Shackleton (2000) found significantly less herbaceous cover and lower vegetation height in communal lands than protected areas, yet the communal lands also had significantly higher species richness.

The functional diversity aspect of biodiversity can often be inferred from structural diversity. Structural complexity has been linked with, amongst others, productivity (Aguiar & Sala 1999; Ishii *et al.* 2004), habitability and species richness (Halaj *et al.* 2000), regulation of edge effects (Harper *et al.* 2005), groundwater regulation (Ilstedt et al., 2016), and ecosystem health and integrity (Manning *et al.* 2006). At landscape levels, the spatial heterogeneity of flora and fauna habitats and their complex interactions in three dimensional space affects the distribution of biodiversity (Tews *et al.* 2004; Hall *et al.* 2011). An often neglected aspect of structural diversity is vertical complexity. It has relevance to ecosystem function as canopy height is related to biomass and productivity (Lefsky *et al.* 2002b), biodiversity (Herremans 1995; Halaj *et al.* 2000; Lumsden & Bennett 2005) and contributes to structural heterogeneity (Hall *et al.* 2011).

Studies of landscape structural characteristics (e. g. structural richness, structural extent and structural diversity) and how they affect landscape biodiversity are essential (Waldhardt, 2003) for natural resource management. In the context of agro-ecological landscapes, evidence suggests that heterogeneous landscapes which resemble natural patterns are more functional and productive than structurally simple landscapes (Fischer *et al.* 2006).

Cattle farming is frequently implicated as a culprit of vegetation structure changes; the shifting grazing localities also mean that the effects of cattle on the landscape (e.g. increasing soil nutrients through defecation, increasing moisture availability & lowering fire frequency through grass removal, high grazer selectivity) are widespread (Moleele *et al.* 2002)…. bush encroachment has been shown to result in lower livestock carrying capacity and decreased survival rate for calves (Oba *et al.* 2000). Moreover, bush encroachment can change the behaviour of ungulates which avoid densely vegetated areas, creating a cascade of effects on the herbaceous vegetation (Riginos & Grace, 2008)

…structural landscape changes could provide different ecological functions, albeit with ecological repercussions (Hobbs et al., 2014; van de Koppel et al., 2002). Loss of tall trees may result in increased forage availability for small ungulates through coppicing shoots; however it reduces the abundance of woodland birds, in particular the canopy specialists (Herremans, 1995). Spatial heterogeneity has been linked to stabilising populations and functional heterogeneity (Owen-Smith, 2004).

.. Elephant-fire contributions to large tree mortality, together with tree seedling suppression in the ‘fire trap’ (*sensu* Higgins *et al.* 2000) and cascading interactions with seedling herbivores (Rutina et al., 2005), have contributed to a reduction in large trees (Barnes, 1983; Eckhardt et al., 2000).

Savanna woody vegetation is largely fire-resilient: vegetation composition is largely unchanged by fire and individuals rarely suffer mortality, but vegetation structure is fire-responsive (S I Higgins et al., 2007; Pellegrini et al., 2015). Lower tree and greater grass biomass on gabbro geology drives more frequent fire returns in this landscape (Figure 5.5), facilitating treefall in previously damaged trees, which substantially increases tree mortality (Shannon et al., 2011). This is particularly pertinent for tree species preferentially targeted by elephants, resulting in large areas with missing size classes of long-lived trees(Helm and Witkowski 2012).

Although this research shows that both elephants and humans are substantial drivers of treefall in savannas and utilize all height classes of woody vegetation, tree loss *per se* does not result in woodland decline unless accompanied by lack of seedling recruitment (Augustine and McNaughton 1988). This occurs directly through loss of mature, seed-bearing trees and seedling herbivory by elephants or human livestock (e.g. elephants: Western and Maitumo 2004, goats: Hester *et al.* 2006), or indirectly, by rendering the trees ‘functionally juvenile’ through repeated hedging. Additionally, changes in woodland structure can trigger a cascade of interactions, such as that in Chobe riverfront, Botswana, where elephant-induced shrubland conversion facilitated increased seedling herbivory by expanding impala, *Aepyceros melampus,* habitat (Rutina et al 2005). Similarly, in human-associated woodlands, increased coppice regrowth and bush encroachment favors browsing goats over grazing cattle. To compound issues of tree seedling survival, human presence is associated with more frequent fires, trapping tree seedlings in the fire layer.

Humans can act as ‘functional megaherbivores’: their impact on savanna vegetation <5m in height exceeds that of both elephants and fire (Wessels et al., 2011) and their contribution to tall tree loss is substantial (Chapter 5). Structural complexity reduction has also been recorded in east African miombo savannas where 50% of the woodlands was lost with an accompanying 599% increase in bushlands as a result of communal land use (Luoga et al., 2005). Based on the findings in this thesis, I posit a relationship between intensity of natural resource use, vegetation dynamics and structural heterogeneity with repercussions for ecosystem and human resilience, as well as biodiversity and ecosystem function (Figure 6.1). At low levels of natural resource use, both height-specific gains and loss of vegetation structural metrics are low and structural heterogeneity of the vegetation is maintained (Figure 6.1). As usage intensity increases, so do losses in vegetation structural metrics; fairly obvious as vegetation is being extracted. However, there are height-specific gains in some vegetation metrics as compensatory growth occurs with increasing harvesting. Intermediate use scenarios may contain increased biodiversity (Shackleton 2000b; Smart *et al.* 2005). The paradoxical relationship strengthens with increasing usage intensity, resulting in a situation of high growth metrics, predominantly in the shrub layers (Figure 6.1). Under such high intensity, loss metrics decrease as there are fewer tall trees to remove.

References

Aguiar, M. R., & Sala, O. E. (1999). Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution*, *14*(7), 273–277.

Augustine, D. J., & McNaughton, S. J. (1988). Ungulate Effects on the Functional Species Composition of Plant Communities : Herbivore Selectivity and Plant Tolerance. *The Journal of Wildlife Management*, *62*(4), 1165–1183.

Barnes, R. F. W. (1983). Effects of elephant browsing on woodlands in a Tanzanian National Park: Measurements, Models and Management. *Journal of Applied Ecology*, *20*, 521–540.

Eckhardt, H. C., Wilgen, B. W. Van, & Biggs, H. C. (2000). Trends in woody vegetation cover in the Kruger National Park , South Africa , between 1940 and 1998, 108–115.

Fischer, J., Lindenmayer, D. B., & Manning, A. D. (2006). Biodiversity, Ecosystem Function, and Resilience: Ten Guiding Principles for Commodity Production Landscapes. *Frontiers in Ecology and the Environment*, *4*(2), 80–86.

Halaj, J., Ross, D. W., & Moldenke, A. R. (2000). Importance of Habitat Structure to the Arthropod Food-Web in Douglas-Fir Canopies. *Oikos*, *90*(1), 139–152.

Hall, F. G., Bergen, K., Blair, J. B., Dubayah, R., Houghton, R., Hurtt, G., Kellndorfer, J., Lefsky, M., Ranson, J., Saatchi, S., Shugart, H. H., & Wickland, D. (2011). Characterizing 3D vegetation structure from space: Mission requirements. *Remote Sensing of Environment*, *115*(11), 2753–2775. https://doi.org/10.1016/j.rse.2011.01.024

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaiteh, M. S., & Esseen, P. (2005). Edge Influence on Forest Structure and Composition in Fragmented Landscapes. *Conservation Biology*, *19*(3), 768–782.

Helm, C. V, & Witkowski, E. T. F. (n.d.). Author ’ s personal copy Forest Ecology and Management Characterising wide spatial variation in population size structure of a keystone African savanna tree. https://doi.org/10.1016/j.foreco.2011.09.024

Herremans, M. (1995). Effects of woodland modification by African elephant Loxodonta africana on bird diversity in northern Botswana. *Ecography*, *18*(4), 440–454. https://doi.org/10.1111/j.1600-0587.1995.tb00147.x

Hester, A. J., Scogings, P. F., & Trollope, W. S. W. (2006). Long-term impacts of goat browsing on bush-clump dynamics in a semi-arid subtropical savanna, 277–290. https://doi.org/10.1007/s11258-005-9039-6

Higgins, S I, Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin, B., Govender, N., Rademan, L., O’Regan, S., Potgieter, A. L. F., Scheiter, S., Sowry, R., Trollope, L., & Trollope, W. S. W. (2007). Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, *88*(5), 1119–1125. https://doi.org/10.1890/06-1664

Higgins, Steven I, Bond, W. J., & Trollope, W. S. W. (2000). Fire, resprouting and variability: a recipe for grass-tree in savanna coexistence. *Journal of Ecology*, *88*(2), 213–229.

Hobbs, R. J., Higgs, E., Hall, C. M., Bridgewater, P., Chapin, F. S., Ellis, E. C., Ewel, J. J., Hallett, L. M., Harris, J., Hulvey, K. B., Jackson, S. T., Kennedy, P. L., Kueffer, C., Lach, L., Lantz, T. C., Lugo, A. E., Mascaro, J., Murphy, S. D., Nelson, C. R., Perring, M. P., Richardson, D. M., Seastedt, T. R., Standish, R. J., Starzomski, B. M., Suding, K. N., Tognetti, P. M., Yakob, L., & Yung, L. (2014). Managing the whole landscape: Historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment*, *12*(10), 557–564. https://doi.org/10.1890/130300

Ilstedt, U., Bargués Tobella, A., Bazié, H. R., Bayala, J., Verbeeten, E., Nyberg, G., Sanou, J., Benegas, L., Murdiyarso, D., Laudon, H., Sheil, D., & Malmer, A. (2016). Intermediate tree cover can maximize groundwater recharge in the seasonally dry tropics. *Nature*, *6*(February 2015), 21930. https://doi.org/10.1038/srep21930

Ishii, H. T., Tanabe, S., & Hiura, T. (2004). Exploring the relationships among canopy structure, stand productivity , and biodiversity of temperate forest ecosystems. *Forest Science*, *50*(3), 342–355.

Lefsky, M. A., Cohen, W. B., Parker, G. G., & Harding, D. J. (2002). Lidar Remote Sensing for Ecosystem Studies. *BioScience*, *52*(1), 19–30.

Lumsden, L. F., & Bennett, A. F. (2005). Scattered trees in rural landscapes : foraging habitat for insectivorous bats in south-eastern Australia, *122*, 205–222. https://doi.org/10.1016/j.biocon.2004.07.006

Luoga, E. J., Witkowski, E. T. F., & Balkwill, K. (2005). Land Cover and Use Changes in Relation to the Institutional Framework and Tenure of Land and Resources in Eastern Tanzania Miombo Woodlands. *Environment, Development and Sustainability*, *7*(1), 71–93. https://doi.org/10.1007/s10668-003-4013-8

Manning, A. D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures – Implications for conservation. *Biological Conservation*, *132*, 311–321. https://doi.org/10.1016/j.biocon.2006.04.023

Moleele, N. M., Ringrose, S., Matheson, W., & Vanderpost, C. (2002). More woody plants ? the status of bush encroachment in Botswana ’ s grazing areas, 3–11. https://doi.org/10.1006/jema.2001.0486

Oba, G., Post, E., Syvertsen, P. O., & Stenseth, N. C. (2000). Bush cover and range condition assessments in relation to landscape and grazing in southern Ethiopia. *Landscape Ecology*, *15*, 535–546.

Owen-Smith, N. (2004). Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, *19*(7), 761–771. https://doi.org/10.1007/s10980-005-0247-2

Pellegrini, A. F. A., Hedin, L. O., Staver, A. C., & Govender, N. (2015). Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry or composition in tropical savanna. *Ecology*, *96*(5), 1275–1285. https://doi.org/10.1890/14-1158.1

Riginos, C., & Grace, J. B. (2008). Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, *89*(8), 2228–2238.

Rutina, L. P., Moe, S. R., Swenson, J. E., & Loxodonta, J. E. E. (2005). Elephant Loxodonta africana driven woodland conversion to shrubland improves dry-season browse availability for impalas Aepyceros melampus, (Rutina 2004), 207–213.

Shackleton, C. M. (2000). Comparison of plant diversity in protected and communal lands in the Bushbuckridge lowveld savanna, South Africa. *Biological Conservation*, *94*, 273–285.

Shannon, G., Thaker, M., Vanak, A. T., Page, B. R., Grant, R., & Slotow, R. (2011). Relative Impacts of Elephant and Fire on Large Trees in a Savanna Ecosystem, 1372–1381. https://doi.org/10.1007/s10021-011-9485-z

Smart, R., Whiting, M. J., & Twine, W. (2005). Lizards and landscapes: integrating field surveys and interviews to assess the impact of human disturbance on lizard assemblages and selected reptiles in a savanna in South Africa. *Biological Conservation*, *122*(1), 23–31. https://doi.org/10.1016/j.biocon.2004.06.016

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

van de Koppel, J., Rietkerk, M., Langevelde, F. Van, Kumar, L., Klausmeier, C. A., Fryxell, J. M., Hearne, J. W., Andel, J. Van, de Ridder, N., Skidmore, A., Stroosnijder, L., & Prins, H. H. T. (2002). Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *The American Naturalist*, *159*(2), 209–218.

Waldhardt, R. (2003). Biodiversity and landscape—summary, conclusions and perspectives. *Agriculture, Ecosystems & Environment*, *98*(1–3), 305–309. https://doi.org/10.1016/S0167-8809(03)00090-2

Wessels, K. J., Mathieu, R., Erasmus, B. F. N., Asner, G. P., Smit, I. P. J., van Aardt, J. A. N., Main, R., Fisher, J., Marais, W., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., & Jacobson, J. (2011). Impact of communal land use and conservation on woody vegetation structure in the Lowveld savannas of South Africa. *Forest Ecology and Management*, *261*(1), 19–29. https://doi.org/10.1016/j.foreco.2010.09.012

Western, D., & Maitumo, D. (2004). Woodland loss and restoration in a savanna park : a 20-year experiment, 111–121.