for the (a) adults size class and along the first and second axes for the (b) saplings and (c) seedlings size classes shown in Appendix S2. The first axis for the adults size class is included in the main text.Scale decreases from the left (large) to the right (small) hand side. Darker bars shows significant spatial variables (MEMs), with p-values for only the highest R^2 explained by the spatial variables.

(a) Adults size class: second axis

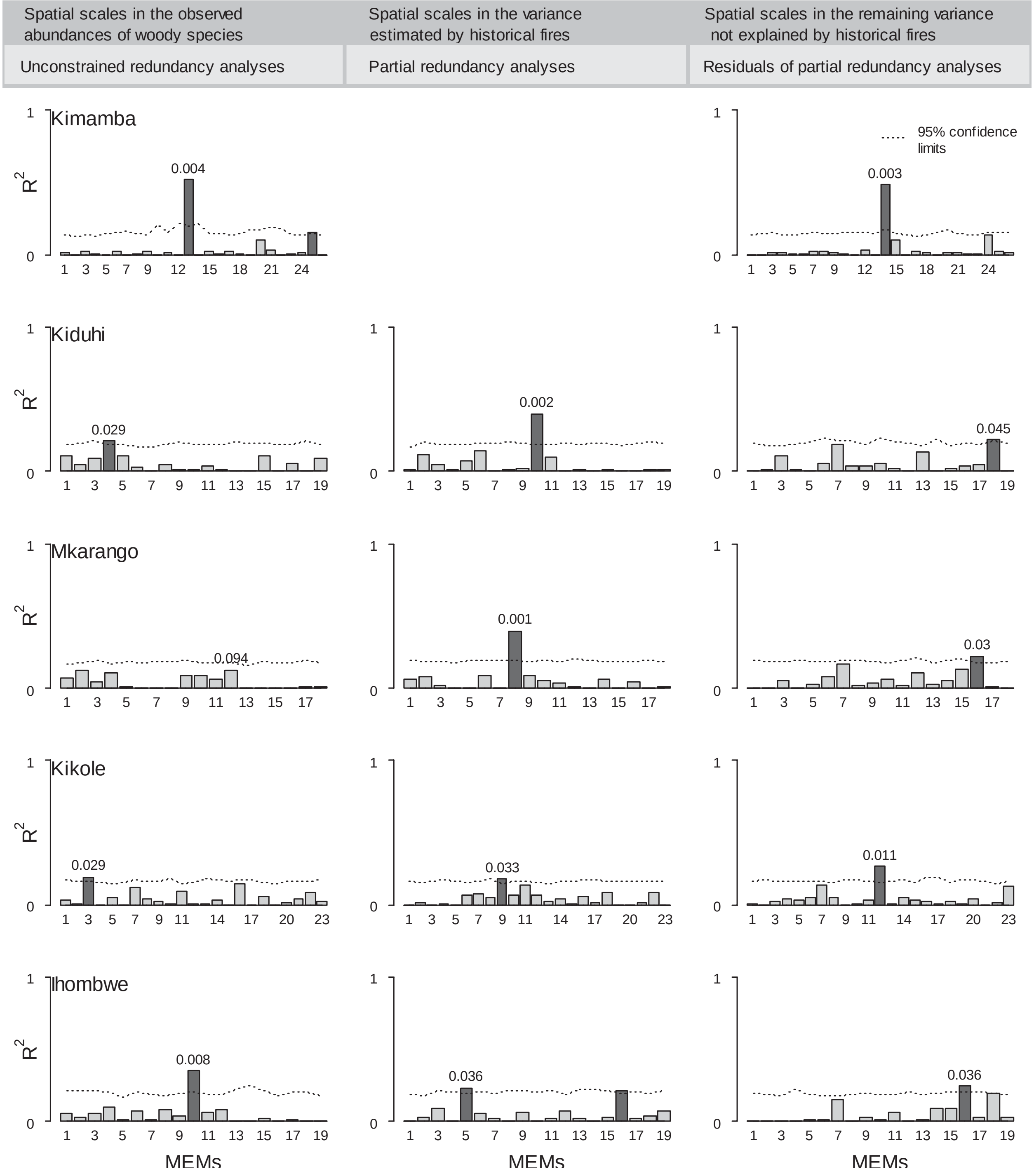
Spatial scales in the observed abundances of woody species	Spatial scales in the variance estimated by historical fires	Spatial scales in the remaining variance not explained by historical fires
Unconstrained redundancy analyses	Partial redundancy analyses	Residuals of partial redundancy analyses



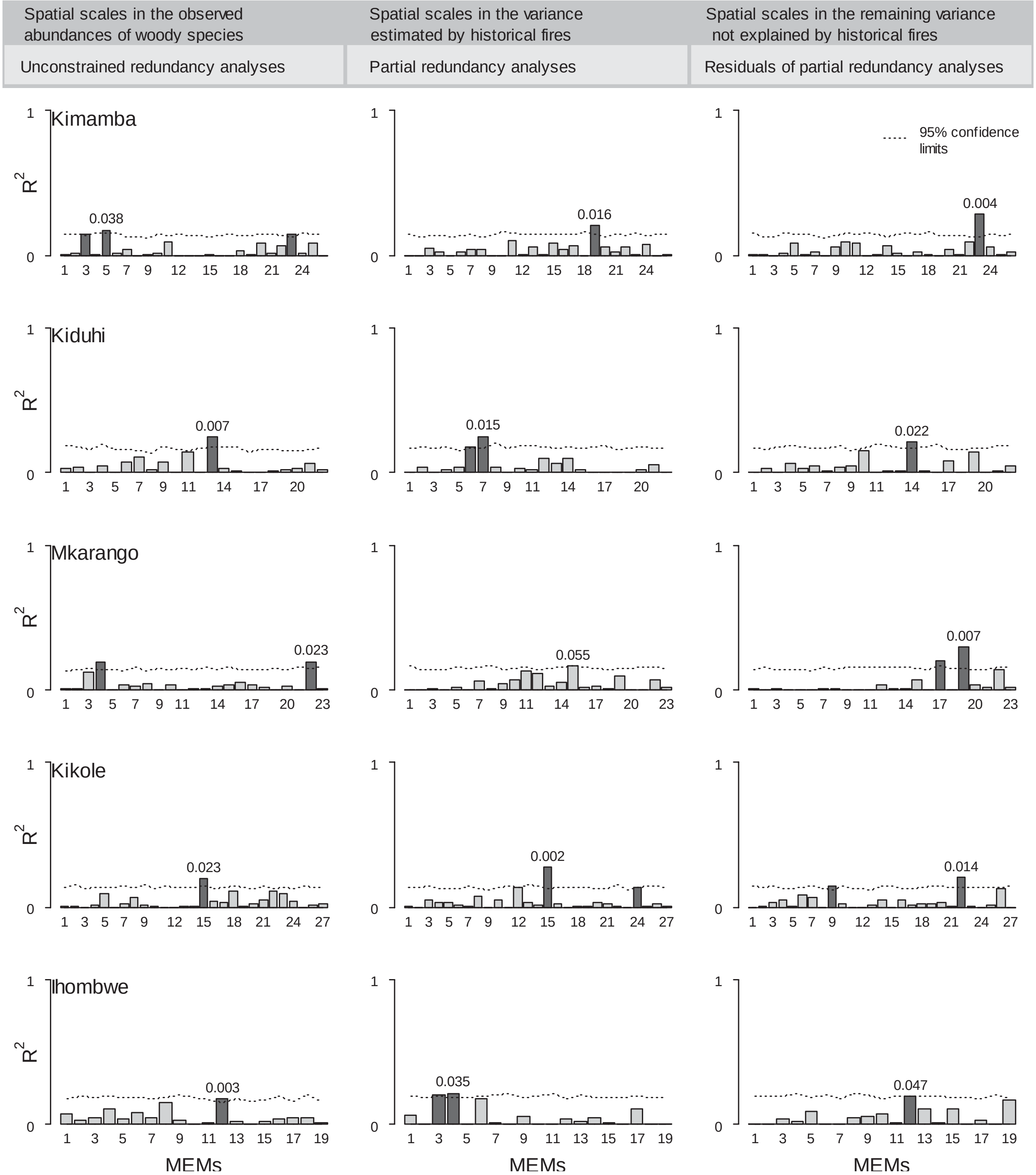
(b) Saplings size class: first axis



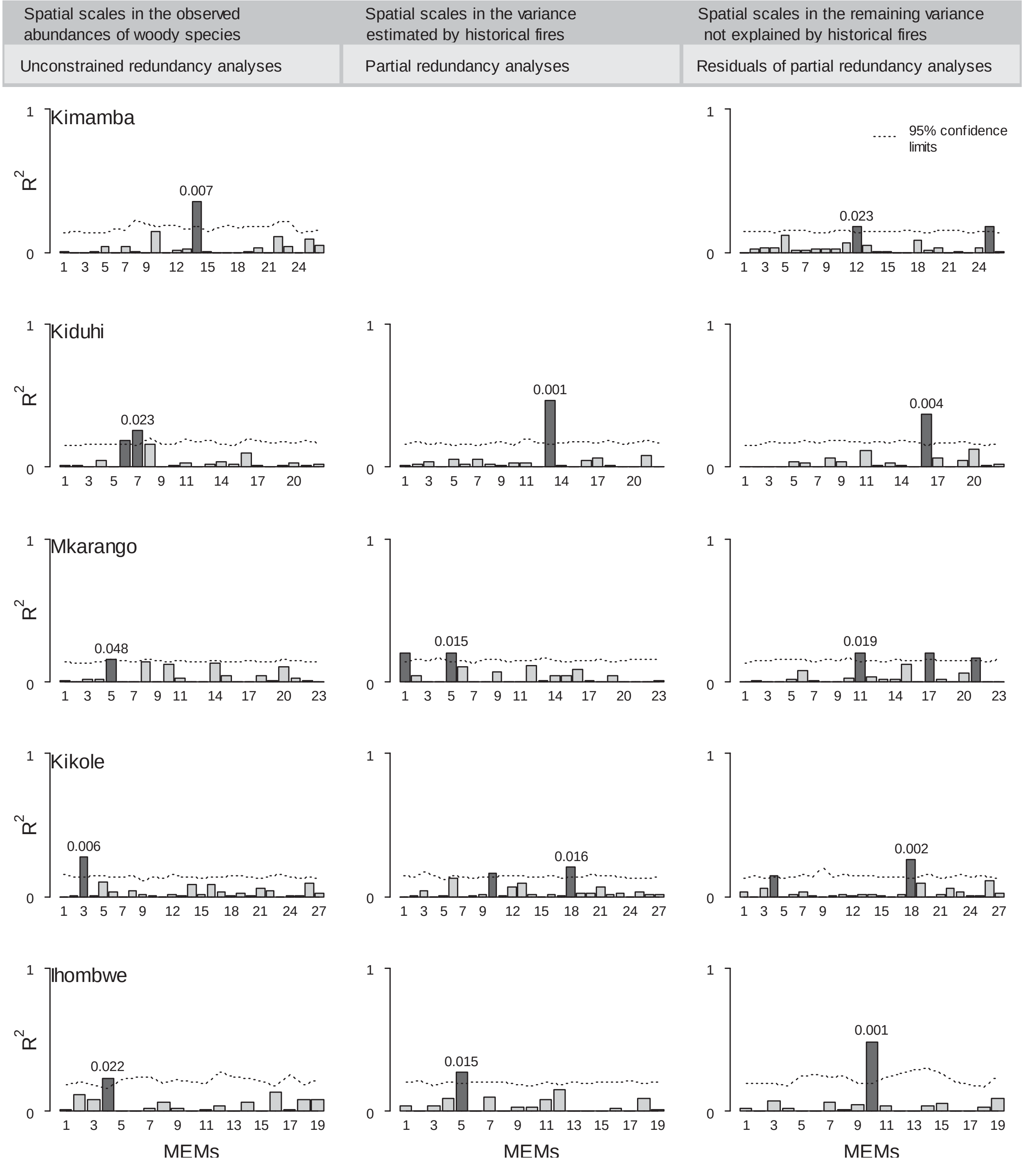
Saplings size class: second axis



(c) Seedlings size class: first axis



Seedlings size class: second axis



Paper III

Anthropogenic fires and land use increase small-scale species diversity and cause large-scale homogenization of species composition in savanna woodlands

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Abstract

Spatial and temporal changes in plant community properties are accelerating due to anthropogenic influences on natural environments. Human utilization of natural resources often creates secondary habitats, which are expanding rapidly – particularly in the tropics – and play a key role in conserving biodiversity. Uncertainties remain regarding the biodiversity and functional value of secondary habitats across spatial and temporal scales, partly due to a lack of long-term datasets. In 2012, we re-sampled woody plant communities that were first sampled in 1977, situated across a spatial mosaic of human utilization in savanna woodlands in Tanzania. We quantified spatial differences and temporal changes in woody plant community properties, and assessed how these differences and changes relate to environmental conditions. We observed an overall increase in alpha diversity, concurrently with a homogenization of the species composition i.e. a decrease in beta diversity, across a large spatial extent during 1977 – 2012. In general, fire was important for both spatial differences and temporal increases in species richness, whereas selective harvesting was an important driver of temporal changes in species composition. Both fire-tolerant and fire-sensitive species increased in abundance between the sampling periods, whereas semi-sensitive species decreased. Our results suggest that fire is an important driver of change in species richness and composition in savanna woodlands. Moreover, although species richness increased at smaller spatial scales during the sampling periods, the interplay between fire and land use lead to a homogenization of species composition over larger spatial scales.

Introduction

Spatial and temporal changes in plant community properties are increasingly central themes in ecology, due to an accelerating anthropogenic influence on natural environments (Corlett 2015, Ellis et al. 2013, Steffen et al. 2011). Indeed, changes in the distribution of species, and the diversity and composition of plant communities, caused by habitat transformation, fragmentation and degradation, are widespread (Chapin III et al. 2000, Lewis 2009, Newbold et al. 2015, Pereira et al. 2012). Consequently, there is an intense research effort on aspects of temporal dynamics of plant communities and how these vary across spatial scales, in order to understand current species distributions and predict future biodiversity patterns (Bernhardt-Römermann et al. 2015, Chown 2010, Dornelas et al. 2014, Dornelas et al. 2012, Magurran and Henderson 2010, Swenson et al. 2012, Vellend et al. 2013). Such efforts are of high importance in the tropics, where much of the global biodiversity reside and human livelihoods are particularly dependent on services provided by natural ecosystems (Lewis 2009, Magurran et al. 2010, Pereira et al. 2012). Human utilization of natural ecosystems often leads to the development of secondary habitats, which are expanding rapidly across the tropics (Achard et al. 2002, Lewis 2009, Wright 2005). Secondary habitats are areas regenerating after human utilization, and are increasingly appreciated for their contribution to global biodiversity conservation (Barlow et al. 2007, Chazdon et al. 2009, Laurance 2007). However, increased human utilization, particularly the expansion of agricultural areas, represents a major driver of biodiversity change and significantly affect the distribution of plant species (Biggs et al. 2008, Chown 2010, Latimer et al. 2004, Murphy and Romanuk 2014, Newbold et al. 2015, Newbold et al. 2014, Pereira et al. 2012). An understanding of the current spatial variability in community properties in these habitats, and the changes they have underwent over time, will help understand the extent of change and its drivers.

Savanna woodlands cover most of the vegetated areas in tropical Africa (Huntley and Walker 2012). These savannas have a long history of human utilization, particularly shifting cultivation through slash and burn practices, where fire plays a key role. The majority of African savanna woodlands are therefore secondary habitats in a regenerating phase after abandonment of agriculture. These habitats occur in a spatial mosaic that is also comprised of agricultural settlements and remnants of savanna woodlands with different histories of protection from human use. In this region, agricultural activities do not always cause complete clearance of the tree cover, but leave behind habitats that still contain a high cover of woody species (Lewis 2009). Moreover, even within cleared agricultural areas, some trees are normally left onsite to form sources of natural regeneration (Laris and Wardell 2006, McNicol et al. 2015). Therefore, agricultural land may regenerate quickly after abandonment, although the emerging species assemblage may differ from the original (Achard et al. 2002, Bowen et al. 2007, McNicol et al. 2015, Newbold et al. 2015, Stromgaard 1986). Because of their large spatial coverage, it is important to better understand the biodiversity and functional value of such secondary habitats, their potential to develop a species composition similar to that in relatively un-disturbed habitats, and whether changes after disturbance are spatially consistent (Barlow et al. 2007, Chazdon et al. 2007, Dent and Wright 2009, Lewis 2009, Morris 2010, Newbold et al. 2015, Sax and Gaines 2003). Although secondary habitats have a high potential for natural regeneration, recurrent fires may modify structural properties, demography and the spatial distribution of woody species, and may thereby contribute to the long-term degradation of these habitats (Barlow et al. 2012, Grady and Hoffmann 2012, Higgins et al. 2000, Levick et al. 2015, Ryan and Williams 2011, Tarimo et al. 2015, Vellend et al. 2013). The historical fire regime may therefore be one of the key drivers of long-term changes in woody plant community properties.

Temporal changes in plant community properties are widely assessed through re-sampling of historical data, which has been done across many ecosystems and spatial scales (Bernhardt-Römermann et al. 2015, Grytnes et al. 2014, Ross et al. 2012, Smith et al. 2012, van de Vijver et al. 1999, Vellend et al. 2013). Here, we re-sample the woody plant community within seventeen sites in savanna woodlands in Tanzania, originally sampled in 1977. In order to understand how fire and agricultural activities drive temporal changes in these communities, and whether such changes are spatially consistent, we quantified the frequency of fires and the change in the extent of agricultural areas during the past ~40 years. We also included other anthropogenic activities, such as harvesting pressure and livestock herbivory, and underlying abiotic factors such as climate and topography, to assess how these conditions contribute to long-term changes in community properties, and how they likely modify effects of fire and agricultural activities. The combined effect of these drivers is likely to vary among species, depending on their resilience and adaptation to such disturbances, and therefore this combined effect may modify the magnitude and direction of changes in community properties (Kalema and Witkowski 2012, Morris 2010, Sax and Gaines 2003, Supp and Ernest 2014, White et al. 2006). Our understanding of how fire, agricultural expansion and other anthropogenic uses have contributed to alter vegetation properties in secondary habitats across large spatial scales is poor in tropical Africa, partly due to the lack of long-term data (Dornelas et al. 2012, Magurran et al. 2010, Sax and Gaines 2003, Supp and Ernest 2014).

We investigated the influence of historical fires and land uses on the spatial differences and temporal changes in woody plant community properties. We tested if woody plant community properties differ between the two sampling periods, and if so, whether these differences relate to the spatial and temporal patterns of fire frequency, land use change and abiotic conditions. We predicted that the magnitude of temporal changes in woody species diversity and composition vary spatially because of the spatial heterogeneity in historical fires and human utilizations (Turner 2010). We also predicted that this magnitude increases with the frequency of historical fires and the degree of land use changes because of the contrasting effects of fire and land use on species that vary in their sensitivity to fire and land use. In addition, the magnitude of change is modified by abiotic conditions due to the inherent distribution of plant species along abiotic gradients.

Materials and methods

Study area

Study sites occur in the Rukwa and Katavi regions (Fig. 1, Table 1) in western Tanzania. The first sampling was conducted in 1977 by Kikula (1979, 1986) in 20 sites within woodland areas. Kikula defined woodland areas based on the height of trees and a canopy cover of more than 20%, but excluded areas where crowns were densely interwoven. He distributed sites in areas of different geomorphology and along topographical gradients. He also considered site accessibility as an important criterion, but excluded areas with noticeable human influences. Kikula considered all the sites to have a similar fire regime, since he did not notice any consistent burning patterns during field reconnaissance trips or in multi-temporal Landsat images.

Sampling of the woody plant community

Sampling in 1977 was done by employing the Point-Centered Quarter Method (PCQM; Cottam and Curtis 1956). The PCQM is a distance-based method that utilizes four quadrants defined at a sample point by a perpendicular line to the transect line (Fig. 1). A ten kilometer transect line was used at each of the 20 sites and sample points were located within an area covering 750 m on each side of the transects. Thus, ca. 1500 ha (i.e. 1.5 x 10 km) was sampled at each site. An average of 30 sample points were randomly positioned along the transect line within this area. At each sample point, the tree that was closest to the sample point in each of the four quadrants was identified to species level and its diameter at breast height (dbh) and distance from the sample point was recorded. In 1977, species composition was recorded at the site level (Kikula 1979), with the density of each species measured as the number of trees per hectare, species mean basal area measured as the mean cross-sectional area (area = $\pi \cdot dbh^2/4$), and species basal density measured as basal area per hectare.

We re-sampled 17 (Fig. 1) of the 20 sites in 2012, following the same sampling strategy as Kikula (1979). Three of the original sites were not re-sampled due to time constraints. The sites were not permanently marked by Kikula, and we therefore utilized coordinates, scaled from a map of the study area, and descriptions of localities that included references to permanent physical features (Kikula 1979). In the field, we located each site with the help of residents, by comparing the locations of the sites indicated by the residents with descriptions of the sites and coordinates documented by Kikula (1979). We also compared the locations of the identified sites with information recorded on topographical maps. Based on these comparisons we are confident that we re-sampled within the same sites as Kikula did in 1977. Similar to Kikula, we sampled 30 randomly selected points in each site. For consistency, we pre-determined the sample points by defining random distances along the transect line, which was then established onsite within the 1.5 x 10 km site sampled in 1977. We identified individual trees to species level in the field and then collected specimens for all the recorded species for identification at the herbarium of the University of Dar es Salaam, Tanzania. We checked the species nomenclature for both sampling periods against The Plant List Database (The Plant List 2013), to ensure consistency of species names over time. Similar to Kikula (1979), we compiled the species composition at site level, with corresponding density, mean basal area and basal density of each species; following Mitchell (2015) and Warde and Petranka (1981). We use the basal density, which is corrected for differences in sampling intensity (i.e. differences in observed distances and sampling points), for further analyses. In order to explain the spatial variation among sites in temporal changes in community properties, we quantified 16 environmental variables (Supplementary material, Appendix 1, Table A1), and grouped them into fire, land use and abiotic categories of explanatory variables.

Fire explanatory variables

We recorded both recent and historical fire occurrences for each site. The recent fire record consisted of ground-observed fire signs, identified within ~20 m on each side of the transect line and recorded at each of the sampling points. We counted the number of trees with soot and those that were burned, but combined the two for further analyses, since very few sites had burned trees. We also recorded the presence of ground fire scars associated with agricultural activities, unidentified ground fire scars, and white ash. We used the total number of trees with fire scars and total number of presences for each level of the categorical variables at site level for further analyses.

The historical fire record, for the past ~40 years, was compiled from Landsat satellite images and MODIS active fire product (MOD14/MYD14). The availability of Landsat satellite data was constrained by the extent of cloud cover, and we therefore did not achieve a complete spatial coverage for the duration of the study. Long periods with missing data were prevalent in the 1970s and 1980s, which has also been the case in other African savannas (Hudak and Brockett 2004). The longest period with missing data ranged from three to ten years at site level. This period is within the range of fire return intervals of one to thirteen years derived from MODIS dataset (Tarimo et al. 2015). Combining Landsat and MODIS datasets provided 23 – 27 years of available data for the sites. All available Landsat satellite images during 1972 – 2011 were analyzed to extract the extent of burned areas (see Tarimo et al. 2015 for details). We determined the number of years each sample point in a site was detected as burned from this dataset. We then scored as burned each sample point within the location of

MODIS detected active fires during 2001 – 2012. The historical fire record, therefore, consisted of the number of years (i.e. frequency) each sample point was detected as burned from the combined dataset. Because of the differences in data availability, we utilized the highest frequency observed among the sample points in each site in the analyses.

Land use explanatory variables

Land use explanatory variables consisted of utilization pressure and disturbances. We measured disturbances through harvesting pressure, quantified as the number and state (fresh or decaying) of stumps, by the presence of wild and domestic animal’s droppings and footsteps, and by the presence of cleared or abandoned farms. These variables were recorded at each sampling point in each site, similar to the recent fire signs. In addition, we used the current human population density and the change in the extent of agricultural areas as measures of disturbance. We quantified changes in the extent of the agricultural areas in an extended area (Fig. 1) around each transect, in order to detect possible large-scale changes associated with the shifting agriculture practices in the area. We then employed the Rapid Land Cover Mapper (RLCM) tool (USGS EROS 2015) to quantify changes in the agricultural area from 1972 to 2010, based on available aerial photographs and Landsat satellite images. The RLCM tool employs a dot grid method and facilitate multi-temporal mapping of land cover from multi-resolution and multi-scale data sources. We selected five-year intervals to map the extent of agricultural areas, in order to accommodate short-term variation that is characteristic of shifting agriculture. Based on data availability, we quantified agricultural extents in the 1970s (combined Landsat and aerial photographs), in 1984, 1990, 1995, 2000, 2003, 2007 and 2011. The resolution of the dot grid was set to 250 m to accommodate the sizes of farms, which are normally less than one hectare (McNicol et al. 2015). We quantified the short-term changes as the difference in the extent of the agricultural areas, at site level, between consecutive intervals, and then summed the differences for the overall change. Initial analyses indicated that the location of agricultural areas changed simultaneously with changes in the extent of these areas. We therefore quantified this change in position, by locating the centroid of the agricultural areas, at site level, in each interval, and measured the linear distance between these centroids in each site. We expect short distances to occur in areas with no change in agricultural extent and location or represent a likely expansion of agricultural areas from a permanent settled area, while long distances likely represent agricultural clearance in a new location combined with abandonment of a previous agricultural area.

Abiotic explanatory variables

Abiotic explanatory variables consisted of mean monthly temperature, total annual rainfall, elevation, and slope at each sample point. Temperature and rainfall data, compiled from average climate data during 1950 – 2000, were sourced from WorldClim (Hijmans et al. 2005), and slope was derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model at 30 m resolution (LP DAAC 2014). Elevation was recorded in the field using a hand held GPS receiver. To account for other spatially structured influences not represented by our explanatory variables, we included each site's latitude in the abiotic group of explanatory variables. An analysis with both latitude and longitude resulted into qualitatively similar results. Therefore, we retained latitude only, given the north-south extent of the study area.

Statistical analyses

Among-sites differences in species composition within each sampling period

The large spatial extent of the study area and the differences in fire history and land uses among sites may have caused spatial differences in species composition and concomitant temporal changes. We therefore assessed the species composition of each site relative to other sites in each sampling period, before assessing temporal changes in the community properties.

We utilized the total variance of the community composition dataset as a measure of spatial differences in species composition among sites in each sampling period (Legendre and Cáceres 2013). This variance was then partitioned to quantify the contribution of each site, as the local contribution to beta diversity (LCBD), and the contribution of each species as the species contribution to beta diversity (SCBD), following Legendre & Cáceres (2013). The local contribution to beta diversity, i.e. LCBD values, represent the degree to which each site is compositionally different relative to the site with mean species composition, while SCBD values represent the degree to which the frequency and abundance of each species vary throughout the study area (Legendre 2014, Legendre and Cáceres 2013, Legendre and Gauthier 2014). We compared the results from the two sampling periods to identify factors that may have influenced certain sites or species more than others during the study period. Furthermore, previous studies have characterized the fire-tolerance levels of woody species in the study region, thus forming fire sensitive-tolerant groups (Chidumayo 1997, Lawton 1978, Trapnell 1959). We utilized these fire sensitive-tolerant groups to assess the influence of fire frequency, which is associated with land uses, on the frequency and abundance of woody species across the sites, although we did not have information on the fire-tolerance levels for all species (Supplementary material Appendix 3, Fig. A3). In this assessment, we compared the SCBD values and the total basal density for each species, and for each group of fire sensitive-tolerant species at each sites, between the sampling periods.

Spatial differences in species composition comprise both spatial turnover and spatial richness difference, i.e. the among-sites differences in the number of species (Carvalho et al. 2012, Legendre 2014). In order to understand the sources of spatial differences in species composition, we partitioned the LCBD values, in each sampling period, into turnover and richness difference portions.

Temporal changes in woody plant community properties

We quantified change in community properties between the two sampling periods by assessing changes in alpha diversity metrics and in species composition. We described alpha diversity as species richness, Shannon species diversity, and Pielou species evenness at each site, and used Student's paired t-tests to quantify changes in the alpha diversity metrics over time.

We employed multivariate analyses to quantify changes in species composition over time, utilizing the basal density as a measure of species abundance. We employed a multiple response permutation procedure (MRPP; Oksanen et al. 2014) to test the null hypothesis of no significant change in species composition between the sampling periods. We also employed a permutational multivariate analysis of variance (ADONIS; Oksanen et al. 2014) to assess if there was a significant contribution of the sampling periods to the change in species composition. We then employed two non-metric multidimensional scaling (NMDS) approaches to quantify temporal changes in species composition; first with the community dataset from the first sampling, and second, with a combined 1977–2012 dataset. We defined the magnitude of change as the length of the displacement vector of each site between 1977 and 2012 and as the difference in the site scores between the sampling periods along the first and second NMDS axes of these two analyses.

We utilized a null model analysis (Chase et al. 2011) to assess if observed changes in species composition were different from changes expected from random community assemblage processes. This was important in order to distinguish changes resulting from sampling effects, differences in alpha diversity and random influences of environmental conditions from those that may be associated with a systematic influence of environmental conditions (Anderson et al. 2011, Baselga et al. 2015, Chase et al. 2011, Kraft et al. 2011, Myers et al. 2015). Specifically, we tested if fire frequency and land use changes have influenced, in a systematic way, the compositional similarity among sites from 1977 to 2012.

One common approach to null model analyses is to compare dissimilarities between the observed and a randomized community, utilizing a presence/absence community dataset (Baselga et al. 2015, Chase et al. 2011, Myers et al. 2013). We defined a pairwise null dissimilarity index to represent a random temporal change in species composition, based on the observed species richness at each site, and the species pool across all sites, following Chase et al. (2011). Thus, observed temporal change in species composition different from that expected at random, as quantified by the pairwise null dissimilarities, may indicate an influence of the change in environmental conditions between 1977 and 2012 (Anderson et al. 2011, Chase et al. 2011). We employed NMDS analysis of the null community, based on the null dissimilarities, and compared compositional similarity among sites in each sampling period. In this analysis, sites in the null community will be more compositionally similar within than between sampling periods if the observed change in species composition is caused by a change in environmental conditions during 1977 – 2012 (Chase et al. 2011, Myers et al. 2015). We used the Mantel test to assess if there is a significant difference in the pairwise null dissimilarities among sites between the two sampling periods (Anderson et al. 2011). We also compared the NMDS based on the null community with another NMDS of the observed community, based on Jaccard dissimilarity index.

We also assessed portions of the observed temporal change in species composition, attributed to turnover and richness difference, following Legendre (2014), in order to gain a better understanding of these sources of temporal change in species composition, and if the changes are related to the environmental conditions. We then quantified the contribution of each site (the LCBD) to the turnover and richness difference portions of the temporal change in species composition in order to gain an understanding of the among-site differences in these sources of change.

Relationship between changes in community properties and environmental variables

Because of the relatively small sample size (17 sites), and to avoid collinearity among variables, we needed to reduce the number of explanatory variables in the statistical models. We therefore conducted separate principal component analyses for each category of environmental variables (i.e. fire, land use and abiotic variables). These analyses indicated that up to four principal components (PCs) would be required to explain at least 75% of the variation in each of the categories of environmental variables. Thus, we utilized variable selection to select PCs in each category of the environmental variables that were included in further statistical analyses, as outlined below.

Before assessing the relationships between temporal changes in the community properties and the environmental variables, we assessed the relationship between the spatial compositional differences and the environmental variables by using a generalized linear model (GLM) with the LCBD values in 2012 as the response.

Thereafter, we assessed the relationship between temporal changes in species composition and the environmental variables by both univariate and multivariate methods. We first assessed the relationship between the change in species composition, quantified by the site scores on each axis of the NMDS analysis of the combined 1977–2012 community dataset, and the environmental variables, using a GLM. We then utilized another GLM to assess the relationship between the observed magnitude of change, quantified as the length of the displacement vector between sampling periods for each site, and the environmental variables. We also assessed the relationship between the difference in sites scores on each axis of the two NMDS analyses and the environmental variables. We then utilized permutational multivariate analysis of variance (ADONIS; Oksanen et al. 2014) to test if the partitioned temporal turnover and richness difference (i.e. temporal gain/loss of species) were related to the environmental variables. We also employed a GLM to test for a relationship between the contribution of each site (the LCBD) to the temporal turnover and richness difference and the environmental variables. In all GLM analyses, we performed variable selection in two steps; first in separate models for PCs in each category of environmental variables, and second with a model combining PCs selected in the separate analyses. In both steps, we selected variables based on the lowest Akaike's Information Criterion (AIC) and a p-value < 0.05. We also performed separate ADONIS analyses for each group of environmental variables as a first step and then a combined analysis with PCs that were significant ($p < 0.05$) in the separate analyses. In all analyses, we also included the alpha diversity metrics from 1977 as a separate group of explanatory variables in the first step, in order to account for the differences in initial diversity among sites that may have influenced temporal changes in community properties. In most cases, none of the alpha diversity metrics were selected in the first step and thus they were not included in further analyses.

All analyses were performed in R version 3.1.2 (R Core Team 2014). Community abundances were Hellinger transformed before analyses.

Results

Among-sites differences in species composition within sampling periods

The contribution of each site (the LCBD) to the observed spatial differences in species composition in each sampling period shows that four sites in 1977 and three sites in 2012 had a significantly different species composition relative to the other sites in the same sampling period (Supplementary material Appendix 2, Fig. A2). Two of the sites in 1977 remained different in 2012 and another site emerged as different from the others in 2012. There were also differences in the amount of spatial variation in the frequency and abundance of each species (the SCBD) among sites in each sampling period. Only three of the ten species with the highest SCBD values occurred in both sampling periods but ranked differently relative to other species in each period. Fire-tolerant species had generally increased in SCBD values and in total basal density in 2012, based on analyses at both species and at site level (Supplementary material Appendix 3, Fig. A3a–c). Similarly, the SCBD values and total basal density of fire-sensitive species had increased from 1977 to 2012 (Supplementary material Appendix 3, Fig. A3a–c). On the other hand, species that are semi-sensitive to fire had generally decreased in 2012 in their SCBD values and total basal density, based on analyses at both species and at site level (Supplementary material Appendix 3, Fig. A3a–c).

Based on the partitioning of the spatial differences in species composition to turnover and richness difference (i.e. spatial gain/loss of species), spatial turnover contributed a larger portion of the spatial differences in species composition than the species gained/lost among sites in both sampling periods (Table 2). However, the portion contributed by the spatial gain or loss of species increased from 16% in 1977 to 30% in 2012, indicating an increasing role of the spatial differences in species richness in determining the among-sites differences in species composition.

Temporal changes in species alpha diversity

In general, alpha diversity was higher in 2012 than in 1977 in all sites, irrespective of the environmental conditions. Only three, two and five sites had lower species richness, Shannon diversity and Pielou evenness, respectively, in 2012 than in 1977. After Holm correction for multiple testing, all the alpha diversity metrics were significantly different ($t > 2.13$, $p < 0.049$) between the sampling periods. Species richness and Shannon diversity in 2012 had a positive relationship with those in 1977, although only marginally significant ($p = 0.064$ and $p = 0.053$, respectively). The relationship between the sampling periods was not significant ($p = 0.312$) for species evenness.

Temporal changes in species composition

A change in species composition had occurred between the sampling periods, detected by both the multiple response permutation procedure (MRPP; p = 0.014) and the permutational multivariate analysis of variance (ADONIS; p = 0.001). Based on the multivariate analysis of variance, 8.3% of the total variation in species composition was attributed to the sampling periods. The direction of the change in species composition indicated an overall reduction in the spatial variation in species composition, i.e. a taxonomic homogenization, from 1977 to 2012 (Fig. 2), where sites were more compositionally similar to each other in 2012 than in 1977.

The null model analysis indicated that the observed changes in species composition were different from those expected at random (Fig. 3). Pairwise null dissimilarities among sites were significantly different between the sampling periods (Mantel; tau=0.28, p = 0.001). Sites within each sampling period were more compositionally similar to each other than they were between the sampling periods in the observed community (Fig. 3). This similarity persisted in the null community (Fig. 3), indicating that the changes in species composition were not solely stochastic.

The temporal differences in species richness that contributed to the temporal change in species composition was in general caused by species gains, as indicated by the increase in species richness. This temporal species gain contributed with 24% of the temporal change in species composition, compared to 76% contributed by the temporal species turnover (Table 2). The LCBD values for the partitioned turnover and richness difference (i.e. species gains) indicated that sites with a higher contribution to the temporal change in species composition, based on temporal species turnover, were different from those with a higher contribution based on temporal species gains.

Relationship between changes in community properties and environmental variables

The initial analyses of the spatial differences in species composition among sites (the LCBD) indicated a significant relationship (GLM; $p < 0.024$) with land use variables. Sites with low harvesting density, but with high human population density, high utilization through agriculture and livestock herbivory, and with small changes in the location of agricultural areas, were compositionally different from other sites (high LCBD). When these spatial differences in species composition were partitioned to turnover and richness difference, both had a significant relationship (ADONIS; $p < 0.040$) with the categories of environmental variables. The spatial species turnover portion was more prominent in the southern parts of the study area. This turnover was moderately related to human population density and was prevalent in sites where fire was not utilized for agricultural purposes, and with low average monthly temperature, at higher elevations and with relatively steep slopes. The richness difference portion, i.e. the among-sites differences in species richness, was more prevalent in sites with a high frequency of historical fires and a high density of recent fires. Fire contributed with a relatively higher proportion (ADONIS; R^2 range: 14.2% – 21.7%) of the variation in spatial turnover and spatial difference in species richness when compared to the other categories of environmental variables (ADONIS; R^2 range: 11.8% – 17.3%).

The temporal change in species composition, as quantified by NMDS site scores from the combined 1977-2012 community dataset, was significantly related to all categories of environmental variables (Fig. 4). Based on GLMs on both NMDS axes ($p < 0.045$), the temporal change in species composition increased towards the south of the study area and with increasing frequency of historical fires, density of recent fires, elevation and slope, and decreasing average monthly temperature. On the other hand, the magnitude of temporal change in species composition, as measured by displacement of sites in the compositional space between 1977 and 2012 (i.e. the length of vectors in Fig. 2), was negatively related to the frequency of historical fires (GLM; $p = 0.043$; Fig. 5). Assessing this magnitude separately for each NMDS axis (i.e. the difference in sites scores between 1977 and 2012) indicated a significant influence of land use variables on the change along the second axis (GLM; $p < 0.026$). Along this axis, the magnitude of change increased with increasing human population density, increasing utilization for agriculture and livestock herbivory, and with decreasing harvesting density. When the temporal change in species composition was partitioned to turnover and richness difference, the richness difference portion (i.e. species gains), significantly increased (ADONIS; $p < 0.016$) with the frequency of historical fires and human population density. Temporal species turnover, on the other hand, significantly increased (ADONIS; $p < 0.023$) with harvesting density in sites with low human population density and low utilization for agriculture and livestock herbivory. Fire contributed to a higher proportion (ADONIS; $R^2 = 39\%$) of the variation in temporal species gains relative to that contributed by land use variables in both the temporal species gains and species turnover (ADONIS; $R^2 = 17.6\%$ and $R^2 = 11.8\%$, respectively). When the temporal species gains and species turnover were partitioned among sites (the LCBD), the among-sites differences based on the species gained, increased significantly with elevation and decreased with steepness (GLM; $p = 0.017$). Furthermore, sites that had little influence from agricultural activities were more compositionally similar and occupied a smaller compositional space in both sampling periods than sites with different extents of agricultural areas (Fig. 6).

Discussion

We found large temporal changes in woody plant community properties between 1977 and 2012 in savanna woodlands of Tanzania. Alpha diversity, as measured by species richness, Shannon diversity and Pielou evenness increased at small spatial scales, whereas temporal changes in species composition resulted in a taxonomic homogenization at the larger spatial scale. In agreement with our prediction, spatial differences in species composition resulted from a higher intensity of land use activities and differences in abiotic conditions. On the other hand temporal changes in community properties resulted from high frequency of fires and high harvesting intensity. Contrary to our prediction, the overall magnitude of temporal change in species composition increased with decreasing frequency of historical fires, however species richness increased with an increase in this frequency. Fire was more important than land use and abiotic conditions, both in the spatial differences between sites and in the temporal changes between sampling periods. Our results are similar to recent studies spanning local to global extents that have shown both temporal increases and decreases in alpha diversity, and a trend towards species homogenization across space (Dornelas et al. 2014, Palmquist et al. 2015, Vellend et al. 2013).

Temporal changes in woody plant community properties

Taxonomic (and in some cases functional) homogenization have occurred over time across plant communities under contrasting utilization pressures (Duvall 2011, Keith et al. 2009, Rooney et al. 2004, Ross et al. 2012, Smart et al. 2006, Vellend et al. 2007). Similarly, an increase in alpha diversity simultaneously with an increase in compositional similarity have occurred in the alpine (Jurasinski and Kreyling 2007, Odland et al. 2010), in secondary habitats of North America (Li and Waller 2015, McCune and Vellend 2013) and across Britain (Smart et al. 2006). One explanation to the concurrent increase in alpha diversity with taxonomic homogenization in secondary habitats is that the species contributing to the increase in alpha diversity are recruited from a limited species pool (Lewis 2009). In such cases, species that are favored by the prevalent environmental conditions, and that belong to a small species pool, disperse among sites, causing sites to be more compositionally similar. Thus, the abundance of species that are strongly constrained by environmental conditions decreases, whereas the abundance of species resilient to disturbances and able to persist under wider environmental conditions increases (Barlow et al. 2007, Devineau 2005, Lewis 2009, McCune and Vellend 2013, McKinney and Lockwood 1999, Rooney et al. 2004). In line with increased abundance of species adapted to fluctuating environmental conditions, we found a general increase in the abundance and amount of spatial variation of fire-tolerant species. This also occurred in oak-hickory forests in the USA, where fire-tolerant species had higher abundances in burned than in un-burned sites after 30 years of prescribed burning (Myers et al. 2015). In our study, species turnover was the main source of both the temporal changes and the spatial variation in species composition (Table 2), despite the increase in species richness. Thus, our results suggest that the temporal increase in species richness converged the diversity of woody species across the spatial extent of the sites.

Drivers of temporal change in woody plant community properties

Species homogenization has previously been attributed to intensified agriculture, increases in the frequency and abundance of native species, high density of selective grazers, and both fire suppression and prescribed burning (Keith et al. 2009, Li and Waller 2015, McCune and Vellend 2013, Myers et al. 2015, Rooney et al. 2004, Vellend et al. 2007). Disentangling the sources of change in species composition in our study revealed drivers of change unique to species turnover and the increase in species richness. Temporal turnover, which was the most important source of change in species composition, was positively related to harvesting density in the recent past (i.e. presence of decaying stumps or both fresh and decaying stumps), in areas with low human population density and less utilized for other land uses. Harvesting of a few selected species for commercial and domestic uses is common within the study area and across the country (Backéus et al. 2006, Luoga et al. 2000, Monela et al. 1993, Schwartz et al. 2002). In neighboring Ugandan forests, sites selectively harvested were compositionally different and contained species rarely found in non-selectively harvested sites (Osazuwa-Peters et al. 2015a). In these Ugandan forests, the rate of temporal turnover in species composition accelerated over time, during a 45-year period (Osazuwa-Peters et al. 2015b). These findings suggest that selective harvesting has caused higher temporal turnover in our study area, but only in areas with a low utilization within other land uses. Additionally, historical fires have modified this relationship between temporal turnover and harvesting intensity, although with marginal statistical significance, since temporal turnover varied spatially and the difference increased (high LCBD) in sites with a high frequency of historical fires. This may indicate that fire suppresses the regeneration of certain species because the density and survival of re-sprouts in these woodlands decreases with fire frequency (Ryan and Williams 2011, Zolho 2005). Higher turnover in the savanna woodlands of Mali in West Africa was caused by agricultural activities and settlements, and by increased abundance of economically important and animal-dispersed woody species (Duvall 2011). On the other hand, the temporal increase in species richness in our study resulted from both a high frequency of historical fires and a high human population density. The topography of sites modified this relationship across space, since species richness increased most (high LCBD) in sites located at higher elevations with relatively gentle slopes. Similarly, species richness increased with fire frequency in grassland and woodland areas in the USA and was modified by edaphic conditions and varied across spatial scales (Palmquist et al. 2015). Thus, the overall temporal change in species composition in our study resulted from both fire, land use and abiotic conditions, which differentially influenced the properties of the woody plant community.

Changes in alpha diversity and increased taxonomic homogenization commonly occur in response to the local invasion of exotic species (Dornelas et al. 2014, Magurran 2007, McKinney and Lockwood 1999, Rooney et al. 2004, Sax and Gaines 2003). However, the species encountered in both sampling periods in our study are native to the study area. Thus, the changes that have occurred are not caused by invasive species. We observed the highest compositional similarity among sites that are not utilized for agriculture, whereas compositional dissimilarity appeared to be highest among sites exposed to agricultural use to a smaller or larger extent (Fig. 6). Similarly, previous findings from the study area suggest that more than half of the areas that are open to human utilization contained species that do not occur in protected areas (Banda et al. 2006). This suggests that land uses in our study area could promote the establishment of certain native woody species, and thus contribute to compositional differentiation between utilized sites and those not utilized. However, the species involved occur within the study area and therefore an overall decrease in compositional diversity, i.e. taxonomic homogenization, has occurred during the recent past. Similarly, historical land use has caused taxonomic homogenization of forests re-grown from abandoned agricultural uses in north-eastern North America and Europe (Vellend et al. 2007), while changes in environmental conditions facilitated taxonomic homogenization of woodlands in Britain (Keith et al. 2009). A recent global meta-analysis shows an increasing trend in species richness at local scales in sites regenerating from disturbances (including fire, severe storms, logging and grazing), whereas a decreasing trend has occurred with the invasion of certain exotic species and with recent climate change (Vellend et al. 2013). Our results, and those from previous studies, suggest that the establishment of exotic species is not the only cause of temporal changes in alpha diversity and taxonomic homogenization, and that the relative roles of the factors causing these changes vary among habitats (Murphy and Romanuk 2014, Olden and Rooney 2006, Pereira et al. 2012).

The among-sites differences in species composition, in which we also observed higher species turnover than differences in species richness, revealed drivers of change similar to those causing temporal changes. In addition, large spatial turnover was associated with abiotic conditions, including high elevations, steep slopes and low temperature. These conditions, and low annual rainfall, were similarly important for the temporal change in species composition (Fig. 4). The combined importance of topography, temperature and rainfall that we have observed may indicate an important influence of average climate conditions on woody plant community properties for the ~50-year duration of the climate data. However, this does not necessarily indicate a direct influence of climate change, because of the likely difference between the long-term average and actual change in climate conditions. Climate change is suggested to be an important driver of change in community properties and a cause of taxonomic homogenization in other plant communities (Jurasinski and Kreyling 2007, Odland et al. 2010, Vellend et al. 2013). Furthermore, the combined topography, rainfall and temperature characteristics of a site may also influence other drivers, such as the probability of ignition and spread of a fire.

The unexpected temporal increase in the amount of spatial variability in the frequency and abundance of fire-sensitive species may be explained by the decrease in the extents of fire-affected areas. The expansion of agricultural areas in African savannas is generally associated with a decrease in fire activity and thus burned areas (Andela and van der Werf 2014, Grégoire et al. 2013, Tarimo et al. 2015). We observed an increase, in the period between 1972 and 2010, in the number of sites influenced by agricultural uses and in the extent of agricultural areas for all sites that were initially influenced by agricultural activities (Table 1). We did not find clear trends, but larger increases in fire-sensitive species occurred in sites utilized for agriculture, and one of the two sites with a decrease in the abundance of fire-sensitive species was little influenced by agricultural activities (Table 1; Supplementary material Appendix 3, Fig. A3a–c). We realize, however, that we had relatively fewer sites with little influence from agriculture. Similarly, changes in the abundance of approximately half of the most common species in secondary forest fallows in Indonesia were consistently related to the number of times each site had been used for shifting cultivation (Lawrence et al. 2005). In the West African savannas of Burkina Faso, a decrease in and a lack of fire in agricultural areas promoted the establishment of species that are not commonly occurring in the area (Devineau et al. 2010). Our results and those from these studies suggest that the long-term expansion of agricultural areas and the associated decrease in fire activity may explain the increase in the frequency and abundance of fire sensitive species in these secondary habitats.

Together with the expansion of agricultural areas, livestock herbivory contributed to the temporal changes in species composition from 1977 to 2012, and to the distinctiveness among sites in their species composition. Livestock grazing and browsing can potentially suppress woody species and thus influence long-term community properties. In the dry savannas of Senegal in West Africa, the abundance of woody species and changes in floristic composition increased substantially after fifteen years of fencing (Hejcmanová et al. 2010). However, regeneration in abandoned grazed areas took a longer time compared to regeneration in areas utilized for other human uses in the tropical forests of Puerto Rico (Aide et al. 1995). This delayed regeneration may contribute to changes in species composition when unpalatable species are able to establish and replace those affected by herbivory. This may explain the observed contribution of livestock herbivory to spatial differences and temporal changes in woody plants community properties in our study.

The comparison between the observed and the randomized communities indicated that individual sites changed position along environmental gradients from 1977 to 2012 (Fig. 3). Sites in 1977 were less similar to those in 2012 than would be expected at random, indicating that environmental conditions that influence the assemblage of species in the study area had changed from 1977 to 2012 (Chase et al. 2011). We observed an increase in agricultural areas between 1977 and 2012. Human population density, and thus the extent of different land uses, has also increased substantially during this period. Furthermore, species turnover, which was more important than increased species richness for the changes in species composition we have observed, reflects a directional influence of environmental conditions on the change in species composition (Anderson et al. 2011, Legendre 2014). In addition, both spatial and temporal changes in species richness occurred with an increase in the frequency of historical fires and the density of recent fires. In general, our results suggest that human activities have changed environmental conditions in ways that systematically constrains the species compositional space across a large spatial extent.

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Supplementary material – Appendix 1–3

Table 1. Description of study sites in Katavi and Rukwa regions in Tanzania (see Fig. 1). Temperature and rainfall were sourced from the WorldClim database (Hijmans et al. 2005). Human population and population density were obtained by combining the total census enumeration areas in which sites occur. Environmental heterogeneity represents the average standardized Euclidean distance of all categories of environmental variables. Site influenced by agricultural activities (P) and those with relatively low influence from agricultural activities (A) were determined based on field observation.

Agricultural areas	Site	Annual rainfall (mm)	Temperature Min-Max (°C)	Elevation Min-Max (m)	Human population 2012	Human population density	Environmental heterogeneity
P	Iku-Katuma	939 - 944	26.0 - 26.1	922.5 - 938.4	29197	49	5.28 ± 2.03
P	Inyonga 1	950 - 958	24.2 - 24.2	1175 -1226	7615	1	5.83 ± 1.41
A	Inyonga 2	927 - 938	23.9 - 24.1	1152 - 1212	14846	2	5.81 ± 1.51
P	Inyonga 3	940 - 947	24.2 - 24.3	1158 - 1196	19852	2	5.71 ± 1.84
P	Kankwale	938 - 948	19.5 - 20.0	1803 - 1885	54566	150	5.21 ± 1.68
P	Kifinga	940 - 944	23.3 - 23.7	845.4 - 991.5	60377	63	5.27 ± 1.50
P	Kasansa	926 - 932	24.9 - 25.1	848.1 - 962.7	23002	97	4.94 ± 1.89
P	Kasanga	1121 - 1127	22.8 - 24.4	1022 - 1160	35819	37	5.34 ± 1.86
P	Laela	942 - 960	19.6 - 20.4	1475 - 1635	39817	46	4.91 ± 1.37
P	Mbizi	973 - 1007	19.7 - 20.1	2023 - 2235	46424	128	5.45 ± 2.07
P	Mamba	922 - 925	25.1 - 25.3	857.4 - 873.5	29475	33	5.84 ± 1.97
A	Mpandule	1103 - 1112	21.5 - 21.8	1374 - 1418	25293	10	5.10 ± 2.00
P	Mpanda	1066 - 1087	24.8 - 25.3	1010 - 1150	25494	23	5.70 ± 1.88
A	Mwese	1051 - 1067	22.3 - 23.3	1161 - 1257	7520	3	5.25 ± 2.10
P	Mwazye	979 - 997	18.8 - 19.2	1760 - 1896	7895	34	5.56 ± 1.77
A	Ugalla	1082 - 1086	23.5 - 23.8	1102 - 1139	8559	5	5.49 ± 1.35
A	Uruwira	989 - 993	25.2 - 25.4	1025 - 1082	6124	3	5.32 ± 1.30

Table 2. The total variation in species composition (beta diversity) partitioned into species turnover and species richness difference for the 17 study sites in Katavi and Rukwa regions in Tanzania (Fig. 1).

Attribute	1977	2012	1977 - 2012
Total beta diversity	0.424	0.407	0.461
Total turnover	0.355 (84%)	0.287 (70.5%)	0.349 (76%)
Total richness difference	0.069 (16%)	0.120 (29.5 %)	0.112 (24%)

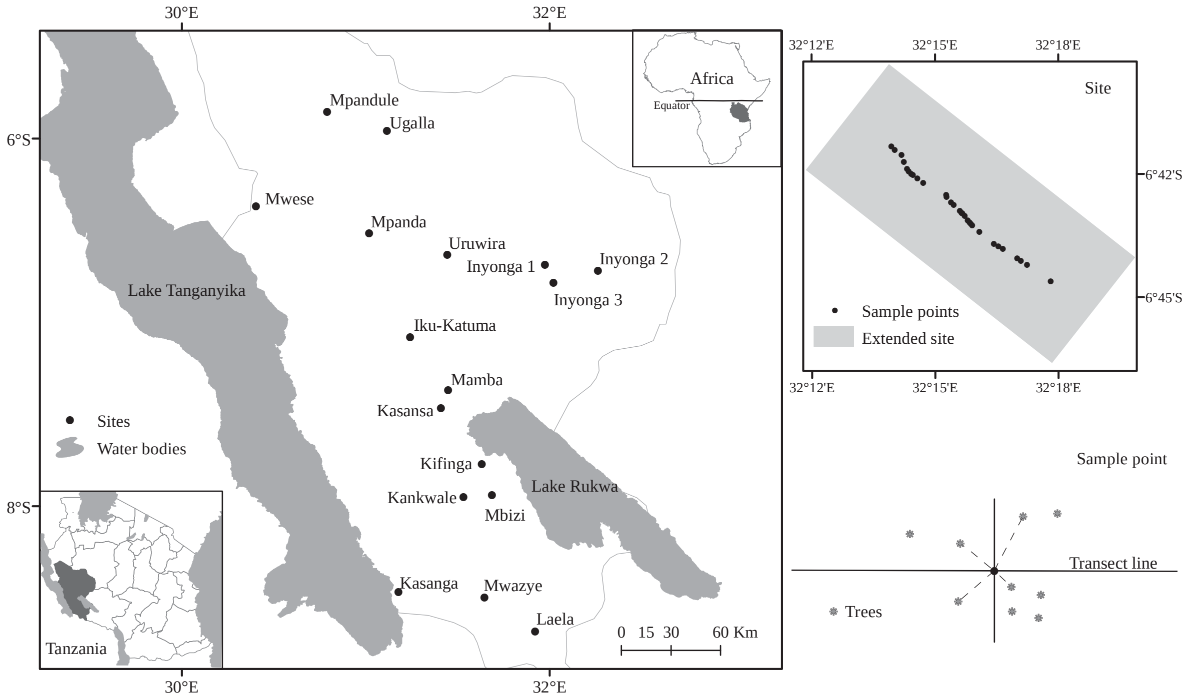

Fig. 1. Location of study sites in the Katavi and Rukwa regions in Tanzania and layout of the study design. Woody species were re-sampled along a transect line (top right) by the Point-Centered Quarter Method. At each sample point (bottom right), one tree closest to the sample point in each of the four quadrants was recorded. The extent of agricultural areas was determined within the extended site.

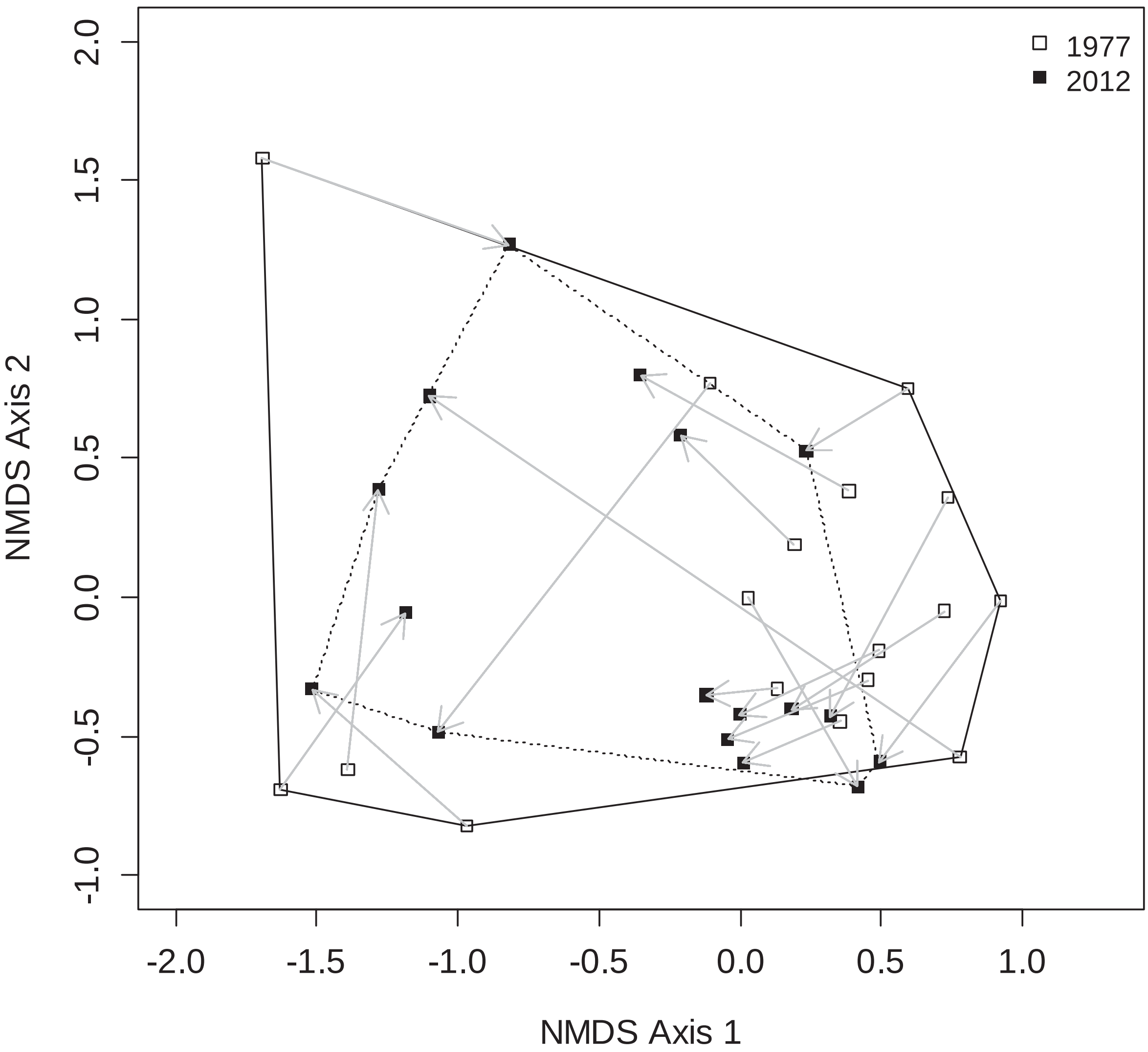

Fig. 2. The location of sites in the compositional space and the direction of change in species composition based on observed abundances of species. Sites in 1977 are from the separate analyses for each sampling period while those in 2012 are from the combined 1977–2012 dataset, sampled in the Katavi and Rukwa regions in Tanzania (Fig. 1).

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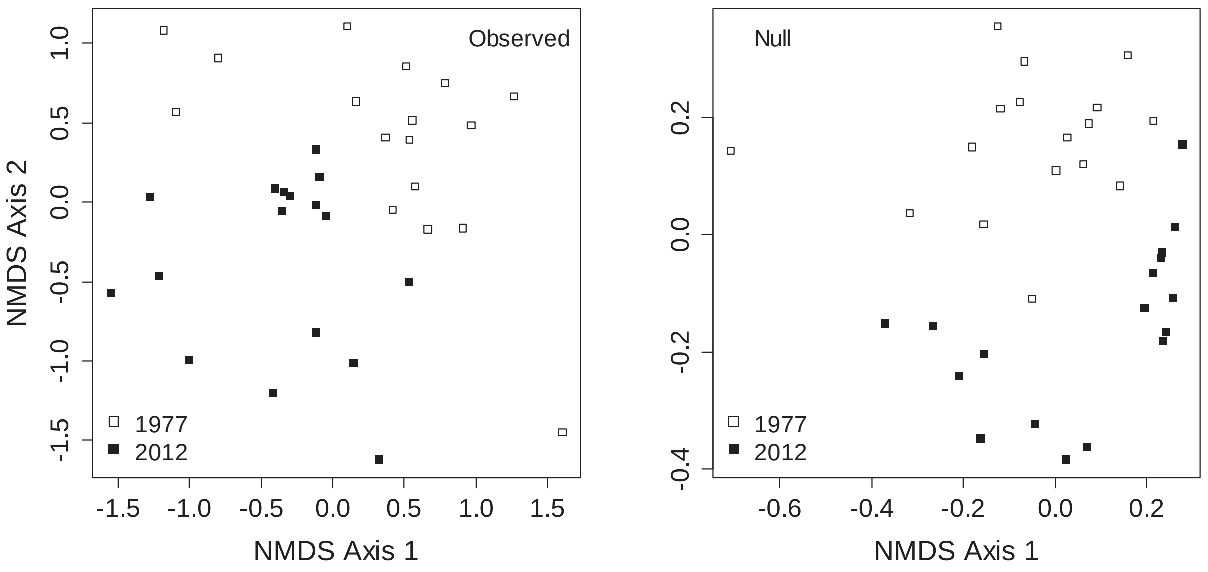

860 Fig. 3. The site locations in the compositional space of the observed and null communities

861 based on the presence/absence of individuals of each species from the combined 1977–2012

862 dataset sampled in the Katavi and Rukwa regions in Tanzania (Fig. 1).

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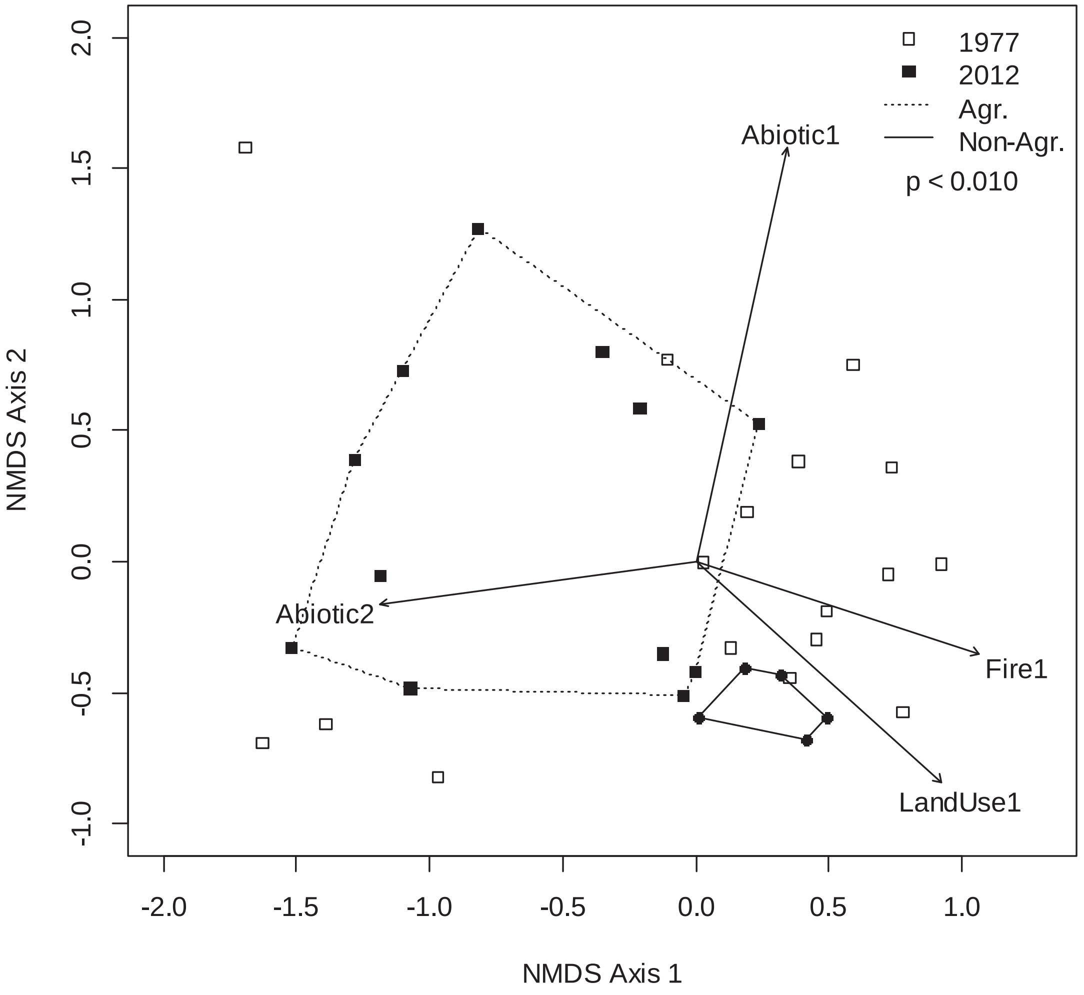

Fig. 4. Relationship between the locations of sites sampled in 2012, in the Katavi and Rukwa regions in Tanzania (fig. 1), in the species composition space and environmental variables. The species composition consists of the combined 1977–2012 community matrix. Fire1 represents high density of recent fires; LandUse1 represents high harvesting density, low utilization for agriculture and livestock herbivory and low human population density; Abiotic1 represents low average monthly temperature, higher elevations and steep slopes, and southern latitudes; Abiotic2 represents low total annual rainfall and southern latitudes. Non-Agr. indicates sites that are less influenced by agricultural activities while Agr. those influenced by agricultural activities (see Table 1).

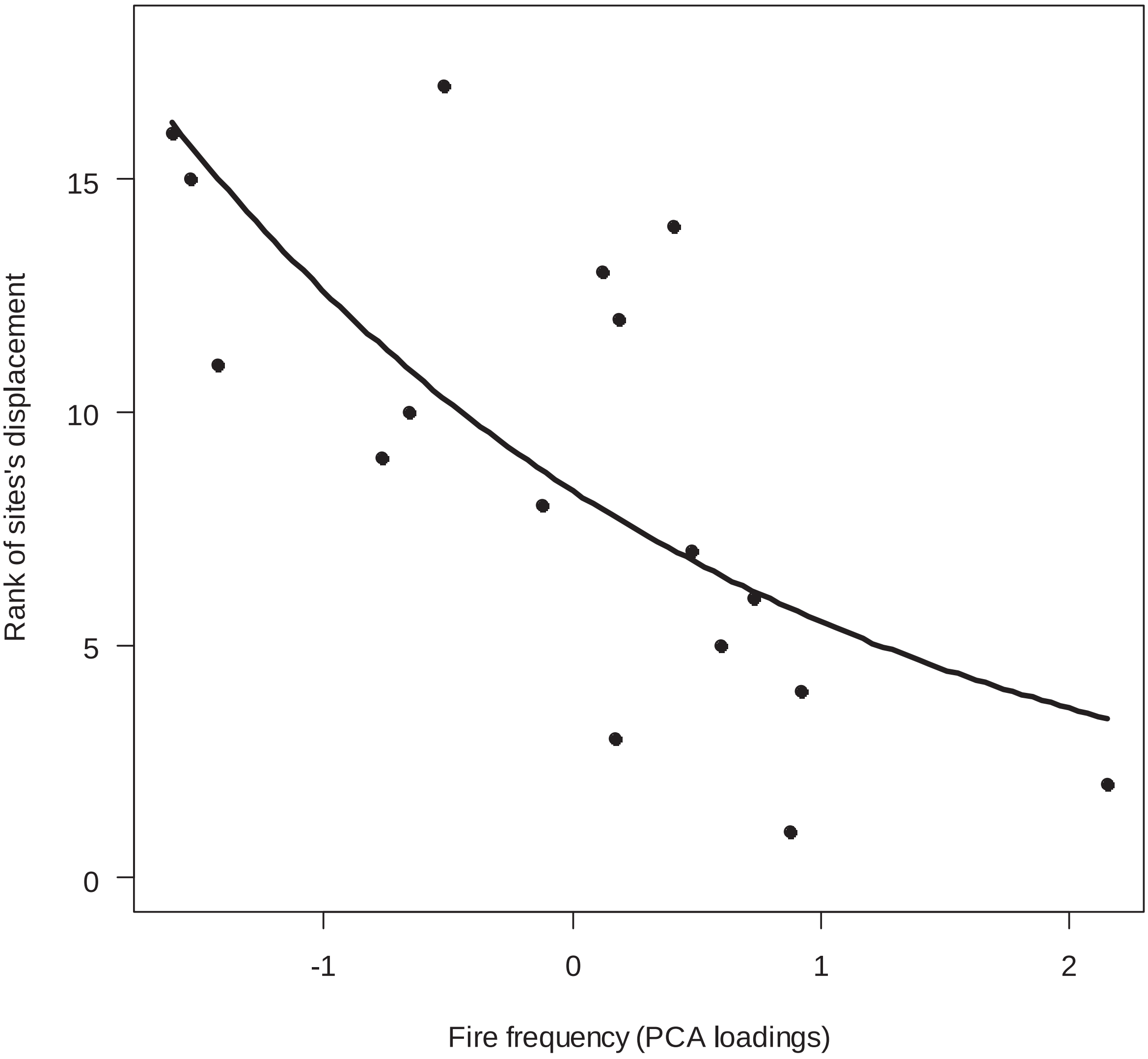

Fig. 5. The relationship between the magnitude of change in species composition and fire in savanna woodlands in Katavi and Rukwa regions in Tanzania (Fig. 1). Sites are ranked based on the magnitude of change, which is quantified as the displacement of sites in the compositional space between 1977 and 2012 (length of vectors in Fig. 2). Rank = 1 represents small displacement. The x-axis represents loadings from principal components analysis, which increases with the frequency of historical fires.

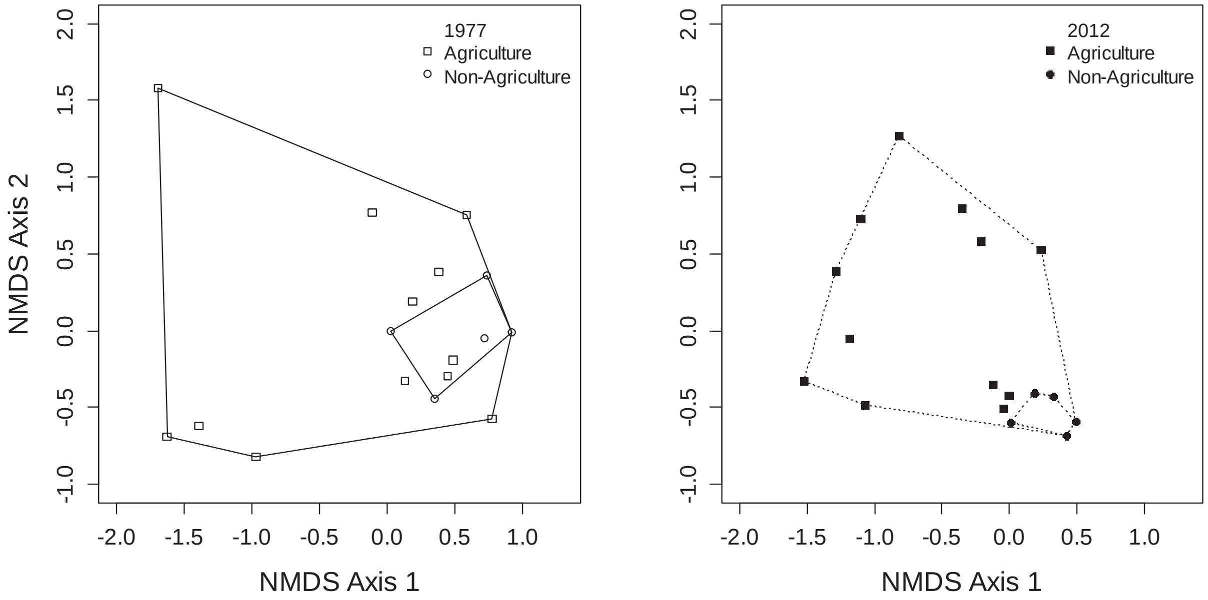

Fig. 6. The location of study sites with relatively little influence from agricultural activities (smaller envelopes) as observed in 2012 in the Katavi and Rukwa regions in Tanzania (Fig. 1). Same sites are shown in 1977 for comparison.

APPENDICES

Appendix 1. Table A1. Environmental variables included in the analyses

Category	Variable	Type	Range of mean values at sites
Fire	Historical fires	Numeric	6 – 18 years
	Recent fire signs on trees	Numeric	0 – 384 trees
	Recent fire signs on the ground	Factor: 4 levels	G, GAR, FA, N
Land use	Extent of agricultural area	Numeric	0 – 65.8 %
	Change in the location of agricultural areas	Numeric	0 – 9.6 km
	Cultivation	Factor: 3 levels	F, AF, N
	Human population density	Numeric	1 – 150
	Number of stumps	Numeric	0 – 60
	Stumps’ condition	Factor: 4 levels	DS, FS, DFS, N
	Domestic animals	Presence / Absence	Presence, Absence
	Wild animals	Presence / Absence	Presence, Absence
Abiotic	Average monthly temperature	Numeric	19.0 – 26.1 ^{o}C
	Total annual rainfall	Numeric	924.1 – 1123.4 mm
	Elevation	Numeric	864.1 – 2122.9 m
	Slope	Numeric	2.1 – 6.1 degrees
	Latitude	Numeric	5.9 – 8.8 degrees

G = unidentified ground fire scars; GAR = ground fire scars associated with agriculture; FA = fresh ash; F = recently cleared farm, AF = abandoned farm; DS = decaying stump; FS = fresh stump; DFS = decaying and fresh stumps; N = none.

Appendix 2: Local contributions to beta diversity (LCBD) for each sampling period.

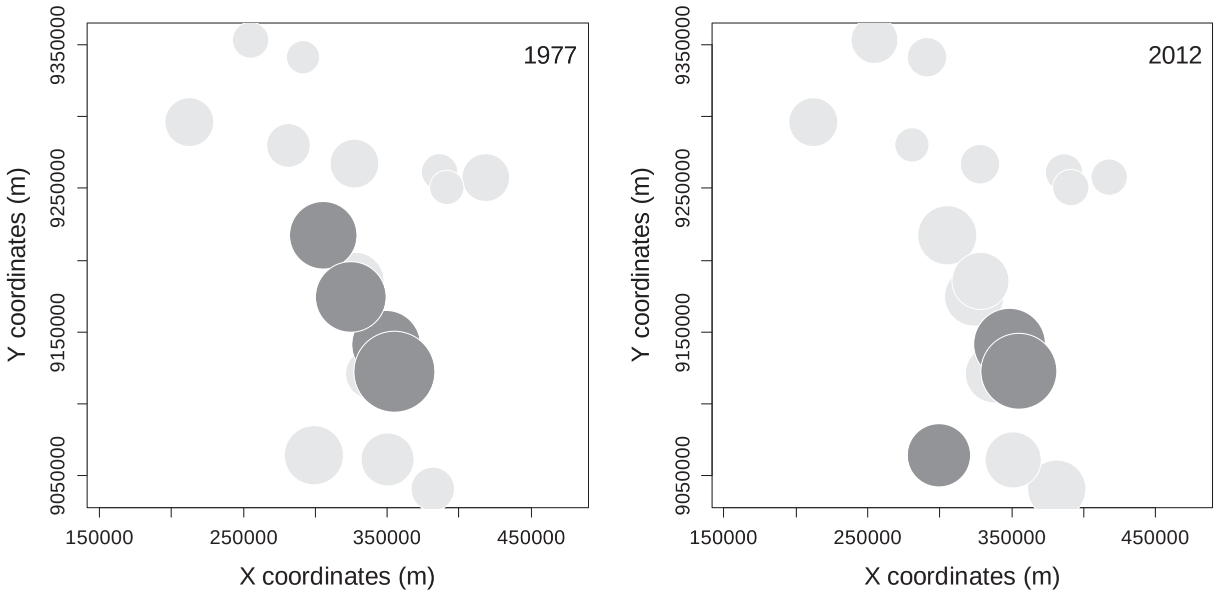

Fig. A2: The contribution of each site (the LCBD) to the observed among-sites differences in species composition in each sampling period. The size of the circles represent the magnitude of the compositional difference for each site relative to the site with mean species composition. Darker circles represents sites with a significant compositional difference relative to other sites.

Appendix 3: Changes in total abundance and degree of variability of individual species observed in both sampling periods and in the total abundance of species with known response to fire at each site.

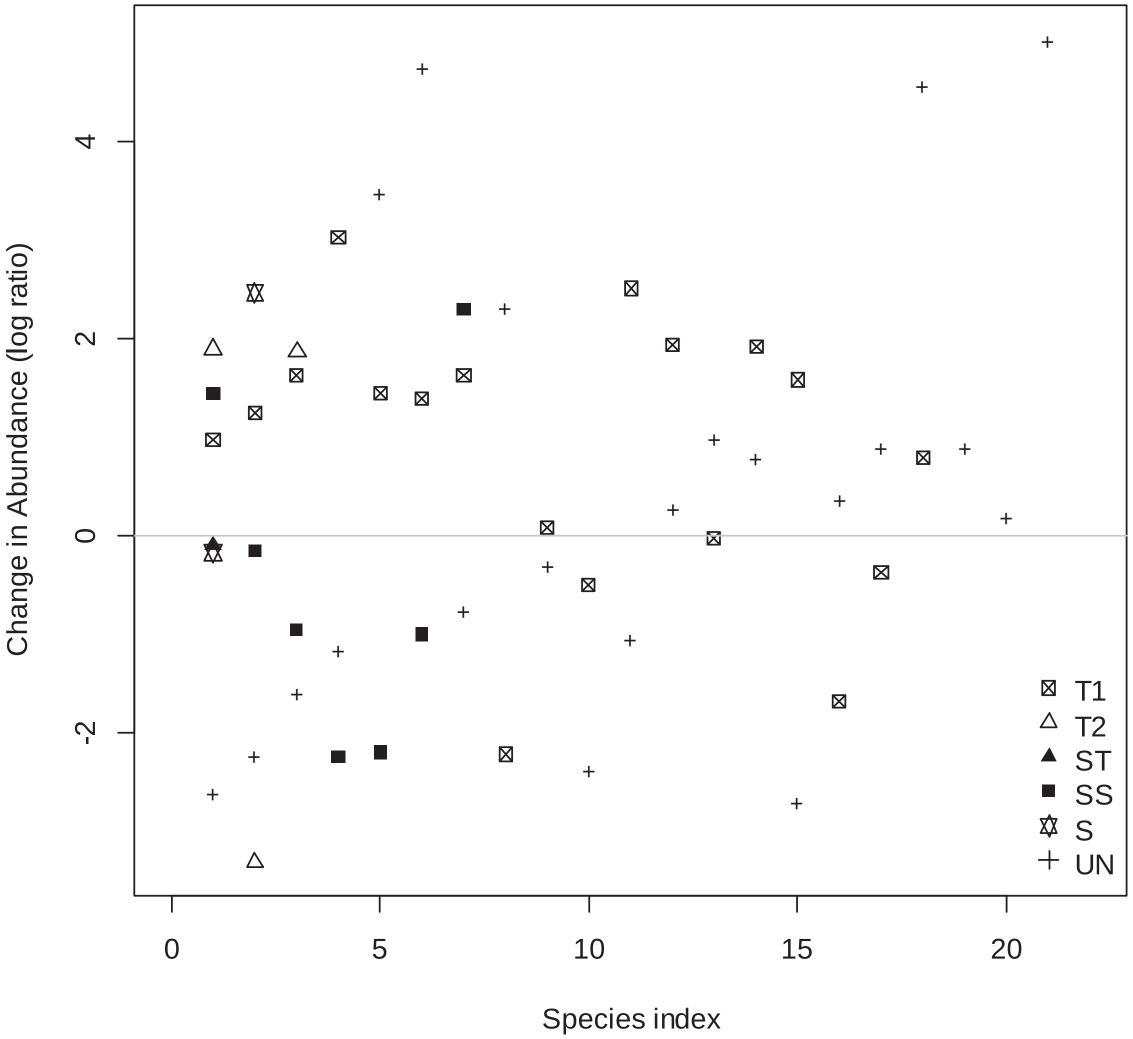

Fig. A3a: Change in total abundance of species encountered in both sampling periods. Abundance in measured as the total basal density of a species during a sampling period. Change is defined as the log ratio (log2012/log1977) of the abundances, thus positive values indicate an increase while negative values indicate a decrease in abundance of each species. T1 = Species tolerant to fire but intolerant to shade; T2 = Species tolerant to fire and shade; ST = Species semi-tolerant to fire; SS = Species semi-sensitive, they require protection from fire at juvenile growth stage; S = Fire sensitive species; UN = Species with unknown response to fire.

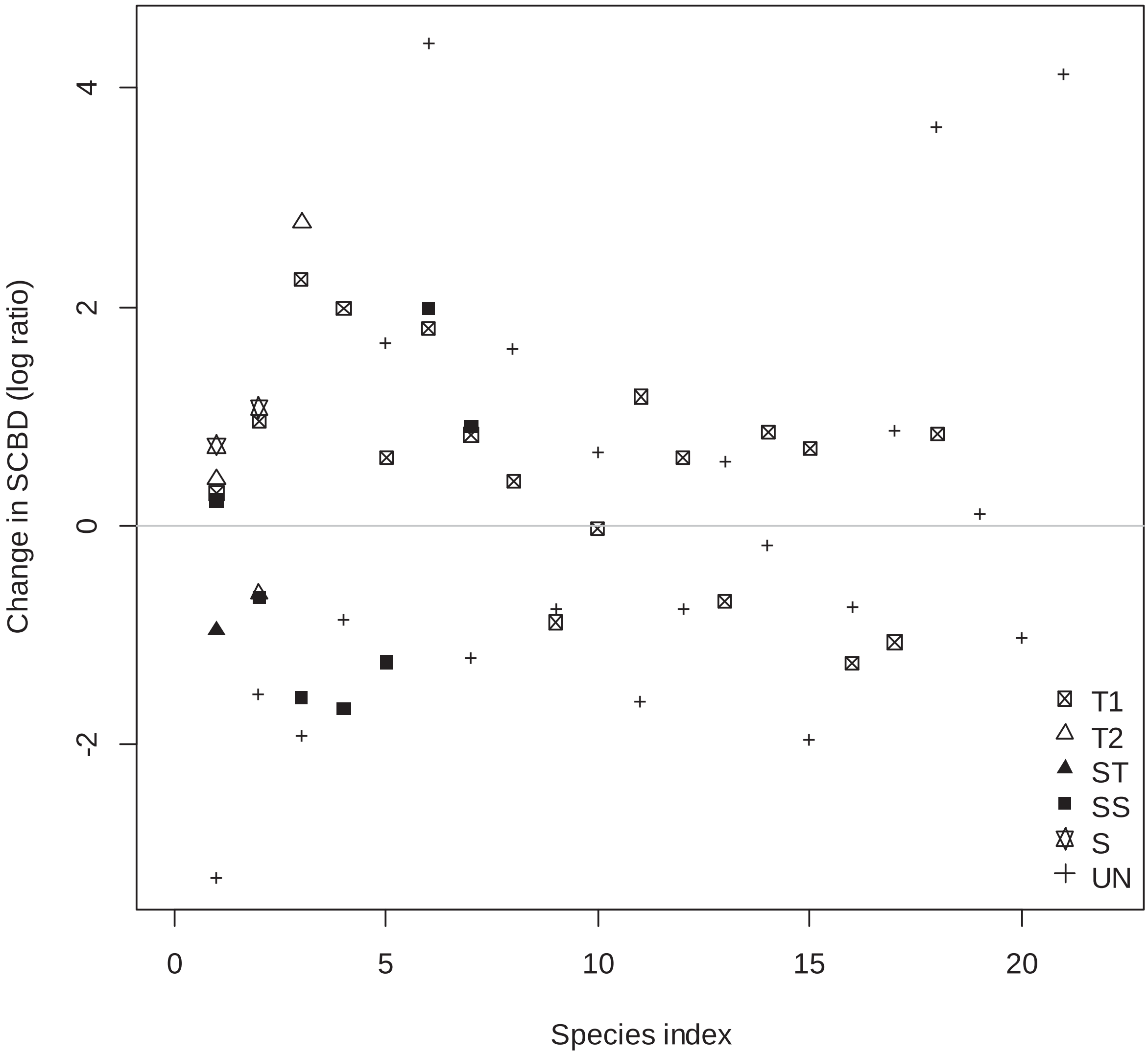

Fig. A3b: Change in the degree of variability (the SCBDs) of species encountered in both sampling periods. Change is defined as the log ratio (log2012/log1977) of the SCBDs, thus positive values indicate an increase while negative values indicate a decrease in degree of variability of each species. T1 = Species tolerant to fire but intolerant to shade; T2 = Species tolerant to fire and shade; ST = Species semi-tolerant to fire; SS = Species semi-sensitive, they require protection from fire at juvenile growth stage; S = Fire sensitive species; UN = Species with unknown response to fire.

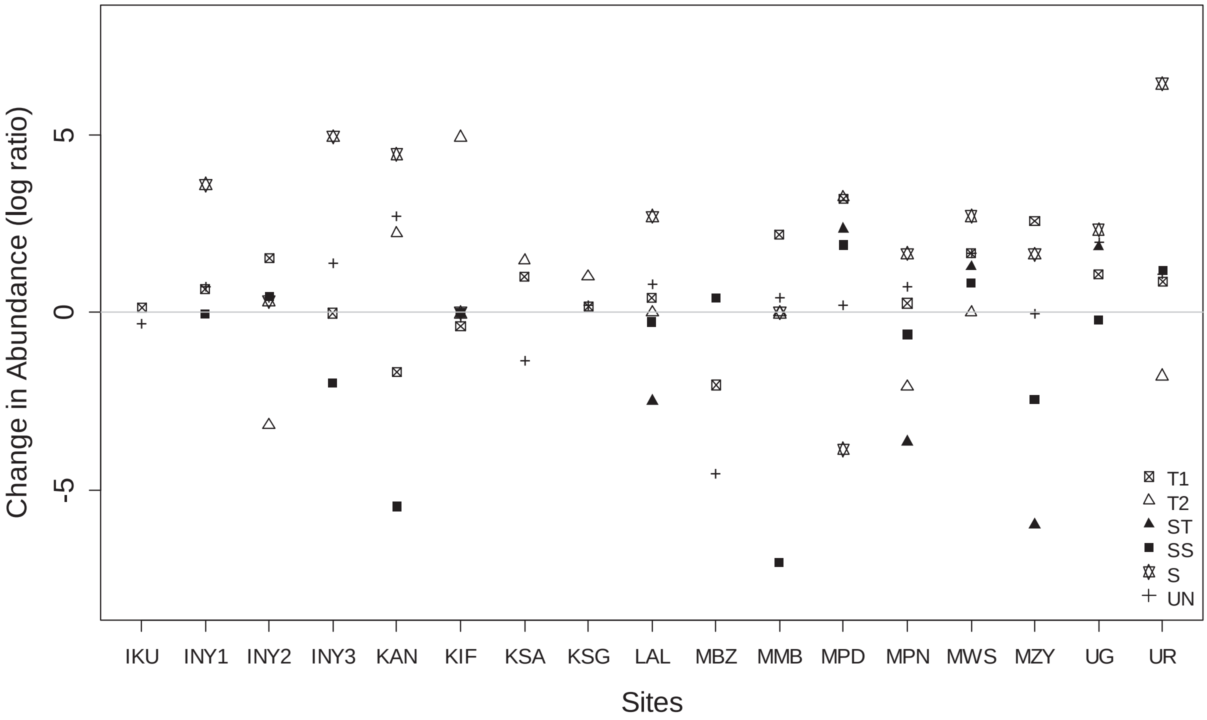

Fig. A3c: Change in total abundance of species with known response to fire at each site. Abundance in measured as the total basal density of a species during a sampling period. Change is defined as the log ratio (log2012/log1977) of the abundances, thus positive values indicate an increase while negative values indicate a decrease in abundance of each species. T1 = Species tolerant to fire but intolerant to shade; T2 = Species tolerant to fire and shade; ST = Species semi-tolerant to fire; SS = Species semi-sensitive, they require protection from fire at juvenile growth stage; S = Fire sensitive species; UN = Species with unknown response to fire. Site names are IKU=Iku-Katuma; INY1-3=Inyonga1-3; KAN=Kankwale; KIF=Kifinga; KSA=Kasansa; KSG=Kasanga; LAL=Laela; MBZ=Mbizi; MMB=Mamba; MPD=Mpandule; MPN=Mpanda; MWS=Mwese; MZY=Mwazye; UG=Ugalla; UR=Uruwira.

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