

BACKGROUND: THE ECOLOGY, BIODIVERSITY, STRUCTURE, AND FUNCTION OF SOUTHERN AFRICAN WOODLANDS

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Introduction

Tropical savannas are expected to experience significant shifts in vegetation structure and biodiversity in the coming century, due primarily to human induced climate change, land use change, and atmospheric carbon concentration (Ross et al., 2021; Scheiter & Higgins, 2009; Moncrieff et al., 2016). Yet we lack a detailed understanding of how biodiversity and vegetation structure vary and affect ecosystem function (i.e. processes controlling fluxes of energy and matter through ecosystem across this highly heterogeneous biome, resulting in large uncertainty in earth system flux estimates across this biome (Ahlstrom et al., 2015)). This thesis examines the role of tree species diversity as a driver of ecosystem function, with a focus on woody biomass and productivity as measures of ecosystem function, in southern African savannas. Biodiversity - Ecosystem Function (BEF) theory predicts positive effects of biodiversity on productivity (Tilman et al., 2014), but it is unclear whether this effect should occur in disturbance-prone and environmentally stressful ecosystems (Steudel et al., 2012; Baert et al., 2018). This chapter provides background on the ecology and biodiversity of tropical savannas and more specifically southern African woodlands, then summarises current literature on biodiversity-ecosystem function theory, to understand in greater depth the rationale for this thesis.

The ecology of savannas

Savannas occupy ~20% of the global land surface (Scholes & Walker, 1993). They are the dominant land cover in the seasonal tropics, covering ~40% of the tropical land surface (Scholes & Archer, 1997) (Figure 1). While debate continues around use of the term ‘savanna’ (Lehmann et al., 2011; Ratnam et al., 2011), the generic definition used in this thesis characterises a savanna by the co-dominance of grass and trees, with a near contiguous grass-dominated understorey, and a closed or discontinuous, but sparse, woody overstorey (Scholes & Archer, 1997; Bond, 2008). Within this broad definition, savannas are highly heterogeneous, across local to continental scales (Bucini & Hanan, 2007), with wide variation in canopy cover (Sankaran et al., 2005; Hirota et al., 2011), the functional and floristic composition of the woody overstorey (Fayolle et al., 2018; Solbrig et al., 1996), and the composition of the herbaceous understorey (Siebert & Dreber, 2019; Van Coller et al., 2018).

Historically, tropical savannas were often mis-represented as severely degraded forests (Veldman, 2016). This view has roots in the nineteenth century idea of Clementsian succession and potential vegetation (Pulsford et al., 2014), which focussed on hierarchical physiognomic vegetation classifications with closed canopy forest at the top, rather than floristic or functional classifications that are in greater use at present (Aleman et al., 2020). The misinterpretation was exacerbated by the vast majority of early studies of savanna ecosystems originating from regions which lacked savanna vegetation. The hangover of this outdated paradigm is still felt today, with tropical savannas receiving less conservation funding (Watson et al., 2016), experiencing the greatest rates of transformation to agriculture of any major biome (Hoekstra et al., 2004; Parr et al., 2014), and being the focus of misplaced reforestation projects (Silveira et al., 2020; Kumar et al., 2020; Laestadius et al., 2011). In recent years there has been a push to acknowledge the value of tropical savannas, both intrinsically as centres of biodiversity and endemism (Kumar et al., 2020; Pennington et al., 2018), and as providers of ecosystem services (Ryan et al., 2016). Savannas proliferated globally during the Pliocene (~3-8 Mya), as a result of climate change, C4 grass proliferation, and an increase in the frequency and intensity of fire, with all three of these causes being inter-linked (Cerling et al., 1997; Beerling & Osborne, 2006; Edwards & Smith, 2010). Rather than being viewed as derived landscapes that may be restored to a more forest-like environment, savannas should be considered a unique biome in their own right, with particular vegetation formations (Torello-Raventos et al., 2013), a distinct evolutionary history (Veldman et al., 2015), and unique responses to global environmental change ().

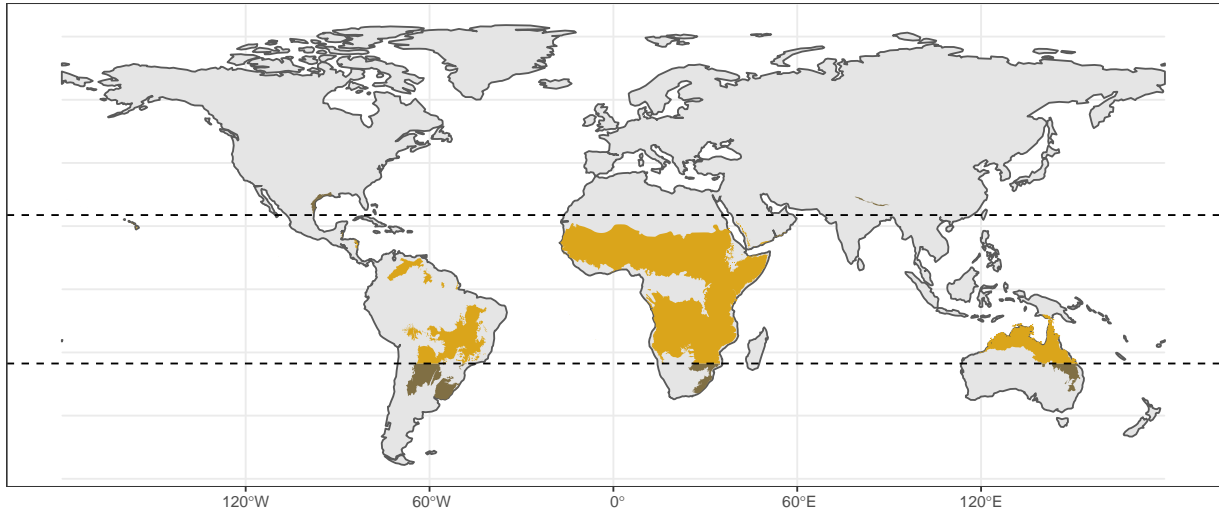


Figure 1: The global distribution of tropical savannas and grasslands (yellow), re-classified from the Terrestrial Ecoregions of the World (Dinerstein et al., 2017). Dashed lines mark the latitudinal extent of the tropics from N23.5° to S23.5°. Brown areas denote extra-tropical vegetation resembling tropical savannas.

Determinants of savanna vegetation

Savanna vegetation may occur as a result of multiple non-exclusive and interacting factors. One of the key questions in savanna ecology concerns identifying the factors driving variation in tree cover and assessing their relative importance in different contexts, thus determining the global distribution of savannas (Higgins et al., 2000; Archibald et al., 2019). Controls on tree cover can be split broadly into ‘disturbance-based’ (e.g. fire, herbivory) or ‘resource-based’ (e.g. precipitation, soil fertility) (Bond, 2008; Staver & Koerner, 2015). Both resource-based and disturbance-based controls on tree cover act simultaneously to varying extents in most savannas, though it is possible to classify savannas into two principal biomes based on their dominant control on tree cover, through their effects on species composition and woodland structure (**Huntley1982**; Torello-Raventos et al., 2013).

Tropical savannas occur in areas of high rainfall seasonality (Lehmann et al., 2011). At the continental scale, available moisture is the most significant determinant of savanna tree cover (Sankaran et al., 2005), setting the upper boundary of tree cover by physiological limitation of tree growth. In wetter mesic savannas, competition between grasses and trees is low, but in arid savannas, grasses may ‘poach’ water from trees by intercepting it closer to the soil surface (Scheiter & Higgins, 2007). While water availability may be the dominant resource-based determinant of savanna vegetation, edaphic properties also affect tree cover across savannas. Tropical savannas are often associated with nutrient-poor soils, especially in higher rainfall areas, where available nutrients are leached from the soil (February et al., 2013). Furthermore soil texture also interacts with rainfall to allow greater woody biomass and less grassy biomass where there is greater drainage (Staver et al., 2011).

While resource availability, particularly moisture sets the upper bounds for tree cover, many savannas exist in areas that are climatically suitable for closed canopy forest (Sankaran et al., 2005; Lehmann et al., 2011; Staver et al., 2011; Murphy & Bowman, 2012). Above $\sim 650 \text{ mm yr}^{-1}$, woody cover in savannas appears to show no dependence on MAP (Figure 2) (Sankaran et al., 2008; Sankaran et al., 2005; Good & Caylor, 2011). In mesic savannas, where climatic conditions are suitable for closed canopy forest, there exists large heterogeneity in woody canopy cover at local spatial scales (Dantas et al., 2015). Mesic savannas often form a complex mosaic of open grassy patches and closed canopy forest-like patches, with their distribution dependent on local edaphic conditions and

historical disturbance patterns (Staver et al., 2011).

The key premise of the “Alternative Stable States” phenomenon is that contrasting ecosystem states may occur under similar environmental conditions, due to strong stabilising positive feedbacks on vegetation structure (Staver et al., 2011). Grass is the main fuel source for fires in mesic savannas. C_4 grasses, which dominate many mesic savannas, particularly in southern Africa (Still et al., 2003), are particularly flammable, but require more light than C_3 grasses, meaning they are highly sensitive to variation in tree canopy cover (Charles-Dominique et al., 2018). In areas with low grassy biomass, fire frequency and intensity are expected to be lower due to a lack of fuel. Simultaneously, juvenile trees are highly sensitive to fire in the grassy understorey layer due to their low stature, meaning that fire increases tree mortality, or ‘top-kill’ of these individuals which must then resprout, keeping individuals small and creating a demographic bottleneck where only a few individuals grow to adults (Bond & Midgley, 1995; Ryan et al., 2011). A positive feedback loop therefore occurs whereby disturbance by fire reduces canopy cover, allowing more frequent and intense fires, further reducing canopy cover as tree growth is suppressed. Alternatively, under reduced fire, trees can escape the ‘fire trap’ in the understorey and grow to canopy trees (Wakeling et al., 2011), which rarely burn due to adaptive traits such as insulating bark and elevated crowns, increasing canopy cover, causing competitive exclusion of grasses (Moustakas et al., 2013), which further reduces disturbance by fire (Figure 3).

Hirota et al. (2011), using remotely sensed measures of tree cover across tropical Africa, South America and Australia, demonstrated a distinctly bi-modal distribution of tree cover within areas of intermediate rainfall (~ 650 - 1500 mm yr^{-1}). Staver et al. (2011) further showed that fire is the main source of this bi-modality. Furthermore, Staver et al. (2017) showed that change in fire return interval, whether the result of management or environmental change, can result in changes in ecosystem structure. Specifically, that longer fire return intervals result in a shift toward a more forest-like ecosystem with greater canopy closure, fewer small trees, and a greater number of large canopy trees.

The factors described above which determine savanna vegetation structure are highly interactive. Moisture availability interacts with fire disturbance, leading, seemingly paradoxically, to a situation where increased resource availability may lead to lower woody biomass above a given threshold resource availability, due to increased grass growth and more intense and frequent fires (Xu et al., 2015). Soil nutrient availability also plays an interactive role with fire, increasing grass recovery rate between fires, which may lead to more frequent fires, increased tree mortality and lower woody biomass (Kellman, 1984). Interactions between environment, disturbance and tree cover, with clear thresholds of resource availability and tipping points of disturbance regime, result in a highly complex model of savanna ecosystem processes.

Adaptations of savanna trees

Savanna trees are subject to a multitude of environmental pressures. To overcome these, savanna trees have a number of adaptations and employ various life history strategies, leading to a high functional diversity within tropical savanna trees (Solbrig et al., 1996), despite their low tree species diversity compared to tropical rainforests (Solbrig et al., 1996), for example.

Seasonal fires are a key determinant of savanna structure in mesic savannas (>650 mm MAP) (Sankaran et al., 2005). Many savanna tree species produce thick corky bark which protects the sapwood from high temperatures during fire (Hoffmann et al., 2012; Lawes et al., 2011; Dantas & Pausas, 2013). Additionally, many savanna trees produce large below-ground root structures that are able to store carbohydrate, allowing individuals to re-sprout following fire (Wigley et al., 2019). There is evidence of adaptation in juveniles of some species that allows them to resprout in the same year following fire, giving them a head-start over competitors which adhere to a more rigid bud production cycle (Wiegand et al., 2006). Natural coppicing of adult savanna trees is common. If one growing tip is damaged due to fire, other stems on the same individual can continue growing, avoiding mortality. Savanna trees also sometimes have insulated buds to prevent fire reaching the

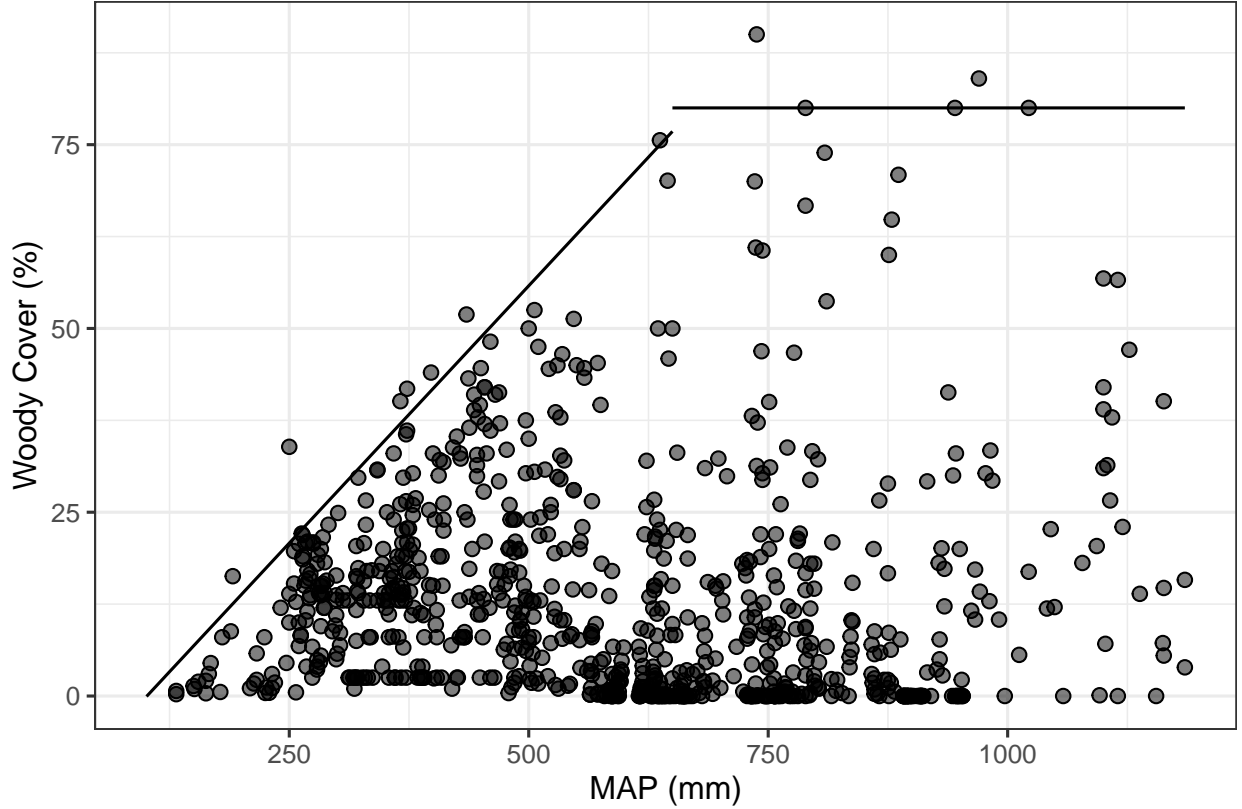


Figure 2: The relationship between rainfall (Mean Annual Precipitation) and proportional tree cover, across 854 savanna sites in Africa, adapted from Sankaran et al. (2005). The line of best fit uses a broken-stick 99th quantile piece-wise linear regression to identify the breakpoint at which rainfall no longer sets the upper limit for tree cover. Above the breakpoint (650 ± 134 mm MAP) other processes such as disturbance by fire and local edaphic limitations are thought to determine tree cover.

sensitive growing tip (Charles-Dominique et al., 2015).

Previously, root niche separation between grasses and trees was thought to be the main method by which trees and grasses coexist in savannas (Walter, 1971). Trees were observed to have deep tap roots while grasses have a greater density of fine near-surface roots (Timberlake et al., 1993). In arid savannas, root niche separation is an important mechanism allowing tree-grass coexistence, with consequences for the timing of seasonal growth in relation to seasonal rainfall intensity. In mesic savannas however, this effect is largely absent, except under specific edaphic conditions (Case et al., 2020; Ketter & Holdo, 2018; Sankaran et al., 2004; Higgins et al., 2000). Recent work has shown that many savanna trees in mesic savannas produce two types of roots, the first are deep tap roots which are used primarily for water uptake and for storing carbohydrates as ligno-tubers to facilitate pre-rain green-up and resprouting following fire. The second are a mesh of finer roots which occur near to the surface and compete directly with grasses. These roots are used primarily for nutrient uptake, as most savanna soils have a distinct vertical nutrient profile (Tomlinson et al., 2012; February et al., 2013). As an additional adaptation to overcome nutrient poor soils, many savanna trees readily produce root nodules with mutualistic *Rhizobia* bacteria capable of fixing atmospheric nitrogen, or have ecto-mycorrhizal associations which improve phosphorus uptake (Hogberg, 1986).

Fire removes much of the grass layer in a savanna, meaning that this is an ideal time for tree seedlings to germinate, as the lack of grass fuel means another fire is unlikely for some time, and the lack of grass cover means less competition for the growing seedling. Many tree species have adapted to having fire-activated seed dispersal (Veldman et al., 2015), with large seeds for long seed residence times, and rapid growth of newly emerged seedlings (Daibes et al., 2019), so that the seedlings can

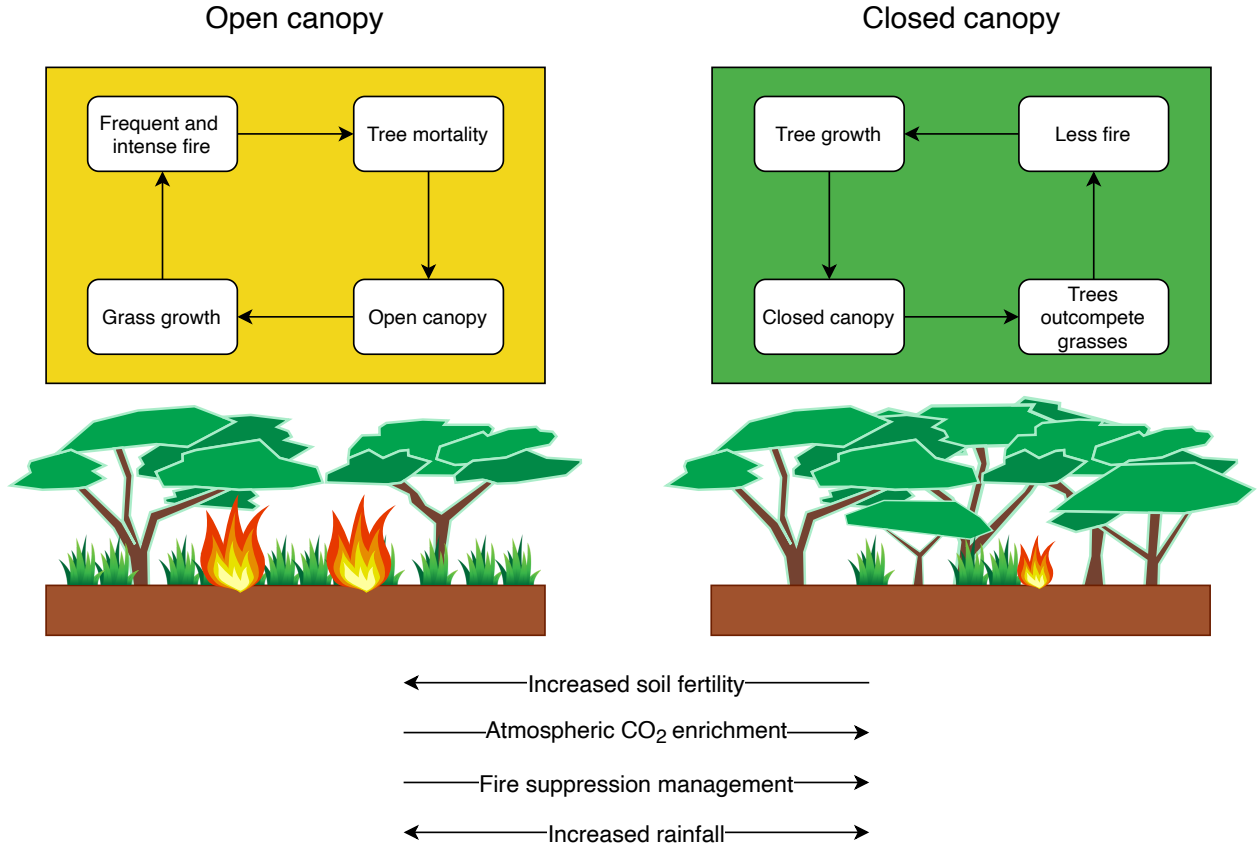


Figure 3: The positive feedback mechanisms which determine the alternative stable states of mesic tropical savannas. Left: increased fire increases tree mortality, which decreases canopy cover, increasing available light for grass growth, leading to more fire and a further reduction in canopy cover. Right: decreased fire decreases tree mortality, which increases canopy cover, reducing available light to the grassy understorey, causing a reduction in grass fuel load, fewer fires and a further increase in canopy cover. Bottom: stabilising feedback loops can be disrupted given a large enough perturbation, causing a switch to another stable state. Some of these perturbations have different outcomes depending on the principal limitation of woody cover. In arid savannas, increased rainfall leads to an increase in woody cover, as more water percolates to deeper tree tap roots, while in a mesic savanna where water is not limiting, increased rainfall may lead to an increase in grass growth and therefore an increase in fire, which reduces woody cover.

grow enough to escape the “fire-trap” before the grass fuel load has increased sufficiently to allow another fire. Wakeling et al. (2015) found that in densely grassy areas, a lack of gaps may prevent the germination of tree seeds, with long seed residence times allowing trees to take advantage of stochastic fire events that open up gaps for rooting. As an alternative to producing seed, many savanna trees reproduce predominantly via clonal growth. Clonal suckers remain connected to the natal tree, allowing rapid growth, as they benefit from the resources of the established carbohydrate-storing root structures (Bond & Midgley, 2003).

Tropical savannas experience highly seasonal patterns of rainfall. Many savanna trees are deciduous, losing their leaves during the dry season to limit transpiration and conserve water (Dahlin et al., 2016). The phenomenon of ‘pre-rain green-up’ has been observed widely across tropical savanna trees (Archibald & Scholes, 2007; Borchert, 1994; Williams et al., 1997), whereby trees produce foliage material in advance of the rainy season. Multiple mechanisms have been suggested to explain pre-rain green-up as an adaptive trait, such as: to avoid competition for light and water (Ryan et al., 2017), to avoid herbivory (Aide, 1988), and to maximise the length of the growing season (Scholes & Walker, 1993).

The many adaptations of savanna trees to disturbance and resource availability represent axes of

functional variation which could lead to a greater contribution to ecosystem function under higher biodiversity. Specifically, greater resilience to disturbances and higher productivity maintained under seasonal variation in climate (Díaz & Cabido, 2001; Mori et al., 2012).

The global carbon cycle and change in savannas

Tropical savannas contribute ~30% of global terrestrial Net Primary Productivity (NPP), i.e. atmospheric carbon fixed into biomass (Grace et al., 2006). Due to their large spatial extent, even a small percentage change in woody cover in savannas is expected to have large effects on the global carbon sink (Williams et al., 2005). Globally, savanna ecosystems are being degraded and lost to agricultural expansion, mining, and urban growth (Parr et al., 2014). Ross et al. (2021) predict biomass loss over most tropical savannas over the coming century, mostly due to land use change. Similarly, Aleman et al. (2016) concluded that land use change in sub-Saharan African savannas will have a greater negative effect on tree cover than changes in annual rainfall and rainfall seasonality. By 2100, the human population of sub-Saharan Africa is expected to double, increasing pressure on savanna ecosystems (Pison, 2017). Despite this, tropical savannas are reportedly the fastest increasing component of the terrestrial carbon sink (Sitch et al., 2015).

By 2050, it is expected that atmospheric CO₂ will have risen high enough that C₄ grasses no longer have a growth advantage over C₃ plants (Bond & Midgley, 2012). An increase in atmospheric CO₂ is expected to lead to faster tree growth rates, allowing saplings to more quickly escape the “fire-trap”, resulting in lower mortality, and a shift towards a closed canopy forest-like environment. Additionally, in arid savannas, the negative effect of CO₂ enrichment on grass transpiration rates (Murphy & Bowman, 2012) is expected to lead to less vigorous root growth and therefore more percolation of water to the deeper tree roots, increasing tree growth.

Various studies, across the country of South Africa (Stevens et al., 2016b), the neotropics (Rosan et al., 2019), and globally (Stevens et al., 2016a), have reported woody encroachment of trees into previously grassland or shrubland areas. However, due to the complex interactive nature of the determinants of savanna carbon cycling, it is still unclear whether these predicted effects of atmospheric CO₂ enrichment will materialise. Lewis et al. (2009) suggested that although existing woodlands are thickening, this does not necessarily extend to encroachment into previously unforested areas, due to the strong stabilising influence of fire. Pelletier et al. (2018) concluded that while more arid savannas will likely experience woody encroachment due primarily to the effects of CO₂ enrichment on transpiration and tree-grass water relations, there is no evidence that the same will happen in non-water limited savannas such as the miombo woodlands of southern Africa. Similarly, (Reich et al., 2014) demonstrated that earth system models may be overly sensitive to the effects of CO₂ enrichment, and that the models suffer from a lack of mechanistic understanding of the effect of resource availability on disturbance. Körner (2017) suggested that CO₂ enrichment may serve only to increase biomass turnover through increased growth offset by fire, with 44% of all carbon emissions in savanna coming from fire (Werf et al., 2010), and 62% of fire carbon emissions coming from savanna (Werf et al., 2017), offsetting the extra carbon sequestered.

Tropical savannas remain the largest source of uncertainty in models of the terrestrial carbon cycle (Ahlstrom et al., 2015). Environmental and land use change is expected to cause drastic changes to the functioning of savanna ecosystems in the coming century. Clearly, there is much work needed to better understand the interactive mechanisms which determine the role of tropical savannas in the global carbon cycle, and how these relations vary across environmental and biogeographic gradients. The wide functional diversity of savanna trees means that ecosystem level responses to global change will be complex, as adaptive traits determine varied individual responses, resulting likely in shifts in carbon storage and turnover of species in response to changes in rainfall, temperature, fire regime, and atmospheric carbon.

Southern African woodlands

This thesis focusses specifically on the mesic savannas of southern Africa, the savanna formations occurring in a latitudinal band south of the Congo basin rainforest, and north of the arid savannas of the country of South Africa (Figure 4). These savannas cover approximately 2.7 million km² (Arino et al., 2010). Hereafter they are referred to as southern African woodlands.

The structure of southern African woodlands is driven primarily by disturbance from fire and herbivory, leading to a highly heterogeneous patchy woodland habitat (Archibald et al., 2019). Fire return interval varies locally, dependent on climate and existing vegetation which determines grass fuel load (Archibald et al., 2010). Large herbivores play an important role in determining the vegetation structure of southern African woodlands. Compared to climatically similar savannas in the neotropics or southeast Asia, large herbivores are common in savannas throughout southern Africa (Asner et al., 2009). It has been suggested that large herbivores may cause disturbance in a manner similar to fires, reducing woody biomass by increasing mortality of juvenile saplings (Bond & Keeley, 2005), though the effects of herbivory are often much more localised than fire, and the spatial distribution of herbivory cannot be predicted with the same detail (Hempson et al., 2015). While the dominant pressure determining the coexistence of grass and trees in savannas globally is moisture availability, within southern African woodlands where rainfall is rarely a limiting factor, competition for light is more important (Vadigi & Ward, 2013). Depending on the disturbance regime, southern African woodlands occasionally form dense closed canopies, while C₄ grasses are highly sensitive to shade. Feedbacks between tree cover and grass growth determine the fire regime and lead to highly heterogeneous woodland structure.

Southern African woodlands support a growing human population, with >150 million people benefitting from ecosystem services provided (Ryan et al., 2016; Wunder et al., 2014). Vast areas of woodland in southern Africa are used for grazing cattle which requires relatively open woodland (Njana et al., 2013), while other areas are used for charcoal production, bushmeat hunting, fruit, vegetable and mushroom foraging, and timber production (Ryan et al., 2016). Wood extraction by humans is increasing in southern Africa (Hansen et al., 2013), with more than 90% of harvested wood used for energy production, mostly as charcoal in a domestic setting (May-Tobin, 2011). Other important ecosystem services provided by these woodlands to the human population include regulation of water availability throughout the dry season (Wilk et al., 2010; Hecky et al., 2003) and the provision of medicinal plants (Ryan et al., 2016; Augustino et al., 2011). Simultaneously, southern African woodlands are inhabited by a high number of charismatic endemic species (Burgess et al., 2004) and are increasingly a destination for international tourists (Vergles et al., 2015; Shackleton et al., 2007). These attributes together make southern African woodlands a hugely important natural asset, both locally and globally.

Southern African mesic savannas can be divided roughly into three dominant vegetation types. Miombo woodlands dominate southern Africa, and are the largest savanna vegetation type in the world (Ryan et al., 2011). They are dominated by species from the Fabaceae family, subfamily Detarioideae, from the genera: *Brachystegia*, *Julbernardia*, and *Isoberlinia*, with the namesake ‘miombo’ coming from the local name for the genus *Brachystegia* in various Bantu languages. These woodlands frequently have tall continuous tree canopies that occasionally close to the point of excluding grasses, and are therefore frequently classified as forest by some forest cover maps (Hansen et al., 2013). Rainfall in miombo woodlands varies between 540-1700 mm yr⁻¹, with a highly seasonal pattern of precipitation. Miombo woodlands are highly diverse, with >8500 vascular plant species, of which >300 are tree species, many of which are endemic to the region (Frost, 1996).

Mopane woodlands form thin bands in the south of Zambia, Zimbabwe, central and southern Mozambique, and also across the border region of Angola and Namibia (Figure 4). They are characterised by the dominance of a single tree species, *Colophospermum mopane*, and generally occur in areas of lower rainfall than miombo woodlands (Palgrave, 2003). Reduced rainfall means that mopane soils are generally more fertile than the surrounding miombo woodlands (Makhado et al., 2014). Mopane woodlands are host to the largest diversity of large mammals in southern Africa, including

populations of charismatic and highly threatened species such as the black rhinoceros (*Diceros bicornis*) and giraffe (*Giraffa camelopardalis*) (Mittermeier et al., 2003). While much of the mopane woodlands exists as short-stature shrubby vegetation, larger ‘cathedral mopane’ exists in some areas, forming a near closed canopy (Makhado et al., 2014).

Baikiaea woodlands occur on sandy soils, in a wide belt along the Angolan-Namibian border to Zimbabwe. They are dominated by *Baikiaea plurijuga*, which grow to large trees at low densities, with a grass and shrub understorey that burns regularly (Werger & Coetzee, 1978). Like *C. mopane*, *B. plurijuga* is also in the Detarioideae subfamily. Baikiaea woodlands are generally less suitable for agriculture than miombo woodlands, with highly sandy soil and low rainfall, though logging pressures have removed many of the largest and oldest trees in some regions (). Like mopane woodlands, Baikiaea woodlands provide habitat for many large herbivores ().

Although this thesis focusses primarily on the mesic savanna types described above, other savannas not dominated by large Detarioideae species also exist in southern Africa. Combretaceae woodlands are dominated by trees from the *Combretum* and *Terminalia*, both arbuscular mycorrhizal genera. Combretaceae woodlands are found in slightly drier but still dystrophic environmental conditions to miombo woodlands, but differ in their woodland structure, lacking large canopy tree species (). Finally, Mimosoideae woodlands occur in drier eutrophic areas, often with higher levels of herbivory from large mammals than other woodlands in the region. Mimosoideae genera such as *Acacia* often display ‘cagey’ and thorny canopy architecture to protect from browsing mammals (Maurin2014).

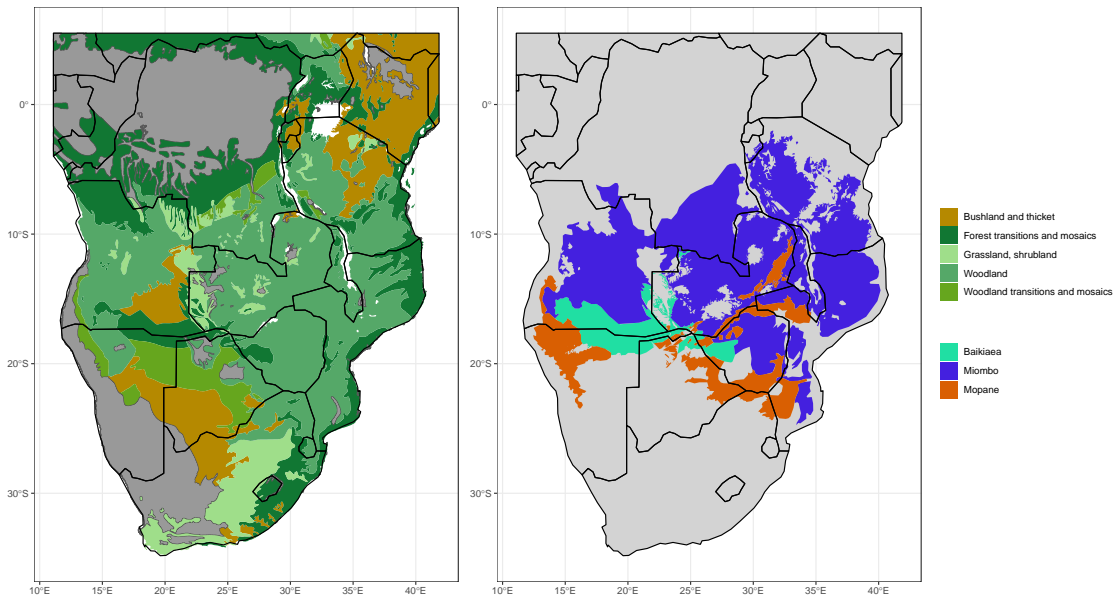


Figure 4: The distribution of key savanna vegetation types within southern Africa. Left: physiognomic classification adapted from White (1983). Right: floristic classification of selected savanna-woodlands adapted from Dinerstein et al. (2017), Terrestrial Ecoregions of the World.

Biodiversity and ecosystem function theory

In 1992, the Earth Summit in Rio de Janeiro discussed the growing concern that global patterns of biodiversity loss might negatively impact the functioning of ecosystems, and importantly damage the ecosystem services provided to humans. Later, researchers gathered in Bayreuth, Germany to discuss the role of biodiversity (B) on ecosystem function (EF) (Schulze & Mooney, 1993). Since then, a thriving field of research has emerged which aims to assess and explain the multiple and complex relationships between biodiversity and ecosystem function (Figure 5), with hundreds of studies exploring biodiversity effects in both experimental and natural systems (Plas, 2019; Newbold

et al., 2016; Tilman et al., 2014). The 1992 Earth Summit defined a paradigm shift in ecological thinking. Previously, biodiversity had mainly been considered a passive result of environmental conditions and ecosystem function, while the research that came after redefined biodiversity as both a driver and result of ecosystem function. BEF theory provides intuitive reasoning as to why increased biodiversity should lead to increased ecosystem function.

BEF theory and supporting empirical evidence has informed global environmental policy by encouraging biodiversity conservation as a means of maintaining ecosystem functionality and its associated ecosystem services such as carbon storage, food provision, soil moisture retention etc. (Balvanera et al., 2014; Naeem et al., 2012). Increasingly, biodiversity conservation is being encouraged as a method of maximising natural capital (perceived value of natural assets, Kareiva et al. 2011) indirectly by maximising ecosystem functionality (Scherer-Lorenzen, 2014; Cardinale et al., 2012). Many conservation policy makers are seeking win-win conservation strategies which will maximise both biodiversity and ecosystem service provision (Howe et al., 2014; Adams, 2004). Research into the role of biodiversity in maintaining ecosystem functionality has become more pertinent in the last 20 years in response to mounting evidence of startling global biodiversity losses (McRae et al., 2017; Butchart et al., 2010; Vitousek et al., 1997). There is trepidation however, that as ecosystems are transformed as a result of conservation meant to maximise ecosystem function, or rather a subset of ecosystem functions that are easily measured and have been identified as valuable, such as carbon sequestration (Duffy et al., 2017), other ecosystem functions and services may suffer and the ecosystem may lose unique characteristics (Brockerhoff et al., 2017; Srivastava & Vellend, 2005).

This thesis aims to understand variation in ecosystem function and community structure in southern African woodlands through the lens of the “Biodiversity - Ecosystem Function Relationship” (BEFR). Ecosystem functions can be defined in broad terms as the rate processes which control the fluxes of energy and matter through an ecosystem (Jax, 2005). This includes basic processes of primary production such as gross primary productivity and atmospheric nitrogen fixation, but can be extended to indirect aggregate measures of function such as resilience of productivity to disturbance. Additionally, ecosystem function can be further extended to ecosystem properties such as forest canopy complexity and trophic complexity, which in turn influence ecosystem processes. In this thesis, I focus only on biomass and productivity of trees as measures of ecosystem function, with the aim of improving our understanding of the carbon dynamics of southern African woodlands.

Niche complementarity, selection effects, and facilitation

There are various mechanisms underlying the observed effect of biodiversity on ecosystem function. Early experiments in artificial grasslands (Tilman & Downing, 1994) and experimental microcosms (Naeem et al., 1994), which involved introducing or removing species from random assemblages concluded that selection effects were the strongest drivers of the BEFR. Assuming random introduction or extinction of species, it is more likely that a diverse community will contain a species which contributes to a given ecosystem function (Huston, 1997). Of course, in natural systems, species introduction and removal is rarely random and may be confounded by a species’ contribution to ecosystem functionality (Smith & Knapp, 2003). Related to selection effects, which place emphasis on the presence of species which contribute to function, Grime (1998) proposed the Mass-Ratio Hypothesis to explain biodiversity effects on ecosystem function. The Mass-Ratio Hypothesis suggests that it is not the breadth of niche space filled by a species assemblage that determines ecosystem functionality, but the ability of the most abundant species to optimise a chosen ecosystem function. Subsequent experimental studies have attempted to partition selection effects from other effects, or to remove selection effects entirely through experimental design, in an attempt to isolate other effects (Loreau, 2001).

The mechanism of niche complementarity has been the main focus of the majority of previous BEFR studies (Wright et al., 2017) (Figure 6). The theory of niche complementarity follows intuitively from early evolutionary theory, that coexisting species must occupy different environmental niches, in order to prevent competitive exclusion of the weaker competitor (Tobner et al., 2016; Levine

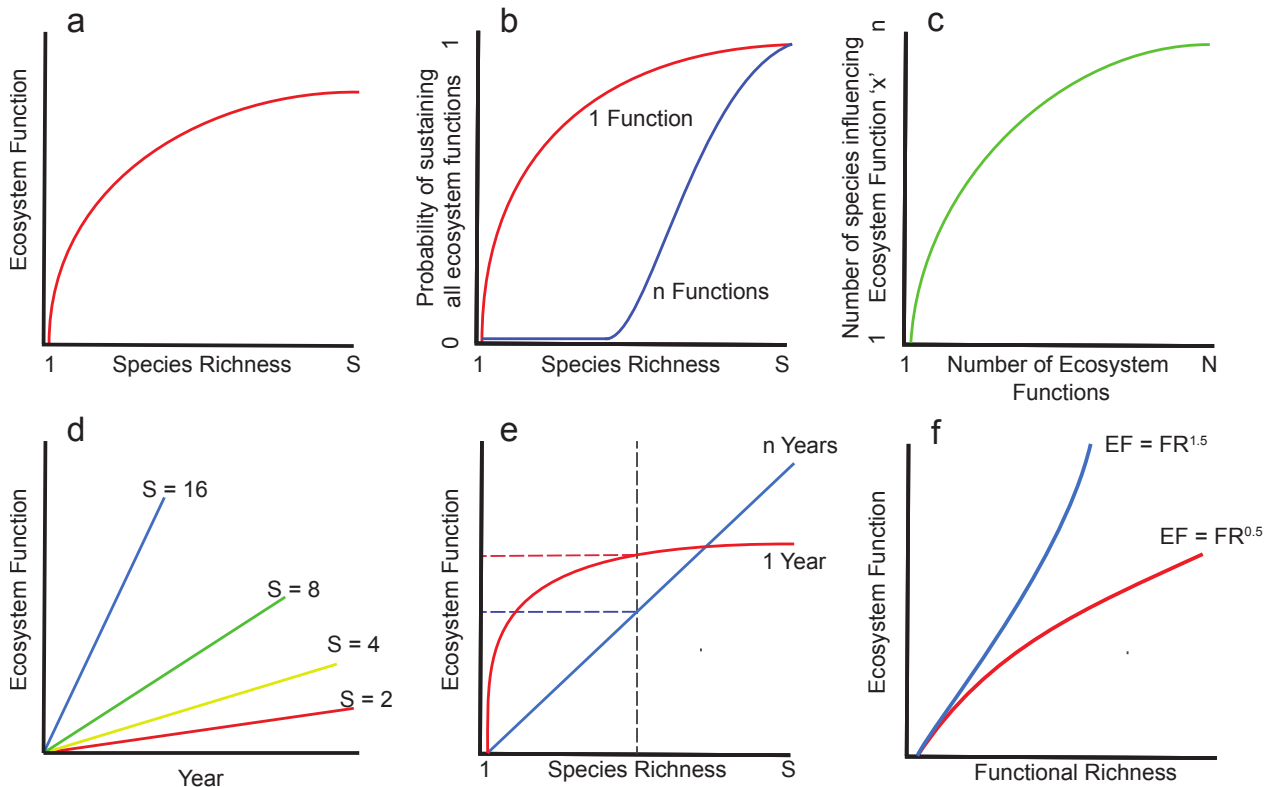


Figure 5: Schematic diagrams illustrating various inferences made on the Biodiversity - Ecosystem Function Relationship by previous studies. a) The classic BEF relationship found by many small scale experiments (Cardinale et al., 2009). b) As more functions are considered simultaneously the minimum species richness needed to maintain overall ecosystem functionality increases, also showing how the proportion of functionally redundant species increases as less functions are considered (i.e. the curve reaches asymptote at a lower species richness) (Hector & Bagchi, 2007). c) The saturating relationship of the number of ecosystem functions considered and the number of species influencing ecosystem multifunctionality (Hector & Bagchi, 2007). d) As studies progress through time the strength of the BEF relationship increases, the rate of increase in ecosystem function increases as species richness (S) grows (Cardinale et al., 2007). e) As studies progress through time the shape of the relationship becomes more linear, saturating at progressively higher species richnesses. Studies averaged over longer periods exhibit a greater loss in ecosystem function in response to an equivalent species richness reduction (Reich et al., 2012). f) When functional richness is used in place of species richness, the relationship reaches asymptote at a higher richness. Additionally the relationship becomes more concave as a power coefficient representing the strength and number of species interactions increases. $FR^{>1}$ (interspecific competition > intraspecific competition (unstable)) results in a convex relationship, while $FR^{<1}$ results in a concave relationship (Mora et al., 2014).

& HilleRisLambers, 2009; MacArthur, 1955; MacArthur & Levins, 1967). Thus, the more species present in a given system, the more environmental niche space is filled, leading to more efficient and complete use of resources, a reduction in density dependent intra-specific competition and ‘higher’ observed values for various ecosystem functions (Isbell et al., 2013). The mechanism of niche complementarity has been corroborated by many studies, but to varying extents depending on biome, whether the study was conducted in an experimental or natural system, duration of study, and what measures of biodiversity and ecosystem function are used (Wright et al., 2017; Cardinale et al., 2009; Cardinale et al., 2011). Niche complementarity can also mediate functionality over time, as different species are able to optimise function at different times under varying environmental conditions; this effect is known as the biodiversity insurance hypothesis (Morin et al., 2014; Bartomeus et al., 2013; Yachi & Loreau, 1999). The insurance hypothesis also postulates that higher biodiversity at the landscape level will increase the rate at which ecosystems recover from

stochastic local disturbances, by providing refugia populations in less perturbed areas (Gonzalez et al., 2009).

Facilitation effects increase the functional contribution of certain species in combination. For example, if grass species A is sensitive to high temperatures, tree species B may provide shade and thus reduce the temperature of the understorey, increasing the productivity of grass species A compared to if it was found in monoculture. Originally this specific example of facilitation was termed “nurse plant syndrome” (Padilla & Pugnaire, 2006). This effect has been studied extensively in dryland ecosystems, where adult trees act as nurse plants for juveniles below, providing shade and reducing mortality. Callaway & Walker (1997), Good et al. (2014) and Weltzin & McPherson (1999) theorised a predictable relationship between environmental stress and the nature of interactions among plants, hypothesising that facilitation effects override competitive effects in highly stressful environments. More recently, Lortie et al. (2021) conducted a meta-analysis of facilitation effects in arid shrublands, concluding that while shrubs do provide facilitative effects, the net effect of species diversity on shrub biomass turned weakly negative under high diversity, due to competitive effects. Facilitation effects remain understudied in the BEFR literature. A history of research into partitioning niche complementarity from selection effects in biodiversity experiments has largely ignored the role of facilitation effects, presumably because they are not expected to drive large scale variation in the BEFR between systems, and because they are often context specific and difficult to test for their presence in natural systems (Wright et al., 2017). Wright et al. (2021) discusses how facilitation effects may have been mistakenly identified as niche complementarity as a result of the simplistic partitioning method used in previous studies.

Global distribution of biodiversity-ecosystem function research

Among the hundreds of published studies of the biodiversity-ecosystem function relationship (BEFR), the majority are from experimental contexts, in small grassland patches or mesocosms. The number of studies in forested ecosystems is growing, but remains restricted predominantly to temperate forests in the global north (Clarke et al., 2017). In particular, there is a paucity of BEFR research in disturbance-prone wooded ecosystems, e.g. the mesic savannas which cover ~20% of the global land surface (Scholes & Walker, 1993). Liang et al. (2016) conducted a meta-analysis of estimates of the BEFR from 777,126 forest sample plots. They found that 99.87% of these estimates followed a monotonic, positive BEFR curve, which saturated at high species richness. However, less than 600 of these plots were located in Africa, and none further south than Tanzania.

Clarke et al. (2017) reviewed four BEFR meta-analyses (Gamfeldt et al., 2015; Griffin et al., 2013; Zhang et al., 2012; Cardinale et al., 2009) and identified only two studies conducted in Africa (Foster et al., 1999; Burleigh & Yamoah, 1997), compared with 69 in Europe and 82 in North America (Figure 7). Both of these African studies are narrow in their scope and do not consider southern African woodland-savanna mosaics. Foster et al. (1999) studied the effect of dietary diversity on a single marine mollusc species in an experimental context. Burleigh & Yamoah (1997) is an agroforestry study primarily investigating the suitability of two Fabaceae tree species as erosion mitigators. Neither of these studies provide an understanding of the BEFR that is relevant to understanding how entire savanna ecosystems respond to changes in biodiversity. In Duffy et al.’s (2017) meta-analysis, only three terrestrial field studies from southern Africa were used to compare the effects of biodiversity to those of environmental factors from a total of 167 field estimates of the BEFR. Given the unique community composition (Lehmann et al., 2011), environmental conditions (Linder, 2003) and strong role of disturbance by fire and herbivory in structuring these savannas, it would be unfeasible to generalise the BEFR found in other systems to this region.

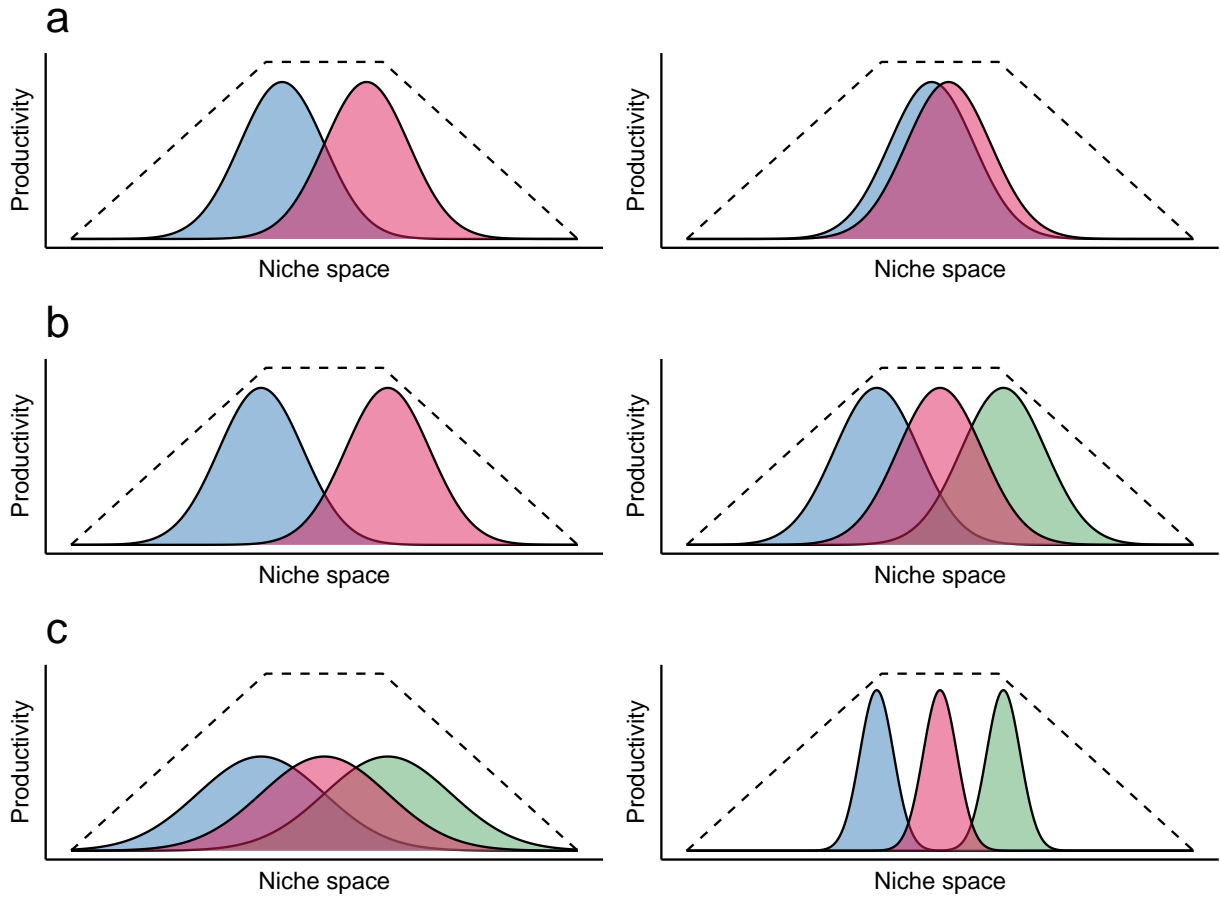


Figure 6: Schematic diagrams demonstrating niche occupation and secondary controls on the mechanism of niche complementarity. Each density plot shows a number of species, each represented by the species functional contribution (productivity) under different environmental conditions (niche space) within the larger environmental niche volume (dashed line). a) shows how the degree of overlap in functional niche of two species affects the total utilisation of the environmental niche volume (area under all species curves). When species are functionally distinct (left), more of the environmental niche volume is utilised. Removal of a species in this case would result in a large reduction in ecosystem productivity, while on the right, where functional redundancy is high, removal of a single species would have negligible effects. b) shows the effect of adding a functionally distinct species to an ecosystem. c) shows the effect of niche breadth on niche volume utilisation. On the left, three generalist species overlap in their functional niche. While each species has relatively incomplete utilisation of the environmental niche volume, this is offset as each species may occupy a wide range of environmental conditions. If the red species was removed, there would be only a marginal reduction in ecosystem productivity. On the right, three specialist species have a narrower niche breadth but a more complete utilisation of the environmental niche under ideal conditions. If a species was removed from this ecosystem, there would be a much greater reduction in ecosystem productivity.

Should we expect biodiversity effects on ecosystem function in southern African woodlands?

Extensive research has linked tree biodiversity to ecosystem function in temperate and tropical forests (Liang et al., 2016), but tropical savannas differ in the environmental pressures they experience, and in the mechanisms which determine ecosystem structure. Conclusions drawn from BEFR research conducted in forests cannot necessarily be directly applied to disturbance driven and resource limited systems.

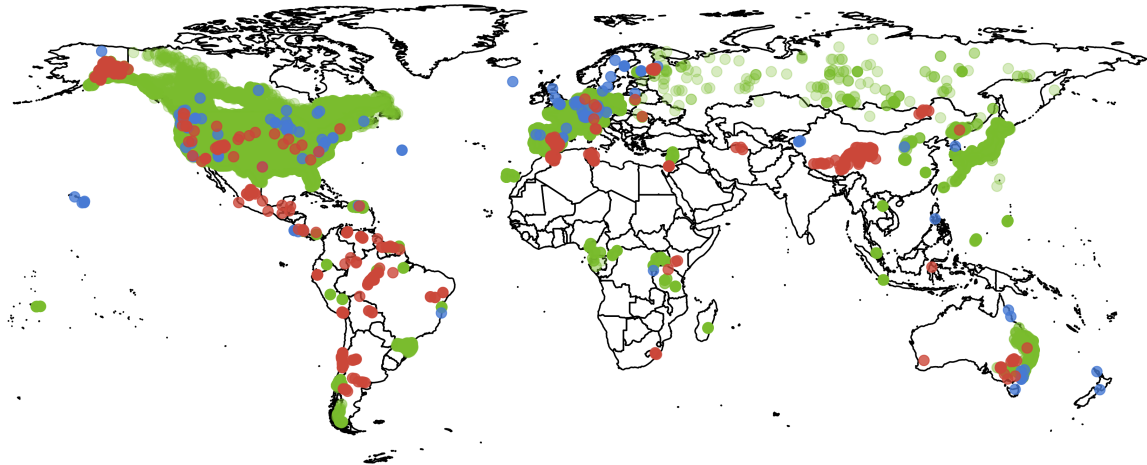


Figure 7: Location of studies of the biodiversity - ecosystem function relationship included in three meta-analyses of BEF research: blue Clarke et al. (2017), green Liang et al. (2016), red Duffy et al. (2017) - 67 field studies.

Despite the current trend in conservation strategy to maximise biodiversity under the assumption that it will ensure ecosystem functionality, it remains unclear how important the BEFR is in determining ecosystem functionality compared to environmental factors (Tilman et al., 2014). It is also unclear to what extent the BEFR itself varies over environmental and biogeographical gradients (Scherer-Lorenzen, 2014). Many observed biodiversity effects could potentially be better explained by variation in unmeasured environmental variables, with which biodiversity merely correlates. Plant biodiversity has been shown to increase in areas with climatic conditions conducive to growth (Fischer et al., 2014; Bunker et al., 2005), and it is clear that temperature and precipitation also have a direct role in determining ecosystem functions such as net primary productivity and woody biomass (Urban et al., 2017; Michaletz et al., 2014).

A strong positive BEFR may not exist in all landscapes, with previous experimental and field studies producing many contrasting results. Duffy et al. (2017) conducted a meta-analysis of 133 estimates of the BEFR from 67 studies, suggesting comparable effects of biodiversity and climate or nutrient availability, but this generalisation remains largely speculative, especially for regions with a paucity of data, such as southern Africa (Figure 7). Resource availability and disturbance frequency/intensity have been identified as two environmental factors that modulate the effect that biodiversity has on ecosystem functionality (Tilman et al., 2012; Tilman et al., 2014; Hooper et al., 2012). In European forests, Ratcliffe et al. (2017) found that the strength of the effect of tree species richness on many ecosystem functions increased as water availability decreased. They suggested that facilitation effects between species became stronger than competitive effects when resource availability was low, with strong facilitation effects being more likely at high species richness. Furthermore, Baert et al. (2018) reported that environmental stress shows a humped relationship with the strength of the BEFR, with the relationship being highest at intermediate levels of stress. They suggest an interplay between niche complementarity and selection effects at low environmental stress levels, which are often accompanied by greater levels of competition due to the lack of growth limitation, and higher facilitative effects at very high levels of environmental stress. These environmental factors, which remain unmeasured in many studies of the BEFR in natural systems may explain some of the variation in the observed strength of the BEFR. Conducting experiments across environmental gradients will improve understanding of how biodiversity effects interact with the environment to

determine ecosystem functionality (Turnbull et al., 2016; Tilman et al., 2014). Cardinale & Palmer (2002) found that in an experimental mesocosm of caddisfly larvae, increased disturbance in the form of random individual mortality led to increased effects of species richness on productivity. They attributed this effect to a decrease in dominance of competitively superior but low productivity taxa. Fire disturbance in forests has been linked to abundance dependent mortality among smaller stems (Roques et al., 2001). A species with more small stems is more likely to experience mortality during a fire. There may therefore be a link between disturbance regime and the strength of the species richness - ecosystem function relationship in fire prone woodland ecosystems. Unlike the caddisfly larvae in Cardinale & Palmer (2002) however, tree species differ in their resilience to fire driven mortality, owing to adaptations such as corky bark (Solbrig et al., 1996). The strength of the BEFR in a given system may therefore be a product of environmental conditions, disturbance regime, and species functional composition.

Biodiversity is often crudely measured as local species richness of a focal trophic level or functional group (e.g. trees). However, more complex measures such as functional richness provide better insight into the tangible organism level processes, which drive apparent species richness effects (Finegan et al., 2015; Scherer-Lorenzen, 2014; Petchey & Gaston, 2006). For example, increased tree species richness appears to cause an increase in the productivity of forest stands, but is this due to there being a higher likelihood of having a productive species (selection effects), canopy packing complementarity, root depth complementarity, facilitative shading effects, or more likely a combination of all the above? It is likely that species richness is merely correlated with many other aspects of biodiversity which actually affect ecosystem function (Mlambo, 2014; Scherer-Lorenzen, 2014). Ultimately, there is no biological reason why two species should exhibit niche complementarity according to differences in species name. Of course, this is not to discount the role of phylogenetic and taxonomic separation as a proxy for degree of potential niche differentiation among species (Flynn et al., 2011; Petchey & Gaston, 2002). Additionally, the distribution of relative contributions to a given function among species within an ecosystem is likely to affect the provision of that ecosystem function, through selection effects and the mass ratio hypothesis (Chisholm et al., 2013). *i.e.* a species with a high photosynthetic capacity will contribute little to overall ecosystem level productivity if it is found at very low abundances, but see Violle et al. (2017) and Soliveres et al. (2016), which suggest that rare species often exhibit the least redundant traits and are therefore as functionally important as common species. Functional diversity should ideally be used to more directly quantify the functional contribution of species and individuals within an ecosystem, to understand better the mechanisms that driver biodiversity effects.

In temperate and wet tropical closed canopy forests trees interact with each other due to their close proximity (Coomes & Allen, 2007; Purves et al., 2007). Overlapping canopies and inter-weaving root networks produce competition for light, water and nutrients between individuals. Southern African woodlands however, exist along a wide gradient of tree cover. At the extreme low end of this gradient, trees are often too far apart for canopy competition to occur, and while the root networks of savanna trees are often extensive (Belsky, 1994), root competition may also approach zero between adult trees in the most sparsely wooded ecosystems. Low tree densities may result from a combination of “resource-based” processes such as low water availability and “disturbance-based” processes of disturbance caused by fire, herbivory, or human land use practices such as selective logging or tree felling for beehive harvesting (Ryan et al., 2016). Figure 2 shows percentage woody cover along a precipitation gradient in Africa from Sankaran et al. (2005). It shows that the majority of plots have a woody cover below the physiological maximum set by precipitation, indicating that many other factors influence woody cover other than water availability. A lack of competition would certainly weaken any effect of tree species diversity on ecosystem productivity, as multiple species can often fill overlapping niches in the absence of competition. Niche differentiation however, would still serve to only allow certain species to establish and optimise productivity in certain micro-habitats, suggesting at least some effect of tree diversity on ecosystem function even in the most sparsely forested ecosystems. Though Dohn et al. (2017) demonstrated strong competitive interactions at neighbourhood scales of up to 5 m for most trees in an East African savanna. Additionally, many

savanna tree species do not grow well under shade (Belsky, 1994), unlike those in forests. Adult savanna trees will therefore compete with seedlings and saplings from their own species and from other species. Differences in competitive interactions amongst trees across tree cover gradients are likely to have an impact on the strength of the BEFR.

Demographic structure, structural diversity and ecosystem function

Disturbance by fire and herbivory, as well as drought and extreme temperature, create a bottleneck in the demographic structure of savannas, with high mortality of juveniles. The extent of this demographic bottleneck effect causes variation in tree canopy structure in different savannas. In the same way that co-existing tree species are expected to occupy different niche space to produce the positive niche complementarity effect on ecosystem function, it can be assumed that individuals occupying different demographic stages and with different canopy occupancy also occupy different niche space. Thus, demographic and physical structure may represent a form of structural diversity that also influences ecosystem function.

In wet tropical forests () and temperate forests (Dănescu et al., 2016), canopy layer diversity has been shown to increase productivity. Presumably an increase in canopy layer diversity

Conclusions

Savannas are complex, and savanna vegetation arises as a result of many interacting factors. Tropical savannas are ecologically complex, but are understudied and represent the largest uncertainty in models of the global carbon cycle. Assumptions about the behaviour of tropical savannas cannot be made based on other tropical forested ecosystems, mainly due the pervasive role of disturbance and resource scarcity as drivers of ecosystem functioning. Previous studies of tropical savannas have focussed predominantly on the role of abiotic environment and disturbance as drivers of ecosystem function, with biodiversity as a passive result of these factors. Biodiversity - Ecosystem Function research reframes the role of biodiversity as both a driver and result of ecosystem function, and provides an intuitive prediction that biodiversity increases ecosystem function. However, BEF research in natural forested ecosystems has shown that both positive and negative biodiversity effects may occur, depending on the function studied and the intensity of environmental stress. It is unclear how biodiversity of tree species in southern African woodlands may affect productivity, but there are multiple reasons why biodiversity effects might be weaker or possibly negative in this biome. This thesis aims to increase our understanding of tree biodiversity in southern African woodlands, the world's largest savanna, through the lens of the Biodiversity-Ecosystem Function Relationship.

References

- Adams, W. M. (2004). 'Biodiversity Conservation and the Eradication of Poverty'. In: *Science* 306.5699, pp. 1146–1149. DOI: 10.1126/science.1097920.
- Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneeth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). 'The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink'. In: *Science* 348.6237, pp. 895–899. DOI: 10.1126/science.aaa1668.
- Aide, T. Mitchell (1988). 'Herbivory as a selective agent on the timing of leaf production in a tropical understory community'. In: *Nature* 336.6199, pp. 574–575. DOI: 10.1038/336574a0.
- Aleman, J. C., A. Fayolle, C. Favier, A. C. Staver, K. G. Dexter, C. M. Ryan, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo et al. (2020). 'Floristic evidence for alternative biome states in tropical Africa'. In: *Proceedings of the National Academy of Sciences* 117.45, pp. 28183–28190. DOI: 10.1073/pnas.2011515117.
- Aleman, Julie C., Olivier Blarquez & Carla A. Staver (2016). 'Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa'. In: *Global Change Biology* 22.9, pp. 3013–3025. DOI: 10.1111/gcb.13299.
- Archibald, S., A. Nickless, N. Govender, R. J. Scholes & V. Lehsten (2010). 'Climate and the inter-annual variability of fire in southern Africa: a meta-analysis using long-term field data and satellite-derived burnt area data'. In: *Global Ecology and Biogeography* 19.6, pp. 794–809. DOI: 10.1111/j.1466-8238.2010.00568.x.
- Archibald, S. & R. J. Scholes (2007). 'Leaf green-up in a semi-arid African savanna -separating tree and grass responses to environmental cues'. In: *Journal of Vegetation Science* 18.4, pp. 583–594. DOI: 10.1111/j.1654-1103.2007.tb02572.x.
- Archibald, Sally, William J. Bond, William Hoffmann, Caroline Lehmann, Carla Staver & Nicola Stevens (2019). *Distribution and Determinants of Savannas*. DOI: 10.1002/9781119081111.ch1.
- Arino, O., J. R. Perez, V. Kalogirou, P. Defourny & F. Achard (2010). 'GlobCover 2009'. In: *ESA Living Planet Symposium*, pp. 1–3.
- Asner, G. P., S. R. Levick, T. Kennedy-Bowdoin, D. E. Knapp, R. Emerson, J. Jacobson, M. S. Colgan & R. E. Martin (2009). 'Large-scale impacts of herbivores on the structural diversity of African savannas'. In: *Proceedings of the National Academy of Sciences* 106.12, pp. 4947–4952. DOI: 10.1073/pnas.0810637106.
- Augustino, S., J. B. Hall, F. B. S. Makonda & R. C. Ishengoma (2011). 'Medicinal Resources of the Miombo woodlands of Urumwa, Tanzania: Plants and its uses'. In: *Journal of Medicinal Plants Research* 5.27. DOI: 10.5897/JMPR10.517.
- Baert, Jan M., Nico Eisenhauer, Colin R. Janssen & Frederik De Laender (2018). 'Biodiversity effects on ecosystem functioning respond unimodally to environmental stress'. In: *Ecology Letters* 21.8. Ed. by Johannes Knops, pp. 1191–1199. DOI: 10.1111/ele.13088.
- Balvanera, Patricia, Ilyas Siddique, Laura Dee, Alain Paquette, Forest Isbell, Andrew Gonzalez, Jarrett Byrnes, Mary I. O'Connor, Bruce A. Hungate & John N. Griffin (2014). 'Linking Biodiversity and Ecosystem Services: Current Uncertainties and the Necessary Next Steps'. In: *BioScience* 64.1, pp. 49–57. DOI: 10.1093/biosci/bit003.
- Bartomeus, Ignasi, Mia G. Park, Jason Gibbs, Bryan N. Danforth, Alan N Lakso & Rachael Winfree (2013). 'Biodiversity ensures plant-pollinator phenological synchrony against climate change'. In: *Ecology Letters* 16.11, pp. 1331–1338. DOI: 10.1111/ele.12170.
- Beerling, D. J. & C. P. Osborne (2006). 'The origin of the savanna biome'. In: *Global Change Biology* 12.11, pp. 2023–2031. DOI: 10.1111/j.1365-2486.2006.01239.x.
- Belsky, A. Joy (1994). 'Influences of Trees on Savanna Productivity: Tests of Shade, Nutrients, and Tree-Grass Competition'. In: *Ecology* 75.4, pp. 922–932. DOI: 10.2307/1939416.
- Bond, W. J. & J. E. Keeley (2005). 'Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems'. In: *Trends in Ecology and Evolution* 20.7, pp. 387–394. DOI: 10.1016/j.tree.2005.04.025.
- Bond, William J. (2008). 'What Limits Trees in C4 Grasslands and Savannas?' In: *Annual Review of Ecology, Evolution, and Systematics* 39.1, pp. 641–659. DOI: 10.1146/annurev.ecolsys.39.110707.173411.
- Bond, William J. & Guy F. Midgley (2012). 'Carbon dioxide and the uneasy interactions of trees and savannah grasses'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 367.1588, pp. 601–612. DOI: 10.1098/rstb.2011.0182.
- Bond, William J. & Jeremy J. Midgley (May 1995). 'Kill Thy Neighbour: An Individualistic Argument for the Evolution of Flammability'. In: 73.1, p. 79. DOI: 10.2307/3545728. URL: <https://doi.org/10.2307/3545728>.
- (2003). 'The Evolutionary Ecology of Sprouting in Woody Plants'. In: *International Journal of Plant Sciences* 164.S3, S103–S114. DOI: 10.1086/374191.
- Borchert, R. (1994). 'Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees'. In: *Ecology* 75.5, pp. 1437–1449. DOI: 10.2307/1937467.
- Brockerhoff, Eckehard G., Luc Barbaro, Bastien Castagnyrol, David I. Forrester, Barry Gardiner, José Ramón González-Olabarria, Phil O'B. Lyver, Nicolas Meurisse, Anne Oxbridge, Hisatomo Taki et al. (2017). 'Forest biodiversity, ecosystem functioning and the provision of ecosystem services'. In: *Biodiversity and Conservation*. DOI: 10.1007/s10531-017-1453-2.
- Bucini, Gabriela & Niall P. Hanan (2007). 'A continental-scale analysis of tree cover in African savannas'. In: *Global Ecology and Biogeography* 16.5, pp. 593–605. DOI: 10.1111/j.1466-8238.2007.00325.x.
- Bunker, D, F DeClerck, J Bradford & R Colwell (2005). 'Species loss and aboveground carbon storage in a tropical forest'. In: *Science* 310.November, pp. 1029–1031. DOI: 10.1126/science.1117682.

- Burgess, Neil, Jennifer D'Amico Hales, Emma Underwood, Eric Dinerstein, David Olson, Illana Itoua, Jan Schipper, Taylor Ricketts & Kate Newman (2004). *Terrestrial Ecoregions of Africa and Madagascar: A Conservation Assessment*. Washington D. C., pp. 20–29.
- Burleigh, J R & C F Yamoah (1997). 'Site factors associated with the performance of *Leucaena leucocephala* (Lam.) de Wit and *Sesbania sesban* (L.) Merrill in pure and mixed stands in the northern highlands of Rwanda'. In: *Agroforestry Systems* 37.2, pp. 121–131. DOI: 10.1023/A:1005861821739.
- Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno et al. (2010). 'Global Biodiversity: Indicators of Recent Declines'. In: *Science* 328.5982, pp. 1164–1168. DOI: 10.1126/science.1187512.
- Callaway, Ragan M. & Lawrence R. Walker (1997). 'Competition and facilitation: a synthetic approach to interactions in plant communities'. In: *Ecology* 78.7, pp. 1958–1965. DOI: 10.1890/0012-9658(1997)078[1958:cafasa]2.0.CO;2.
- Cardinale, Bradley J., Justin P Wright, Marc W Cadotte, Ian T Carroll, Andy Hector, Diane S Srivastava, Michel Loreau & Jerome J Weis (2007). 'Impacts of plant diversity on biomass production increase through time because of species complementarity.' In: *Proceedings of the National Academy of Sciences of the United States of America* 104.46, pp. 18123–8. DOI: 10.1073/pnas.0709069104.
- Cardinale, Bradley J., J. Emmett Duffy, Andrew Gonzalez, David U. Hooper, Charles Perrings, Patrick Venail, Anita Narwani, Georgina M. Mace, David Tilman, David A. Wardle et al. (2012). 'Biodiversity loss and its impact on humanity'. In: *Nature* 489.7415, pp. 326–326. DOI: 10.1038/nature11373.
- Cardinale, Bradley J., Kristin L. Matulich, David U. Hooper, Jarrett E. Byrnes, Emmett Duffy, Lars Gamfeldt, Patricia Balvanera, Mary I. O'Connor & Andrew Gonzalez (2011). 'The functional role of producer diversity in ecosystems'. In: *American Journal of Botany* 98.3, pp. 572–592. DOI: 10.3732/ajb.1000364.
- Cardinale, Bradley J. & Margaret A. Palmer (2002). 'Disturbance Moderates biodiversity-ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms'. In: *Ecology*, 83 (7)-1915-1927 83.7, pp. 1915–1927. DOI: 10.1890/0012-9658(2002)083[1915:DMBEFR]2.0.CO;2.
- Cardinale, Bradley J., Diane S. Srivastava, J. Emmett Duffy, Justin P. Wright, Amy L. Downing, Mahesh Sankaran, Claire Jouseau, Marc W Cadotte, Ian T. Carroll, Jerome J. Weis et al. (2009). 'Effects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipulations of species richness'. In: *Ecology* 90.3, pp. 854–854. DOI: 10.1890/08-1584.1.
- Case, Madelon F., Jesse B. Nippert, Ricardo M. Holdo & A. Carla Staver (2020). 'Root-niche separation between savanna trees and grasses is greater on sandier soils'. In: *Journal of Ecology* 108.6. Ed. by Imma Oliveras, pp. 2298–2308. DOI: 10.1111/1365-2745.13475.
- Cerling, Thure E., John M. Harris, Bruce J. MacFadden, Meave G. Leakey, Jay Quade, Vera Eisenmann & James R. Ehleringer (1997). 'Global vegetation change through the Miocene/Pliocene boundary'. In: *Nature* 389.6647, pp. 153–158. DOI: 10.1038/38229.
- Charles-Dominique, Tristan, Heath Beckett, Guy F. Midgley & William J. Bond (2015). 'Bud protection: a key trait for species sorting in a forest/savanna mosaic'. In: *New Phytologist* 207.4, pp. 1052–1060. DOI: 10.1111/nph.13406.
- Charles-Dominique, Tristan, Guy F. Midgley, Kyle W. Tomlinson & William J. Bond (2018). 'Steal the light: shade vs fire adapted vegetation in forest-savanna mosaics'. In: *New Phytologist* 218.4, pp. 1419–1429. DOI: 10.1111/nph.15117.
- Chisholm, Ryan A, Helene C. Muller-Landau, Kassim Abdul Rahman, Daniel P. Bebb, Yue Bin, Stephanie A Bohlman, Norman A Bourg, Joshua Brinks, Sarayudh Bunyavechewin, Nathalie Butt et al. (2013). 'Scale-dependent relationships between tree species richness and ecosystem function in forests'. In: *Journal of Ecology* 101.5. Ed. by David Coomes, pp. 1214–1224. DOI: 10.1111/1365-2745.12132.
- Clarke, D. A., P. H. York, M. A. Rasheed & T. D. Northfield (2017). 'Does biodiversity-ecosystem function literature neglect tropical ecosystems?'. In: *Trends in Ecology & Evolution* 32.5, pp. 320–323. DOI: 10.1016/j.tree.2017.02.012.
- Coomes, David A. & Robert B. Allen (2007). 'Effects of size, competition and altitude on tree growth'. In: *Journal of Ecology* 95.5, pp. 1084–1097. DOI: 10.1111/j.1365-2745.2007.01280.x.
- Dahlin, Kyla M., Dominick Del Ponte, Emily Setlock & Ryan Nagelkirk (2016). 'Global patterns of drought deciduous phenology in semi-arid and savanna-type ecosystems'. In: *Ecography* 40.2, pp. 314–323. DOI: 10.1111/ecog.02443.
- Daibes, L Felipe, Juli G Pausas, Nathalia Bonani, Jessika Nunes, Fernando A O Silveira & Alessandra Fidelis (2019). 'Fire and legume germination in a tropical savanna: ecological and historical factors'. In: *Annals of Botany* 123.7, pp. 1219–1229. DOI: 10.1093/aob/mcz028.
- Dănescu, Adrian, Axel T. Albrecht & Jürgen Bauhus (2016). 'Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany'. In: 182.2, pp. 319–333. DOI: 10.1007/s00442-016-3623-4.
- Dantas, V. L., M. Hirota, R. S. Oliveira & J. G. Pausas (2015). 'Disturbance maintains alternative biome states'. In: *Ecology Letters* 19.1, pp. 12–19. DOI: 10.1111/ele.12537.
- Dantas, V. L. & J. G. Pausas (2013). 'The lanky and the corks: fire-escape strategies in savanna woody species'. In: *Journal of Ecology* 101.5. Ed. by Peter Bellingham, pp. 1265–1272. DOI: 10.1111/1365-2745.12118.
- Díaz, Sandra & Marcelo Cabido (2001). 'Vive la différence: plant functional diversity matters to ecosystem processes'. In: *Trends in Ecology & Evolution* 16.11, pp. 646–655. DOI: 10.1016/S0169-5347(01)02283-2.
- Dinerstein, Eric, David Olson, Anup Joshi, Carly Vynne, Neil D. Burgess, Eric Wikramanayake, Nathan Hahn, Suzanne Palminteri, Prashant Hedao, Reed Noss et al. (2017). 'An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm'. In: *BioScience* 67.6, pp. 534–545. DOI: 10.1093/biosci/bix014.

- Dohn, Justin, David J. Augustine, Niall P. Hanan, Jayashree Ratnam & Mahesh Sankaran (2017). 'Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna'. In: *Ecology* 98.2, pp. 478–488. DOI: 10.1002/ecy.1659.
- Duffy, J. Emmett, Casey M. Godwin & Bradley J. Cardinale (2017). 'Biodiversity effects in the wild are common and as strong as key drivers of productivity'. In: *Nature* 549.7671, pp. 261–264. DOI: 10.1038/nature23886.
- Edwards, E. J. & S. A. Smith (2010). 'Phylogenetic analyses reveal the shady history of C4 grasses'. In: *Proceedings of the National Academy of Sciences* 107.6, pp. 2532–2537. DOI: 10.1073/pnas.0909672107.
- Fayolle, A., M. D. Swaine, J. Aleman, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo, J. P. G. M. Cromsigt, H. Dessard, M. Finkch et al. (2018). 'A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas'. In: *Journal of Biogeography* 46, pp. 1–12. DOI: 10.1111/jbi.13475.
- February, Edmund C., Steven I. Higgins, William J. Bond & Louise Swemmer (2013). 'Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses'. In: *Ecology* 94.5, pp. 1155–1164. DOI: 10.1890/12-0540.1.
- Finegan, Bryan, Marielos Peña-Claros, Alexandre de Oliveira, Nataly Ascarrunz, M. Sydonia Bret-Harte, Geovana Carreño-Rocabado, Fernando Casanoves, Sandra Díaz, Paul Eguiguren Velepucha, Fernando Fernandez et al. (2015). 'Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses'. In: *Journal of Ecology* 103.1, pp. 191–201. DOI: 10.1111/1365-2745.12346.
- Fischer, Rico, Amanda Armstrong, Herman H. Shugart & Andreas Huth (2014). 'Simulating the impacts of reduced rainfall on carbon stocks and net ecosystem exchange in a tropical forest'. In: *Environmental Modelling and Software* 52, pp. 200–206. DOI: 10.1016/j.envsoft.2013.10.026.
- Flynn, Dan F. B., Nicholas Mirotnick, Meha Jain, Matthew I. Palmer & Shahid Naeem (2011). 'Functional and phylogenetic diversity as predictors of biodiversity ecosystem-function relationships'. In: *Ecology* 92.8, pp. 1573–1581. DOI: 10.1890/10-1245.1.
- Foster, G. G., A. N. Hodgson & M. Balarin (1999). 'Effect of diet on growth rate and reproductive fitness of *Turbo sarmaticus* (Mollusca: Vetigastropoda: Turbinidae)'. In: *Marine Biology* 134.2, pp. 307–315. DOI: 10.1007/s002270050548.
- Frost, P. (1996). 'The ecology of miombo woodlands'. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B.M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.
- Gamfeldt, Lars, Jonathan S. Lefcheck, Jarrett E. K. Byrnes, Bradley J. Cardinale, J. Emmett Duffy & John N. Griffin (2015). 'Marine biodiversity and ecosystem functioning: What's known and what's next?' In: *Oikos* 124.3, pp. 252–265. DOI: 10.1111/oik.01549.
- Gonzalez, Andrew, Nicolas Mouquet & Michel Loreau (2009). 'Biodiversity as spatial insurance: The effects of habitat fragmentation and dispersal on ecosystem functioning'. In: *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*. DOI: 10.1093/acprof:oso/9780199547951.003.0010.
- Good, Megan K., Peter J. Clarke, Jodi N. Price & Nick Reid (2014). 'Seasonality and facilitation drive tree establishment in a semi-arid floodplain savanna'. In: *Oecologia* 175.1, pp. 261–271. DOI: 10.1007/s00442-014-2886-x.
- Good, S. P. & K. K. Caylor (2011). 'Climatological determinants of woody cover in Africa'. In: *Proceedings of the National Academy of Sciences* 108.12, pp. 4902–4907. DOI: 10.1073/pnas.1013100108.
- Grace, John, Jose San Jose, Patrick Meir, Heloisa S. Miranda & Ruben A. Montes (2006). 'Productivity and carbon fluxes of tropical savannas'. In: *Journal of Biogeography* 33.3, pp. 387–400. DOI: 10.1111/j.1365-2699.2005.01448.x.
- Griffin, John N., Jarrett E K Byrnes & Bradley J. Cardinale (2013). 'Effects of predator richness on prey suppression: A meta-analysis'. In: *Ecology* 94.10, pp. 2180–2187. DOI: 10.1890/13-0179.1.
- Grime, J. P. (1998). 'Benefits of plant diversity to ecosystems: Immediate, filter and founder effects'. In: *Journal of Ecology* 86.6, pp. 902–910. DOI: 10.1046/j.1365-2745.1998.00306.x.
- Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland et al. (2013). 'High-Resolution Global Maps of 21st-Century Forest Cover Change'. In: *Science* 342.6160, pp. 850–853. DOI: 10.1126/science.1244693.
- Hecky, Robert E., Harvey A. Bootsma & Murray L. Kingdon (2003). 'Impact of Land Use on Sediment and Nutrient Yields to Lake Malawi/Nyasa (Africa)'. In: *Journal of Great Lakes Research* 29, pp. 139–158. DOI: 10.1016/s0380-1330(03)70544-9.
- Hector, Andy & Robert Bagchi (2007). 'Biodiversity and ecosystem multifunctionality'. In: *Nature* 448.7150, pp. 188–190. DOI: 10.1038/nature05947.
- Hempson, G. P., S. Archibald & W. J. Bond (2015). 'A continent-wide assessment of the form and intensity of large mammal herbivory in Africa'. In: *Science* 350.6264, pp. 1056–1061. DOI: 10.1126/science.aac7978.
- Higgins, Steven I., William J. Bond & Winston S. W. Trollope (2000). 'Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna'. In: *Journal of Ecology* 88.2, pp. 213–229. DOI: 10.1046/j.1365-2745.2000.00435.x.
- Hirota, M., M. Holmgren, E. H. Van Nes & M. Scheffer (2011). 'Global resilience of tropical forest and savanna to critical transitions'. In: *Science* 334, pp. 232–235. DOI: 10.1126/science.1210657.
- Hoekstra, Jonathan M., Timothy M. Boucher, Taylor H. Ricketts & Carter Roberts (2004). 'Confronting a biome crisis: global disparities of habitat loss and protection'. In: *Ecology Letters* 8.1, pp. 23–29. DOI: 10.1111/j.1461-0248.2004.00686.x.
- Hoffmann, William A., Erika L. Geiger, Sybil G. Gotsch, Davi R. Rossatto, Lucas C. R. Silva, On Lee Lau, M. Haridasan & Augusto C. Franco (2012). 'Ecological thresholds at the savanna-forest boundary: how plant traits,

- resources and fire govern the distribution of tropical biomes'. In: *Ecology Letters* 15.7. Ed. by Francisco Lloret, pp. 759–768. DOI: 10.1111/j.1461-0248.2012.01789.x.
- Hogberg, P. (1986). 'Nitrogen-Fixation and Nutrient Relations in Savanna Woodland Trees (Tanzania)'. In: *The Journal of Applied Ecology* 23.2, p. 675. DOI: 10.2307/2404045.
- Hooper, David U., E. Carol Adair, Bradley J. Cardinale, Jarrett E. K. Byrnes, Bruce a. Hungate, Kristin L. Matulich, Andrew Gonzalez, J. Emmett Duffy, Lars Gamfeldt & Mary I. O'Connor (2012). 'A global synthesis reveals biodiversity loss as a major driver of ecosystem change'. In: *Nature* 486.7401, pp. 105–108. DOI: 10.1038/nature11118.
- Howe, Caroline, Helen Suich, Bhaskar Vira & Georgina M. Mace (2014). 'Creating win-wins from trade-offs? Ecosystem services for human well-being: A meta-analysis of ecosystem service trade-offs and synergies in the real world'. In: *Global Environmental Change* 28.1, pp. 263–275. DOI: 10.1016/j.gloenvcha.2014.07.005.
- Huston, M. A. (1997). 'Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity'. In: *Oecologia* 110.4, pp. 449–460. DOI: 10.1007/s004420050180.
- Isbell, Forest, Peter B Reich, David Tilman, Sarah E Hobbie, Stephen Polasky & Seth Binder (2013). 'Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity'. In: *Proceedings of the National Academy of Sciences of the United States of America* 110.29, pp. 11911–6. DOI: 10.1073/pnas.1310880110.
- Jax, Kurt (2005). 'Function and "functioning" in ecology: what does it mean?'. In: *Oikos* 111.3, pp. 641–648. DOI: 10.1111/j.1600-0706.2005.13851.x.
- Kareiva, P., H. Tallis, T. H. Ricketts, G. C. Daily & S. Polasky (2011). 'Natural Capital: Theory and Practice of Mapping Ecosystem Services'. In: *Progress in Physical Geography* 35.5, pp. 701–704. DOI: 10.1177/0309133311417953.
- Kellman, Martin (1984). 'Synergistic Relationships Between Fire and Low Soil Fertility in Neotropical Savannas: A Hypothesis'. In: *Biotropica* 16.2, p. 158. DOI: 10.2307/2387850.
- Ketter, Benjamin L. & Ricardo M. Holdo (2018). 'Strong competitive effects of African savanna C4 grasses on tree seedlings do not support rooting differentiation'. In: *Journal of Tropical Ecology* 34.1, pp. 65–73. DOI: 10.1017/s0266467418000020.
- Körner, Christian (2017). 'A matter of tree longevity'. In: *Science* 355.6321, pp. 130–131. DOI: 10.1126/science.aal2449.
- Kumar, Dushyant, Mirjam Pfeiffer, Camille Gaillard, Liam Langan, Carola Martens & Simon Scheiter (2020). 'Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change'. In: *Biological Conservation* 241, p. 108293. DOI: 10.1016/j.biocon.2019.108293.
- Laestadius, L., S. Maginnis, S. Minnemeyer, P. Potapov, C. Saint-Laurent & N. Sizer (2011). 'Opportunities for forest landscape restoration'. In: *Unasylva* 62, pp. 1–238.
- Lawes, Michael J., Hylton Adie, Jeremy Russell-Smith, Brett Murphy & Jeremy J. Midgley (2011). 'How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness'. In: *Ecosphere* 2.4, art42. DOI: 10.1890/es10-00204.1.
- Lehmann, C. E. R., S. A. Archibald, W. A. Hoffmann & W. J. Bond (2011). 'Deciphering the distribution of the savanna biome'. In: *New Phytologist* 191.1, pp. 197–209. DOI: 10.1111/j.1469-8137.2011.03689.x.
- Levine, Jonathan M. & Janneke HilleRisLambers (2009). 'The importance of niches for the maintenance of species diversity'. In: *Nature* 461.7261, pp. 254–257. DOI: 10.1038/nature08251.
- Lewis, Simon L., Gabriela Lopez-Gonzalez, Bonaventure Sonké, Kofi Affum-Baffoe, Timothy R. Baker, Lucas O. Ojo, Oliver L. Phillips, Jan M. Reitsma, Lee White, James A. Comiskey et al. (2009). 'Increasing carbon storage in intact African tropical forests'. In: *Nature* 457.7232, pp. 1003–1006. DOI: 10.1038/nature07771.
- Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). 'Positive biodiversity-productivity relationship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: 10.1126/science.aaf8957.
- Linder, H. Peter (2003). 'The radiation of the Cape flora, southern Africa'. In: *Biological Reviews of the Cambridge Philosophical Society* 78.2003, pp. 597–638. DOI: Doi10.1017/S1464793103006171.
- Loreau, M. (2001). 'Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges'. In: *Science* 294.5543, pp. 804–808. DOI: 10.1126/science.1064088.
- Lortie, Christopher J., Mario Zuliani, Nargol Ghazian, Stephanie Haas, Jenna Braun, Malory Owen, Florencia Miguel, Merav Seifan, Alessandro Filazzola & Jacob Lucero (2021). 'Too much of a good thing: Shrub benefactors are less important in higher diversity arid ecosystems'. In: *Journal of Ecology* 109.5. Ed. by Alexandra Wright, pp. 2047–2053. DOI: 10.1111/1365-2745.13596.
- MacArthur, Robert (1955). 'Fluctuations of Animal Populations and a Measure of Community Stability'. In: *Ecology* 36.3, p. 533. DOI: 10.2307/1929601.
- MacArthur, Robert & Richard Levins (1967). 'The Limiting Similarity, Convergence, and Divergence of Coexisting Species'. In: 101.921, pp. 377–385. DOI: 10.1086/282505.
- Makhado, Rudzani, Martin Potgieter, Jonathan Timberlake & Davison Gumbo (2014). 'A review of the significance of mopane products to rural people's livelihoods in southern Africa'. In: *Transactions of the Royal Society of South Africa* 69.2, pp. 117–122. DOI: 10.1080/0035919x.2014.922512.
- May-Tobin, C. (2011). 'Wood for Fuel'. In: *The root of the problem: What's driving tropical deforestation today?* Ed. by D. Boucher, P. Elias, K. Lininger, C. May-Tobin, S. Roquemore & E. Saxon. Cambridge MA, USA: Union of Concerned Scientists, pp. 79–87.

- McRae, Louise, Stefanie Deinet & Robin Freeman (2017). 'The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator'. In: *PLOS ONE* 12.1. Ed. by Hideyuki Doi, e0169156. DOI: 10.1371/journal.pone.0169156.
- Michaletz, Sean T., Dongliang Cheng, Andrew J. Kerkhoff & Brian J. Enquist (2014). 'Convergence of terrestrial plant production across global climate gradients'. In: *Nature* 512.1, pp. 39–43. DOI: 10.1038/nature13470.
- Mittermeier, R. A., C. G. Mittermeier, T. M. Brooks, J. D. Pilgrim, W. R. Konstant, G. A. B. da Fonseca & C. Kormos (2003). 'Wilderness and biodiversity conservation'. In: *Proceedings of the National Academy of Sciences* 100.18, pp. 10309–10313. DOI: 10.1073/pnas.1732458100.
- Mlambo, Musa C. (2014). 'Not all traits are 'functional': Insights from taxonomy and biodiversity-ecosystem functioning research'. In: *Biodiversity and Conservation* 23.3, pp. 781–790. DOI: 10.1007/s10531-014-0618-5.
- Moncrieff, Glenn R., Simon Scheiter, Liam Langan, Antonio Trabucco & Steven I. Higgins (2016). 'The future distribution of the savannah biome: model-based and biogeographic contingency'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150311. DOI: 10.1098/rstb.2015.0311.
- Mora, Camilo, Roberto Danovaro & Michel Loreau (2014). 'Alternative hypotheses to explain why biodiversity-ecosystem functioning relationships are concave-up in some natural ecosystems but concave-down in manipulative experiments'. In: *Scientific Reports* 4.1. DOI: 10.1038/srep05427.
- Mori, Akira S., Takuya Furukawa & Takehiro Sasaki (2012). 'Response diversity determines the resilience of ecosystems to environmental change'. In: *Biological Reviews* 88.2, pp. 349–364. DOI: 10.1111/brv.12004.
- Morin, Xavier, Lorenz Fahse, Claire de Mazancourt, Michael Scherer-Lorenzen & Harald Bugmann (2014). 'Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics'. In: *Ecology Letters* 17.12. Ed. by Marcel Rejmanek, pp. 1526–1535. DOI: 10.1111/ele.12357.
- Moustakas, Aristides, William E. Kunin, Tom C. Cameron & Mahesh Sankaran (2013). 'Facilitation or Competition? Tree Effects on Grass Biomass across a Precipitation Gradient'. In: *PLoS ONE* 8.2. DOI: 10.1371/journal.pone.0057025.
- Murphy, Brett P. & David M J S Bowman (2012). 'What controls the distribution of tropical forest and savanna?' In: *Ecology Letters* 15.7, pp. 748–758. DOI: 10.1111/j.1461-0248.2012.01771.x.
- Naeem, S., J. E. Duffy & E. Zavaleta (2012). 'The functions of biological diversity in an age of extinction'. In: *Science* 336.6087, pp. 1401–1406. DOI: 10.1126/science.1215855.
- Naeem, Shahid, L. J. Thompson, S. P. Lawler, J. H. Lawton & R. M. Woodfin (1994). 'Declining biodiversity can alter the performance of ecosystems'. In: *Nature* 368, pp. 734–737.
- Newbold, Tim, Lawrence N Hudson, Andrew P Arnell, Sara Contu, Adriana De Palma, Simon Ferrier, Samantha L L Hill, Andrew J Hoskins, Igor Lysenko, Helen R P Phillips et al. (2016). 'Has land use pushed terrestrial biodiversity beyond the planetary boundary?' In: *Science* 353.6296, pp. 288–91.
- Njana, Marco Andrew, George Chamungwana Kajembe & Rogers Ernest Malimbwi (2013). 'Are miombo woodlands vital to livelihoods of rural households? Evidence from Urumwa and surrounding communities, Tabora, Tanzania'. In: *Forests Trees and Livelihoods* 22.2, pp. 124–140. DOI: 10.1080/14728028.2013.803774.
- Padilla, Francisco M. & Francisco I. Pugnaire (2006). 'The role of nurse plants in the restoration of degraded environments'. In: *Frontiers in Ecology and the Environment* 4.4, pp. 196–202. DOI: 10.1890/1540-9295(2006)004[0196:tronpi]2.0.co;2.
- Palgrave, K. C. (2003). *Trees of southern Africa*. Cape Town, South Africa: Struik Publications.
- Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann & A. N. Andersen (2014). 'Tropical grassy biomes: Misunderstood, neglected, and under threat'. In: *Trends in Ecology and Evolution* 29, pp. 205–213. DOI: 10.1016/j.tree.2014.02.004.
- Pelletier, J., A. Paquette, K. Mbindo, N. Zimba, A. Siampale, B. Chendauka, F. Siangulube & J. W. Roberts (2018). 'Carbon sink despite large deforestation in African tropical dry forests (miombo woodlands)'. In: *Environmental Research Letters* 13, p. 094017. DOI: 10.1088/1748-9326/aadc9a.
- Pennington, R. T., C. E. R. Lehmann & L. M. Rowland (2018). 'Tropical savannas and dry forests'. In: *Current Biology* 28.9, R541–R545. DOI: 10.1016/j.cub.2018.03.014.
- Petchey, Owen L. & Kevin J. Gaston (2002). 'Functional diversity (FD), species richness and community composition'. In: *Ecology Letters* 5.3, pp. 402–411. DOI: 10.1046/j.1461-0248.2002.00339.x.
- (2006). 'Functional diversity: back to basics and looking forward'. In: *Ecology Letters* 9.6, pp. 741–758. DOI: 10.1111/j.1461-0248.2006.00924.x.
- Pison, G. (2017). 'The population of the world (2017)'. In: *Population and Societies* 547, pp. 1–9.
- Plas, F. van der (2019). 'Biodiversity and ecosystem functioning in naturally assembled communities'. In: *Biological Reviews* 94, pp. 1220–1245. DOI: 10.1111/brv.12499.
- Pulsford, Stephanie A., David B. Lindenmayer & Don A. Driscoll (2014). 'A succession of theories: purging redundancy from disturbance theory'. In: *Biological Reviews* 91.1, pp. 148–167. DOI: 10.1111/brv.12163.
- Purves, Drew W., Jeremy W. Lichstein & Stephen W. Pacala (2007). 'Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species'. In: *PLoS ONE* 2.9. DOI: 10.1371/journal.pone.0000870.
- Ratcliffe, S., C. Wirth, T. Jucker, F. van der Plas, M. Scherer-Lorenzen, K. Verheyen, E. Allan, R. Benavides, H. Bruelheide, B. Ohse et al. (2017). 'Biodiversity and ecosystem functioning relations in European forests depend on environmental context'. In: *Ecology Letters* 20, pp. 1414–1426. DOI: 10.1111/ele.12849.

- Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins & M. Sankaran (2011). 'When is a 'forest' a savanna, and why does it matter?' In: *Global Ecology and Biogeography* 20, pp. 653–660. DOI: 10.1111/j.1466-8238.2010.00634.x.
- Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. B. Flynn & N. Eisenhauer (2012). 'Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades'. In: *Science* 336.6081, pp. 589–592. DOI: 10.1126/science.1217909.
- Reich, Peter B., Sarah E. Hobbie & Tali D. Lee (2014). 'Plant growth enhancement by elevated CO₂ eliminated by joint water and nitrogen limitation'. In: *Nature Geoscience* 7.12, pp. 920–924. DOI: 10.1038/ngeo2284.
- Roques, K. G., T. G. O'Connor & A. R. Watkinson (2001). 'Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence'. In: *Journal of Applied Ecology* 38.2, pp. 268–280. DOI: 10.1046/j.1365-2664.2001.00567.x.
- Rosan, Thais M., Luiz E. O. C. Aragão, Imma Oliveras, Oliver L. Phillips, Yadvinder Malhi, Emanuel Gloor & Fabien H. Wagner (2019). 'Extensive 21st-Century Woody Encroachment in South America's Savanna'. In: *Geophysical Research Letters* 46.12, pp. 6594–6603. DOI: 10.1029/2019gl082327.
- Ross, C. Wade, Niall P. Hanan, Lara Prihodko, Julius Anchang, Wenjie Ji & Qiuyan Yu (2021). 'Woody-biomass projections and drivers of change in sub-Saharan Africa'. In: *Nature Climate Change* 11.5, pp. 449–455. DOI: 10.1038/s41558-021-01034-5.
- Ryan, C. M., M. Williams & J. Grace (2011). 'Above- and belowground carbon stocks in a miombo woodland landscape of Mozambique'. In: *Biotropica* 43.4, pp. 423–432. DOI: 10.1111/j.1744-7429.2010.00713.x.
- Ryan, C. M., M. Williams, J. Grace, E. Woollen & C. E. R. Lehmann (2017). 'Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation'. In: *New Phytologist* 213.2, pp. 625–633. DOI: 10.1111/nph.14262.
- Ryan, Casey M., Rose Pritchard, Iain McNicol, Matthew Owen, Janet A Fisher & Caroline Lehmann (2016). 'Ecosystem services from southern African woodlands and their future under global change'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150312. DOI: 10.1098/rstb.2015.0312.
- Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig et al. (2005). 'Determinants of woody cover in African savannas'. In: *Nature* 438.8, pp. 846–849. DOI: 10.1038/nature04070.
- Sankaran, Mahesh, Jayashree Ratnam & Niall Hanan (2008). 'Woody cover in African savannas: the role of resources, fire and herbivory'. In: *Global Ecology and Biogeography* 17.2, pp. 236–245. DOI: 10.1111/j.1466-8238.2007.00360.x.
- Sankaran, Mahesh, Jayashree Ratnam & Niall P. Hanan (2004). 'Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models'. In: *Ecology Letters* 7.6, pp. 480–490. DOI: 10.1111/j.1461-0248.2004.00596.x.
- Scheiter, S. & S. I. Higgins (2009). 'Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach'. In: *Global Change Biology* 15.9, pp. 2224–2246. DOI: 10.1111/j.1365-2486.2008.01838.x.
- Scheiter, Simon & Steven I. Higgins (2007). 'Partitioning of Root and Shoot Competition and the Stability of Savannas'. In: *The American Naturalist* 170.4, pp. 587–601. DOI: 10.1086/521317.
- Scherer-Lorenzen, M (2014). *The functional role of biodiversity in the context of global change*, pp. 195–238.
- Scholes, R. J. & S. R. Archer (1997). 'Tree grass interactions in savannas - Scholes and Archer - 1997'. In: *Annual Review of Ecology and Systematics*.
- Scholes, R. J. & B. H. Walker (1993). *An African savanna. Synthesis of the Nylsvley Study*. Cambridge, United Kingdom: Cambridge University Press.
- Schulze, E. D. & H. A. Mooney (1993). *Biodiversity and Ecosystem Function*. Berlin, Germany: Springer Berlin Heidelberg.
- Shackleton, Charlie M., Sheona E. Shackleton, Erik Buiten & Neil Bird (2007). 'The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa'. In: *Forest Policy and Economics* 9.5, pp. 558–577. DOI: 10.1016/j.forpol.2006.03.004.
- Siebert, Frances & Niels Dreber (2019). 'Forb ecology research in dry African savannas: Knowledge, gaps, and future perspectives'. In: *Ecology and Evolution* 9.13, pp. 7875–7891. DOI: 10.1002/ece3.5307.
- Silveira, Fernando A. O., André J. Arruda, William Bond, Giselda Durigan, Alessandra Fidelis, Kevin Kirkman, Rafael S. Oliveira, Gerhard E. Overbeck, Jerônimo B. B. Sansevero, Frances Siebert et al. (2020). 'Myth-busting tropical grassy biome restoration'. In: *Restoration Ecology* 28.5, pp. 1067–1073. DOI: 10.1111/rec.13202.
- Sitch, S., P. Friedlingstein, N. Gruber, S. D. Jones, G. Murray-Tortarolo, A. Ahlström, S. C. Doney, H. Graven, C. Heinze, C. Huntingford et al. (2015). 'Recent trends and drivers of regional sources and sinks of carbon dioxide'. In: *Biogeosciences* 12.3, pp. 653–679. DOI: 10.5194/bg-12-653-2015.
- Smith, Melinda D. & Alan K. Knapp (2003). 'Dominant species maintain ecosystem function with non-random species loss'. In: *Ecology Letters* 6.6, pp. 509–517. DOI: 10.1046/j.1461-0248.2003.00454.x.
- Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.
- Soliveres, Santiago, Peter Manning, Daniel Prati, Martin M. Gossner, Fabian Alt, Hartmut Arndt, Vanessa Baumgartner, Julia Binkenstein, Klaus Birkhofer, Stefan Blaser et al. (2016). 'Locally rare species influence grassland ecosystem multifunctionality'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1694, p. 20150269. DOI: 10.1098/rstb.2015.0269.

- Srivastava, Diane S. & Mark Vellend (2005). 'Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation?' In: *Annual Review of Ecology, Evolution, and Systematics* 36.1, pp. 267–294. DOI: 10.1146/annurev.ecolsys.36.102003.152636.
- Staver, A. C., S. Archibald & S. A. Levin (2011). 'The Global Extent and Determinants of Savanna and Forest as Alternative Biome States'. In: *Science* 334.6053, pp. 230–232. DOI: 10.1126/science.1210465.
- Staver, A. C. & S. E. Koerner (2015). 'Top-down and bottom-up interactions determine tree and herbaceous layer dynamics in savanna grasslands'. In: *Trophic Ecology: Bottom-up and Top-Down Interactions Across Aquatic and Terrestrial Systems*. Ed. by K. J. La Pierre & T. C. Hanley. Cambridge, United Kingdom: Cambridge University Press, pp. 86–106.
- Staver, A. Carla, Judith Botha & Lars Hedin (2017). 'Soils and fire jointly determine vegetation structure in an African savanna'. In: *New Phytologist* 216.4, pp. 1151–1160. DOI: 10.1111/nph.14738.
- Studel, Bastian, Andy Hector, Thomas Friedl, Christian Löffke, Maike Lorenz, Moritz Wesche & Michael Kessler (2012). 'Biodiversity effects on ecosystem functioning change along environmental stress gradients'. In: *Ecology Letters* 15.12. Ed. by Mark Gessner, pp. 1397–1405. DOI: 10.1111/j.1461-0248.2012.01863.x.
- Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2016a). 'Savanna woody encroachment is widespread across three continents'. In: *Global Change Biology* 23.1, pp. 235–244. DOI: 10.1111/gcb.13409.
- Stevens, Nicola, B. F. N. Erasmus, S. Archibald & W. J. Bond (2016b). 'Woody encroachment over 70 years in South African savannas: overgrazing, global change or extinction aftershock?' In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150437. DOI: 10.1098/rstb.2015.0437.
- Still, Christopher J., Joseph A. Berry, G. James Collatz & Ruth S. DeFries (2003). 'Global distribution of C3 and C4 vegetation: Carbon cycle implications'. In: *Global Biogeochemical Cycles* 17.1, pp. 6–16–14. DOI: 10.1029/2001gb001807.
- Tilman, D. & J. A. Downing (1994). 'Biodiversity and stability in grasslands'. In: *Nature* 367, pp. 363–365. DOI: 10.1038/367363a0.
- Tilman, D., F. Isbell & J. M. Cowles (2014). 'Biodiversity and ecosystem functioning'. In: *Annual Review of Ecology, Evolution, and Systematics* 45, pp. 471–493. DOI: 10.1146/annurev-ecolsys-120213-091917.
- Tilman, D., P. B. Reich & F. Isbell (2012). 'Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory'. In: *Proceedings of the National Academy of Sciences* 109.26, pp. 10394–10397. DOI: 10.1073/pnas.1208240109.
- Timberlake, J. R., G. M. Calvert, J. A. Morris & Forestry Commission (1993). *Preliminary root atlas for Zimbabwe and Zambia*. Forest Research Centre.
- Tobner, C. M., A. Paquette, D. Gravel, P. B. Reich, L. J. Williams & C. Messier (2016). 'Functional identity is the main driver of diversity effects in young tree communities'. In: *Ecology Letters* 19, pp. 638–647. DOI: 10.1111/ele.12600.
- Tomlinson, Kyle W., Frank J. Sterck, Frans Bongers, Dulce A. da Silva, Eduardo R. M. Barbosa, David Ward, Freek T. Bakker, Martijn van Kaauwen, Herbert H. T. Prins, Steven de Bie et al. (2012). 'Biomass partitioning and root morphology of savanna trees across a water gradient'. In: *Journal of Ecology* 100.5, pp. 1113–1121. DOI: 10.1111/j.1365-2745.2012.01975.x.
- Torello-Raventos, Mireia, Ted R. Feldpausch, Elmar Veenendaal, Franziska Schrodt, Gustavo Saiz, Tomas F. Domingues, Gloria Djangbletey, Andrew Ford, Jeanette Kemp, Beatriz S. Marimon et al. (2013). 'On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions'. In: *Plant Ecology and Diversity* 6.1, pp. 101–137.
- Turnbull, Lindsay A., Forest Isbell, Drew W. Purves, Michel Loreau & Andy Hector (2016). 'Understanding the value of plant diversity for ecosystem functioning through niche theory'. In: *Proceedings of the Royal Society B: Biological Sciences* 283.1844, p. 20160536. DOI: 10.1098/rspb.2016.0536.
- Urban, Josef, Miles Ingwers, Mary Anne McGuire & Robert O. Teskey (2017). 'Stomatal conductance increases with rising temperature'. In: *Plant Signaling and Behavior* 12.8, pp. 1–4. DOI: 10.1080/15592324.2017.1356534.
- Vadigi, Snehalatha & David Ward (2013). 'Shade, nutrients, and grass competition are important for tree sapling establishment in a humid savanna'. In: *Ecosphere* 4.11, art142. DOI: 10.1890/ES13-00239.1.
- Van Coller, H., F. Siebert, P. F. Scogings & S. Ellis (2018). 'Herbaceous responses to herbivory, fire and rainfall variability differ between grasses and forbs'. In: *South African Journal of Botany* 119, pp. 94–103. DOI: 10.1016/j.sajb.2018.08.024.
- Veldman, Joseph W., Elise Buisson, Giselda Durigan, G Wilson Fernandes, Soizig Le Stradic, Gregory Mahy, Daniel Negreiros, Gerhard E Overbeck, Robin G Veldman, Nicholas P Zaloumis et al. (2015). 'Toward an old-growth concept for grasslands, savannas, and woodlands'. In: *Frontiers in Ecology and the Environment* 13.3, pp. 154–162. DOI: 10.1890/140270.
- Veldman, Joseph W. (2016). 'Clarifying the confusion: old-growth savannas and tropical ecosystem degradation'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150306. DOI: 10.1098/rstb.2015.0306.
- Vergles, E., H. Djoudi, R R Blackie, C Koffi Koame & D Gautier (2015). 'Dry Forests, Livelihoods and Poverty Alleviation: Understanding Current Trends'. In: *International Forestry Review* 17.S2, pp. 54–69. DOI: 10.1505/146554815815834868.
- Violle, Cyrille, Wilfried Thuiller, Nicolas Mouquet, François Munoz, Nathan J. B. Kraft, Marc W. Cadotte, Stuart W. Livingstone & David Mouillot (2017). 'Functional Rarity: The Ecology of Outliers'. In: *Trends in Ecology and Evolution* 32.5, pp. 356–367. DOI: 10.1016/j.tree.2017.02.002.

- Vitousek, Peter M, Harold a Mooney, Jane Lubchenco & Jerry M Melillo (1997). 'Human Domination of Earth' s Ecosystems'. In: *Science* 277.5325, pp. 494–499. DOI: 10.1126/science.277.5325.494.
- Wakeling, J. L., W. J. Bond, M. Ghau & E. C. February (2015). 'Grass competition and the savanna-grassland 'treeline': A question of root gaps?' In: *South African Journal of Botany* 101, pp. 91–97. DOI: 10.1016/j.sajb.2014.09.007.
- Wakeling, Julia L., A. Carla Staver & William J. Bond (2011). 'Simply the best: The transition of savanna saplings to trees'. In: *Oikos* 120.10, pp. 1448–1451. DOI: 10.1111/j.1600-0706.2011.19957.x.
- Walter, H. (1971). *Ecology of tropical and sub-tropical vegetation*. Edinburgh, United Kingdom: Oliver and Boyd.
- Watson, James E. M., Kendall R. Jones, Richard A. Fuller, Moreno Di Marco, Daniel B. Segan, Stuart H. M. Butchart, James R. Allan, Eve McDonald-Madden & Oscar Venter (2016). 'Persistent Disparities between Recent Rates of Habitat Conversion and Protection and Implications for Future Global Conservation Targets'. In: *Conservation Letters* 9.6, pp. 413–421. DOI: 10.1111/conl.12295.
- Weltzin, Jake F. & Guy R. McPherson (1999). 'FACILITATION OF CONSPECIFIC SEEDLING RECRUITMENT AND SHIFTS IN TEMPERATE SAVANNA ECOTONES'. In: *Ecological Monographs* 69.4, pp. 513–534. DOI: 10.1890/0012-9615(1999)069[0513:focsra]2.0.co;2.
- Werf, G. R. van der, J. T. Randerson, L. Giglio, G. J. Collatz, M. Mu, P. S. Kasibhatla, D. C. Morton, R. S. DeFries, Y. Jin & T. T. van Leeuwen (2010). 'Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009)'. In: *Atmospheric Chemistry and Physics* 10.23, pp. 11707–11735. DOI: 10.5194/acp-10-11707-2010.
- Werf, Guido R. van der, James T. Randerson, Louis Giglio, Thijs T. van Leeuwen, Yang Chen, Brendan M. Rogers, Mingquan Mu, Margreet J. E. van Marle, Douglas C. Morton, G. James Collatz et al. (2017). 'Global fire emissions estimates during 1997–2016'. In: *Earth System Science Data* 9.2, pp. 697–720. DOI: 10.5194/essd-9-697-2017.
- Werger, M. J. A. & B. J. Coetsee (1978). 'The Sudano-Zambezian Region'. In: *Biogeography and Ecology of Southern Africa*. Springer Netherlands, pp. 301–462. DOI: 10.1007/978-94-009-9951-0_10.
- White, F. (1983). *The Vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*. Paris, France: UNESCO. DOI: 10.2307/2260340.
- Wiegand, K., D. Saltz & D. Ward (2006). 'A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna'. In: *Perspectives in Plant Ecology, Evolution and Systematics* 7.4, pp. 229–242. DOI: 10.1016/j.ppees.2005.10.001.
- Wigley, Benjamin J., A. Carla Staver, Roma Zytowskiak, Andrzej M. Jagodzinski & Corli Wigley-Coetsee (2019). 'Root trait variation in African savannas'. In: *Plant and Soil* 441.1-2, pp. 555–565. DOI: 10.1007/s11104-019-04145-3.
- Wilk, J., L. Andersson, P. Wolski, D. Kgathi, S. Ringrose & C. Vanderpost (2010). 'Changing Flow in the Okavango Basin: Upstream Developments and Downstream Effects'. In: *Integrated Watershed Management: Perspectives and Problems*. Ed. by E. Beheim, G. S. Rajwar, M. J. Haigh & J. Kreček. Dordrecht, Netherlands: Springer. Chap. Changing F, pp. 99–113.
- Williams, Mathew, Paul A. Schwarz, Beverly E. Law, James Irvine & Meredith R. Kurpius (2005). 'An improved analysis of forest carbon dynamics using data assimilation'. In: *Global Change Biology* 11.1, pp. 89–105. DOI: 10.1111/j.1365-2486.2004.00891.x.
- Williams, R. J., B. A. Myers, W. J. Muller, G. A. Duff & D. Eamus (1997). 'LEAF PHENOLOGY OF WOODY SPECIES IN A NORTH AUSTRALIAN TROPICAL SAVANNA'. In: *Ecology* 78.8, pp. 2542–2558. DOI: 10.1890/0012-9658(1997)078[2542:lpowsi]2.0.co;2.
- Wright, A. J., W. D. A. Wardle, W. R. Callaway & A. Gaxiola (2017). 'The overlooked role of facilitation in biodiversity experiments'. In: *Trends in Ecology and Evolution* 32, pp. 383–390. DOI: 10.1016/j.tree.2017.02.011.
- Wright, Alexandra J., Kathryn E. Barry, Christopher J. Lortie & Ragan M. Callaway (2021). 'Biodiversity and ecosystem functioning: Have our experiments and indices been underestimating the role of facilitation?' In: *Journal of Ecology* 109.5. Ed. by Mark Rees, pp. 1962–1968. DOI: 10.1111/1365-2745.13665.
- Wunder, Sven, Arild Angelsen & Brian Belcher (2014). 'Forests, Livelihoods, and Conservation: Broadening the Empirical Base'. In: *World Development* 64, S1–S11. DOI: 10.1016/j.worlddev.2014.03.007.
- Xu, Xiangtao, David Medvigy & Ignacio Rodriguez-Iturbe (2015). 'Relation between rainfall intensity and savanna tree abundance explained by water use strategies'. In: *Proceedings of the National Academy of Sciences* 112.42, pp. 12992–12996. DOI: 10.1073/pnas.1517382112.
- Yachi, S. & M. Loreau (1999). 'Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis'. In: *Proceedings of the National Academy of Sciences* 96.4, pp. 1463–1468. DOI: 10.1073/pnas.96.4.1463.
- Zhang, Yu, Han Y. H. Chen & Peter B. Reich (2012). 'Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis'. In: *Journal of Ecology* 100.3, pp. 742–749. DOI: 10.1111/j.1365-2745.2011.01944.x.