Utrecht University

Faculty of Geosciences
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The associations between grazing, soil N:P stoichiometry and carbon pools in Hluhluwe-iMfolozi Park

Master's thesis

to achieve the academical degree
"Master of Science"
in the degree course "Sustainable Development"

submitted by
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Utrecht, August 2020

Preface

You will be reading my Master's thesis on the associations between grazing, soil N:P stoichiometry and carbon pools in Hluhluwe-iMfolozi Park, the basis of which is an analysis of soil samples from the named game reserve in South Africa. I wrote it to fulfil the graduation requirements of the Sustainable Development programme at Utrecht University and was engaged in researching and writing this thesis from November 2019 to August 2020.

As far as I am concerned, two of the world's most pressing problems are climate change and the loss of biodiversity. In this project, I had the chance to contribute to research on both issues. What started with an interest in savanna ecosystems ended in an appreciation of the diverse and often endangered African wildlife. The thesis showed me the importance of wildlife in shaping and maintaining ecosystems, and that its function and protection are not only relevant for the preservation of intact ecosystems but may also create opportunities for climate change mitigation. Besides, the process taught me how to approach and conduct research in ecology and trained me in analytical and conceptual thinking, scientific writing, cooperative working, and self-learning. After all, I feel I have developed as an ecologist and as a researcher and I am motivated to pursue work in conservation after graduation.

Without the great support I was provided, I am certain that I could not have finalized the project as it has become. A special thanks goes to Joris Cromsigt for his excellent guidance and support and his valuable advice and high input during the process. I would like to greatly thank Olli Hyvärinen for letting me undertake a side project to his PhD dissertation, for always being available for questions and discussions and helping me out, and for his encouraging words. Many thanks also to Mariska te Beest for giving me the opportunity to work on my desired project and to Ezemvelo KwaZulu-Natal Wildlife for letting me conduct my research in Hluhluwe-iMfolozi Park. Furthermore, I am grateful for the active support I received and the people that sweated with me during the hard fieldwork in South Africa. These include Phumlani Mangethe (field technician), Eric Khumalo and Falake Dlamini (rangers), and Emilia Malmström (research assistant). Thanks for sharing your knowledge about the bush and its species, for keeping me save and making the work yet so enjoyable. Lastly, I appreciate the willingness of Mara Baudena to review this thesis.

Katharina Jüdt
Utrecht, 30th August 2020

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Summary

Climate change mitigation measures currently concentrate on forests to increase carbon sequestration in aboveground biomass. We should however share the focus with savannas that exhibit a large storage potential of soil organic carbon (SOC) and cover 20% of the land surface. Herbivory represents a main driver of savannas and influences SOC pools via SOC input and via nutrient availability. However, we know little about the influence of wild large herbivores on SOC pools in savannas. As opposed to livestock grazing, grazing by wild large mammals could maintain or enhance SOC sequestration. In fact, previous studies suggested that SOC sequestration increases with increasing grazing intensity in C_4-grasslands due to, at least partly, the stimulation of fine root production and arbuscular mycorrhizal (AM) associations through an increased nutrient demand of grasses after defoliation. In this regard, the return of nutrients to the soil by excretion may specifically influence SOC sequestration via plant productivity and via microbial activity. Studies found dung nitrogen:phosphorus (N:P) ratios to increase with increasing herbivore body size so that the dominance of mesoherbivores or megaherbivores could lead to N or P limitation, respectively. In this thesis, I examined two treatments – grazing intensity with three levels (intense, intermediate, light) and latrine type with two levels (impala, white rhino) – in Hluhluwe-iMfolozi Park, South Africa, and took soil samples in blocks and at two depths (0-5 cm, 5-15 cm) to explore grass (fine) root:shoot ratios, AM grass root infection rates, SOC pools, and soil N:P ratios. I used linear mixed-effect models to analyse the data. SOC pools increased under light versus intermediate grazing in the lower soil layer, although did not differ under intense grazing. (Fine) root:shoot ratios and AM infection rates tended to increase under intense grazing and therefore did not explain this variation in SOC pools. In both layers, SOC pools were higher around white rhino than impala latrines, probably due to a larger SOC and total nutrient input via dung. Furthermore, AM root infection rates increased around impala latrines in the lower layer, possibly explained by the evident increase of soil N:P ratios compared to white rhino latrines, suggesting a minor impact of dung N:P supply ratios on soil N:P ratios around latrines. I concluded that due to a low sample size but clear trends in the data, this research might provide a basis for further research, prior recommendations on management of herbivory and climate models.

Keywords: grazing intensity, N:P stoichiometry, SOC pools, arbuscular mycorrhizal fungi, root:shoot ratio, latrine, megaherbivores, white rhino, African savanna, Hluhluwe-iMfolozi Park

1 Introduction

1.1 Savannas within the climate debate

It has been widely recognized that anthropogenic carbon dioxide emissions largely drive global warming (Rockström et al., 2009). Land use changes and soil degradation represent a major carbon source and may result in the depletion of soil organic carbon (SOC) pools (Lal, 2004). SOC pools retain more carbon than the atmosphere and vegetation together (Stocker et al., 2013), and we therefore need nature conservation, land management and sustainable agricultural practices to prevent large SOC losses. In addition, maintaining and increasing the carbon sequestration potential of unsaturated soils represents an approach to mitigate climate change (Lal, 2004). With a high aboveground biomass, the current focus of climate change mitigation measures lies on forests whereas savannas and grasslands, that may store large amounts of carbon belowground, receive much less attention in the literature and in conservation efforts (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014). This poses a problem since savannas cover approximately 20% of the terrestrial world and store 15% of the terrestrial carbon (Parr et al., 2014).

Abiotic factors, such as rainfall, fire and soil, and biotic factors, such as herbivory by large mammals, shape and maintain savannas (Staver, Archibald, & Levin, 2011), characterized by the coexistence of grasses and trees with a varying tree cover of up to 80% (Parr et al., 2014). As one of the system drivers, large mammals are thought to shape the carbon storage capacity of savannas by grazing (Schmitz et al., 2018). Here, grazing is defined as grassland utilization and includes foraging, trampling and excretion. Current studies are strongly biased towards studying the effect of grazing on SOC sequestration in temperate, livestock-dominated C_3-grasslands and proposed SOC sequestration to negatively respond to grazing intensity (Zhou et al., 2017; McSherry & Ritchie, 2013). Livestock-dominated systems often represent a SOC source due to overgrazing, which is problematic since domesticated mammals graze on most grasslands (Reid et al., 2003). Wild large herbivores, however, are thought to increase carbon sequestration (Doughty et al., 2016) and could be managed to contribute towards mitigating climate change (Cromsigt et al., 2018). In addition, studies suggested that SOC sequestration increases with increasing grazing intensity in C_4-grasslands (McSherry & Ritchie, 2013). Since the world is facing a loss of wild large herbivores (Ripple et al., 2015) and a general decrease of mammalian body size (Dirzo et al., 2014) due to hunting and land use change, it is thus crucial to explore the influence of wild large herbivores on SOC sequestration to better understand the climate change mitigation potential of herbivore-dominated savannas. This knowledge is important for the management of herbivory in those grasslands as well as for climate projections.

Furthermore, studies suggested varying mechanisms driving the system responses to variation in grazing intensity (Zhou et al., 2017; McSherry & Ritchie, 2013). Principally, there are two ways: via plant productivity and via microbial activity. Plant productivity determines SOC input which is higher from below- than aboveground litter (Vidal et al., 2018). Microbial activity affects litter decomposition

and thus SOC release. Arbuscular mycorrhizal (AM) fungi represent a special kind of microbes and the dominant type of mycorrhizae in grasslands (Read & Perez-Moreno, 2003). In contrast to bacteria, they acquire carbohydrates from the plant in return for nutrients (Johnson, 2010). We therefore need to improve our understanding of the role of root productivity and AM symbioses in influencing SOC pools in herbivore-dominated savannas.

In addition to the direct impacts on SOC sequestration, the influence of herbivores on the availability of other nutrients, such as nitrogen (N) and phosphorus (P), provides another mechanism through which herbivores affect SOC sequestration. For instance, herbivores transport nutrients due to a spatial decoupling of grazing and defecation and thereby, change nutrient availability. However, they do not only transport nutrients but also change the nutrient stoichiometry (i.e. relative availability of different chemical elements) of savanna ecosystems (Cromsigt et al., 2018) due to different diets and body requirements (le Roux, van Veenhuisen, Kerley, & Cromsigt, in press; Sitters et al., 2017). Studies showed that those stoichiometric variations influence plant productivity and diversity (Valdés-Correcher, Sitters, Wassen, Brion, & Olde Venterink, 2019), microbial activity (Güsewell & Gessner, 2009) and AM biomass and colonization of roots (Johnson, Rowland, Corkidi, Egerton-Warburton, & Allen, 2003). Moreover, climate models, that incorporate the combined effect of N and P limitation on primary production, showed a reduced global average carbon uptake of 25% compared to simulations that neglected nutrient limitation (Goll et al., 2012). Therefore, we need to better understand how herbivore-driven changes in nutrient availability affect SOC sequestration. This again will give improved insight into the climate change mitigation potential of herbivore-dominated savannas.

1.2 Research objectives and question

With this research, I aimed to evaluate (1) the relation between wild ungulate grazing intensity and SOC levels, and (2) the relation between mesoherbivore (100-1000 kg) versus megaherbivore (>1000 kg) utilization, soil N:P stoichiometry and SOC levels in Hluhluwe-iMfolozi Park, South Africa. Furthermore, my objectives were to assess the impact of grazing intensity and herbivore-induced N:P stoichiometry on (A) grass (fine) root:shoot ratios and (B) AM grass root infection rates. I hereby addressed the knowledge gap between grazing, nutrient availability, and SOC pools in savannas. I achieved the research objectives by comparing (A) grass (fine) root:shoot ratios, (B) AM grass root infection rates, and (C) SOC pools in the upper two soil layers (0-5 cm, 5-15 cm) between (1) different levels of grazing intensity and (2) impala (*Aepyceros melampus*; 45 kg) and white rhino (*Ceratotherium simum*; 1600 kg; Owen-Smith, 1988) latrines. The latrine study additionally investigated differences in (D) soil N:P ratios between the two latrine types. While I analysed (fine) root:shoot ratios as proxies for fine root production, AM root infection rates worked as a proxy for AM biomass.

Accordingly, I asked the following research question and sub-questions:

How do grazing intensity and herbivore-induced soil N:P stoichiometry influence carbon pools in savanna soils in in Hluhluwe-iMfolozi Park?

a. How do grass (fine) root:shoot ratios and arbuscular mycorrhizal (AM) grass root infection rates vary among different levels of grazing intensity?
b. How does soil N:P stoichiometry differ between areas utilized by mesoherbivores versus megaherbivores?
c. How do grass (fine) root:shoot ratios and AM grass root infection rates vary with this herbivore-induced soil N:P stoichiometry?
d. How do soil organic carbon (SOC) pools vary with grass (fine) root:shoot ratios and AM grass root infection rates?
e. How do grass (fine) root:shoot ratios, AM grass root infections rates, soil N:P stoichiometry, and SOC pools vary with mean annual rainfall (MAR), fire frequency, soil texture and depth?

2 Theoretical background

2.1 Impact of grazing on soil organic carbon (SOC) and nutrient pools

Ecosystems, SOC and nutrient pools respond to grazing intensity in diverse ways. In Figure 1, I depicted a summary of the mechanisms that may drive those responses. According to the theory of balanced growth, plants allocate biomass to the organ that they need to overcome resource limitation (Shipley & Meziane, 2002). This explains the compensatory growth of aboveground biomass after defoliation (Bardgett & Wardle, 2003). Due to decreased photosynthesis rates, grazing may also lead to the dieback of roots (Klumpp et al., 2009) and AM hyphae (Johnson, 2010) because of carbon starvation. This results in a supply to SOC and nutrient pools and a nutrient loss for plants (Fujita, de Ruiter, Wassen, & Heil, 2010b). Therefore, the nutrient demand of grasses rises after defoliation which stimulates their release of root exudates and may make them invest into fine roots and mycorrhizae (Bardgett & Wardle, 2003). The uptake of root exudates by microbes increases microbial activity which leads to enhanced nutrient mineralization rates and acquisition by plants (Bardgett & Wardle, 2003). A meta-analysis of livestock grazing in global C_3- and C_4-grasslands by Zhou et al. (2017) proposed this effect for lightly grazed systems. Light grazing hereby increased SOC and N stocks, explained by an induced higher above- and belowground biomass production, resulting in an enhanced SOC input via root exudates and root biomass. Intermediate and high grazing intensities, however, reduced SOC and N pools because the grass removal decreased microbial biomass (Liu, Kan, Yang, & Zhang, 2015). The loss of potential SOC input from litter at intermediate and high grazing intensities limited the effect of root exudates on microbial activity and decreased nutrient mineralization (Sankaran & Augustine, 2004). Like root exudates, fine roots and mycorrhizae facilitate nutrient acquisition to support grass growth by increasing the plants' rhizosphere (Bardgett & Wardle, 2003). Following this reasoning, a meta-analysis by McSherry and Ritchie (2013) showed that increases in grazing intensity increased SOC contents in C_4- and mixed grasslands but decreased them in C_3-grasslands. In C_4-grasses, grazing stimulated the production of fine, shallow roots more strongly than in C_3-grasses (Derner, Boutton, & Briske, 2006) and therefore, the already higher root:shoot ratios increased with increasing grazing intensity (Reeder, Schuman, Morgan, & LeCain, 2004). In addition, the development of mycorrhizal hyphae, which is likewise more strongly associated with C_4- than C_3-grasses (Wilson & Harnett, 1998), enhanced with increasing grazing intensity and an increasing nutrient demand for grass regrowth (Eom, Wilson, & Hartnett, 2001). Both senescent fine roots and mycorrhizal hyphae provided input to SOC pools in C_4-grasslands.

Finally, higher SOC pools in C_4-grasslands, as opposed to C_3-grasslands (McSherry & Ritchie, 2013), might also originate from the fact that fires generally occur more frequently in C_4-grasslands (Keeley & Rundel, 2005). These can provide a higher fraction of organic material, that microbes incorporate into the soil, like the incorporation of dung (Dungait, Bol, Bull, & Evershed, 2009). Fire might also lead to an enhanced plant productivity by removing plant litter and thereby increasing light

and soil temperature (Knapp & Seastedt, 1986) which potentially increases SOC input. Several studies however suggested SOC reductions with increasing fire frequency, driven by carbon dioxide and N emissions from vegetation combusted by fire (Pellegrini et al., 2018; Bird, Veenendaal, Moyo, Lloyd, & Frost, 2000). The decline of N pools leads to a decreased plant productivity and therefore to further losses of SOC input (Pellegrini et al., 2018). In addition, herbivores may themselves either reduce or promote fire frequency by removing grass fuel or increasing grass cover in place of tree cover, respectively (Archibald & Hempson, 2016). For the impact of mean annual rainfall (MAR) on rangelands of the Great Plains, Derner and Schuman (2007) found that SOC pools increased with MAR, associated with an enhanced plant productivity and specifically increased fine root biomass in the upper soil layer (Derner et al., 2006). Likewise, clayey soils promote plant productivity by retaining larger amounts of water and nutrients than sandy soils and therefore exhibit larger SOC pools (Bird et al., 2000). In addition, they have a higher potential to stabilize SOC through the adsorption of SOC by fine mineral particles (Bird et al., 2000).

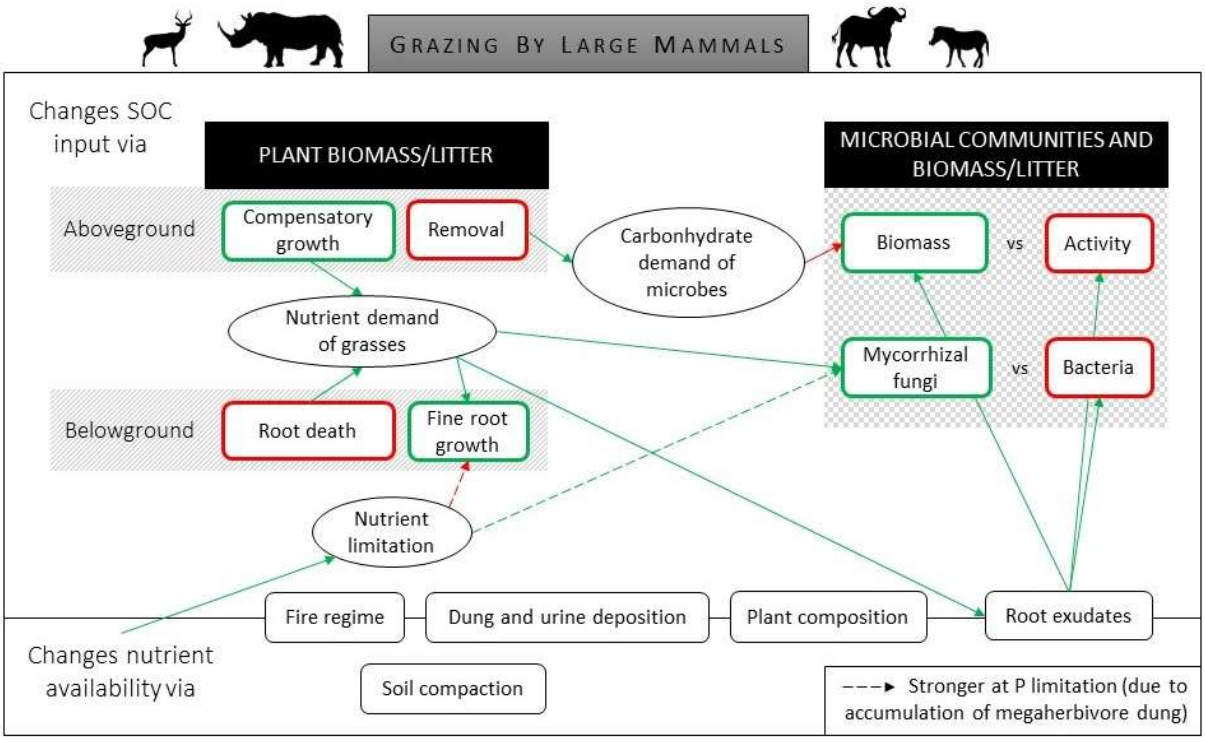

Figure 1: Conceptual framework of impact of grazing by large mammals on soil organic carbon (SOC) pools. Green and red marked variables indicate positive and negative associations between variables and SOC pools, respectively; green and red arrows represent positive and negative effects between variables, respectively.

Furthermore, the removal, transport and return of nutrients affects vegetation which then influences SOC sequestration. In that sense, herbivory influences nutrient cycling rates by returning easily released nutrients in form of dung and urine to the soil (Pastor, Cohen, & Hobbs, 2006). Some savanna ungulates

typically defecate in latrines which are territorial, communal defecating areas (Waldram, Bond, & Stock, 2008; Miller, 1996). Latrines therefore provide extreme examples of nutrient concentration via dung deposition. Herbivory also alters nutrient availability by changing litter composition through selective browsing or a triggered shift in plant composition (Pastor et al., 2006). Moreover, the herbivore-induced establishment of either more trampling-tolerant or trampling-resistant species leads to varying nutrient cycling rates (du Toit & Olff, 2014). Trampling also compacts the soil, which decreases soil moisture especially on clayey soils, and results in lower N mineralization rates. Defoliation reinforces this mechanism by increasing evaporation and reducing infiltration rates (Schrama et al., 2012). Finally, large herbivores may cause shifts in the stoichiometry of savannas (Cromsigt et al., 2018). The return of nutrients to the soil by defecation varies in its N:P ratio, depending on forage quality and body size of the herbivore (le Roux et al., in press; Sitters et al., 2017). Herbivores require N and P for their metabolism which leads to rising N and P requirements with increasing body size. P is an important component of bone tissue (Gillooly et al., 2004) and the proportion of skeleton to body mass increases with herbivore body size (Anderson, Rahn, & Prange, 1979). At constant forage N:P ratios, megaherbivores should therefore have an increased P demand relative to N, compared to mesoherbivores, because they need to invest more P in their skeleton. Le Roux et al. (in press) and Sitters, Maechler, Edwards, Suter, and Olde Venterink (2014) showed megaherbivores to consequently have higher dung N:P ratios than mesoherbivores. The accumulation of megaherbivore relative to mesoherbivore dung thus also influences the return of N and P to the soil (le Roux et al., in press). Megaherbivore dominance may therefore drive grasslands towards P limitation whereas mesoherbivore dominance may support N limitation which likely affects plant productivity and SOC pools.

2.2 Impact of soil N:P stoichiometry on SOC pools

The limitation of one nutrient, that plants require, may limit plant productivity if other nutrient demands are satisfied (Daufresne & Loreau, 2001). Therefore, herbivore-induced N and P limitation might limit root production and hence SOC input from litter. However, grasses are more sensitive to P than N limitation (Fujita, Robroek, de Ruiter, Heil, & Wassen, 2010a; 2010b; Güsewell, 2004). On the one hand, grasses react to P limitation by releasing the enzyme phosphatase to make P plant-available (Fujita et al., 2010a; 2010b). On the other hand, Fujita et al. (2010a; 2010b) observed increased plant root mortality due to P undersupply, compared to N undersupply. Therefore, grass root biomass likely increases with a sufficient availability of P. On the contrary, one might associate P limitation with higher root mortality and/or a prior reduction of root growth to avoid nutrient losses (Olde Venterink & Güsewell, 2010).

Plants can also invest into AM fungi which are especially efficient in acquiring P (Johnson et al., 2003). AM fungi fully depend on carbohydrate provision by plants and form symbioses with plants by providing them with inorganic nutrients. The advantage for plants is that AM hyphae grow beyond the depletion zone of plant roots and can make nutrients, and especially immobile P, plant-available

(Johnson, 2010; Thirkell, Cameron, & Hodge, 2016). The allocation of carbon to AM fungi thus benefits plants the most under P limitation (Johnson et al., 2003). In total, 15% of the SOC pool can consist of extrametrical hyphae of AM fungi (Wilson, Rice, Rillig, Springer, & Hartnett, 2009). Moreover, glomalin, a glycoprotein contained in hyphal walls, represents a stable carbon storage after hyphae senescence (Wilson et al., 2009) and can account for 5% of the SOC pool (Treseder & Turner, 2007). Furthermore, glomalin functions as a long-term binding agent of soil aggregates (Vidal et al., 2018; Wilson et al., 2009; Rillig, 2004), making AM fungi important for SOC persistence through physical protection from decomposition.

2.3 Process of SOC sequestration

Recent studies suggested that SOC persists in soil in various polymer sizes, rather than as distinct pools (Lehmann & Kleber, 2015; Schmidt et al., 2011). The progressive decomposition of those SOC compounds depends on their susceptibility to decomposition due to their molecular chemical composition. In addition, abiotic and biotic factors, such as soil properties, microbial communities, and climatic conditions, determine decomposition because the binding of SOC can physically and chemically protect SOC from decomposition (Lehmann & Kleber, 2015; Schmidt et al., 2011). This process requires the preceding degradation of SOC compounds since mineral surfaces increasingly adsorb SOC of decreasing polymer size, as well as SOC of decreasing polymer size increasingly forms aggregates (Lehmann & Kleber, 2015). Soil enzymes and microbes cannot access bound SOC so that the binding protects it from decomposition (Hemingway et al., 2019; Plaza, Fernández, Pereira, & Polo, 2012). Different kinds of decomposers participate in the process of SOC sequestration at different polymer sizes: soil fauna, exoenzymes (enzymes functioning outside cells) and microbes (Lehmann & Kleber, 2015). Microbes play a fundamental role in this process and influence SOC dynamics through metabolic activity and community structure (Schmidt et al., 2011). They inhabit less than 1% of the soil pores which means that the physical disconnection with decomposers can selectively preserve SOC (Schmidt et al., 2011). The rhizosphere represents the hotspot of sequestration and turnover processes (Vidal et al., 2018). The SOC input from plants, which is higher from below- than aboveground (Vidal et al., 2018; Schmidt et al., 2011), drives this microbial concentration. Roots contain about half of the belowground allocated SOC, roots and microbes respire about one-third, and plants transfer more than 10% to microbial biomass (Jones, Nguyen, & Finlay, 2009). Root products, such as litter and exudates, and microbial litter represent a major source of SOC pools (Vidal et al., 2018; Lehmann & Kleber, 2015). In addition, specific rhizosphere processes bind SOC on mineral surfaces (Vidal et al., 2018).

2.4 Hypotheses

I expected that

a. grazing stimulates AM root colonization and fine root production, and therefore AM grass root infection rates and grass (fine) root:shoot ratios increase with increasing grazing intensity (Figure 2.1).
b. dung N:P ratios increase with increasing herbivore body size, and therefore the contrast in soil N:P ratios is the highest between impala and white rhino latrines with low and high ratios, respectively (Figure 2.2).
c. increases in soil N:P ratios are associated with increases in AM grass root infection rates due to the P acquisition efficiency of AM fungi, and with decreases or no change in grass (fine) root:shoot ratios, due to the enhanced grass root death or an increased P uptake through AM symbioses at P limitation, respectively.
d. increases in AM grass root infection rates and grass (fine) root:shoot ratios are associated with increases in SOC pools via litter. SOC pools hence increase with grazing intensity, too.
e. MAR and soil clay content increase grass productivity, and as a result, increases in MAR and soil clay content are associated with increasing SOC pools whereas the association between fire frequency and SOC pools can be both ways. Either fire frequency supports grass productivity and/or provides carbon for SOC sequestration or it promotes carbon and nutrient losses.

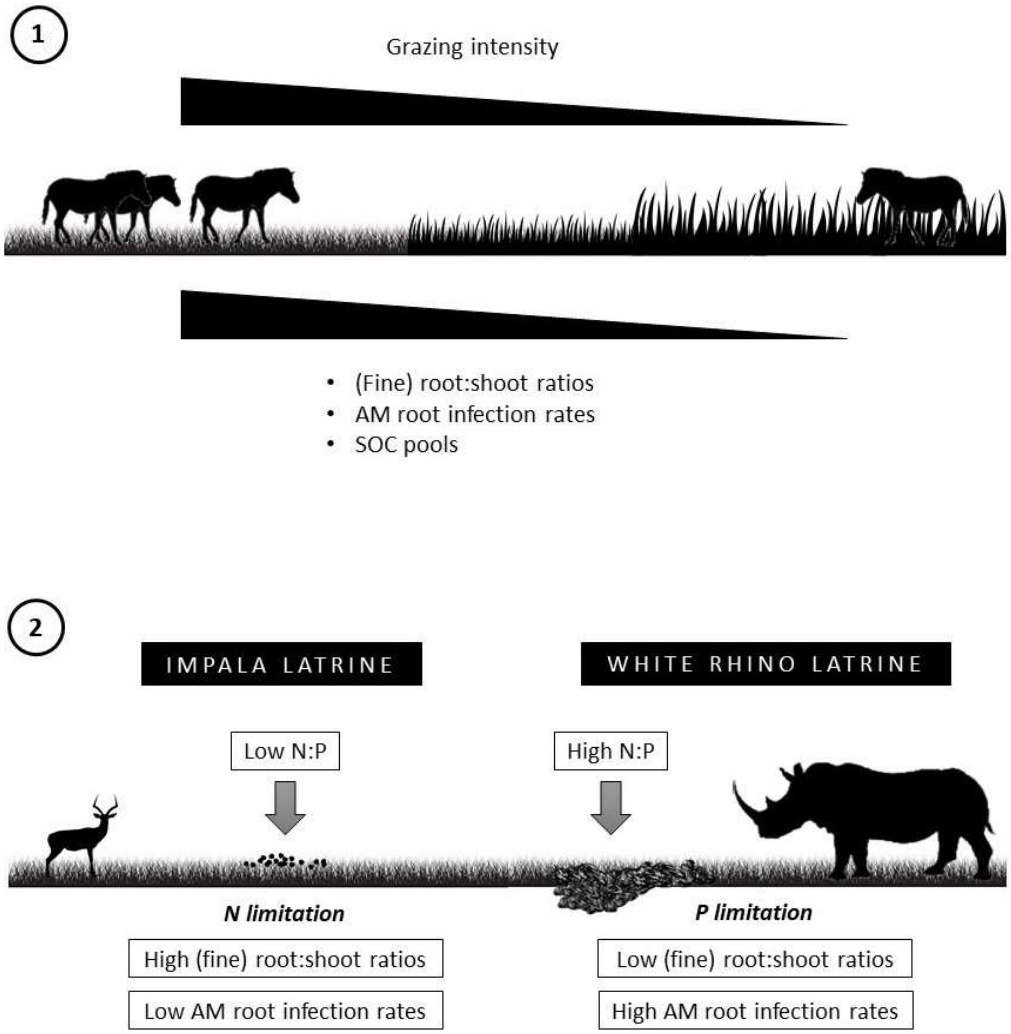

Figure 2: Conceptual framework of hypotheses. Impact of **(1)** grazing intensity and **(2)** dung N:P supply ratios on (fine) root:shoot ratios, arbuscular mycorrhizal (AM) root infection rates, and SOC pools.

3 Material and methods

3.1 Research area

I performed the research in Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa. The reserve covers an area of 90 000 ha and is located in a sub-tropical climate between 28°0'0"S, 28°26'00"S, 31°41'00'E and 32°09'00"E (Figure 3). The altitude in HiP ranges from 20 to 580 m above sea level. Mesic savanna and MAR of 750 mm characterize Hluhluwe, the northern part of the park. On hilltops, MAR may be as high as 1000 mm and generates closed gallery forests. iMfolozi, the southern part of HiP, is drier with MAR of about 600 mm, supporting semi-arid savanna. The vegetation in HiP ranges from grassland to *Acacia* woodland, with grasslands exhibiting the feature of grazing lawns (Waldram et al., 2008). Grazing lawns cover approximately 6.9% of the whole park (Cromsigt et al., 2017). However, in the drier savanna grasslands of iMfolozi, the proportion of grazing lawns may be as high as 20-30% of the total vegetation (Cromsigt et al., 2017). Short, prostrate-growing grass species, such as *Digitaria longiflora*, *Digitaria argyrograpta*, *Urochloa mosambicensis*, *Panicum coloratum* and *Sporobolus nitens*, dominate those lawns. On the contrary, the surrounding tall tussock grassland typically consists of *Themeda triandra*, *Sporobolus pyramidalis* and/or *Hyparrhenia filipendula* (Waldram et al., 2008). HiP possesses a full body-size spectrum of large mammalian herbivores at high densities and is therefore suitable for studying impacts of mesoherbivore versus megaherbivores on the savanna system (le Roux et al., in press).

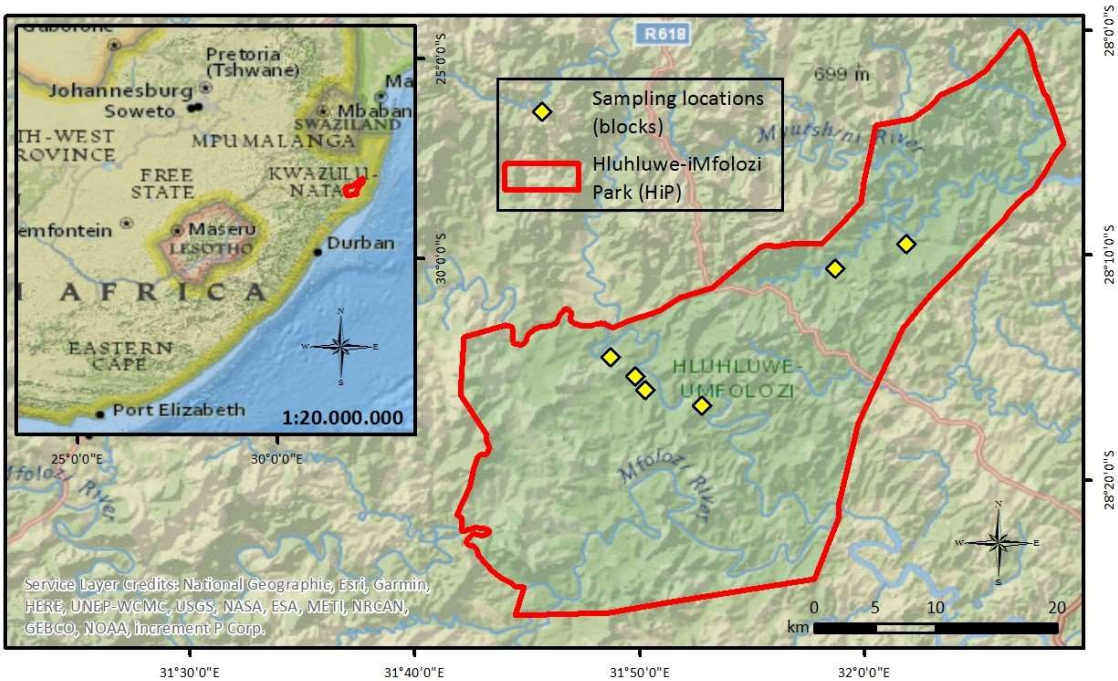

Figure 3: Hluhluwe-iMfolozi Park and sampling locations.

3.2 Research design

The project consisted of two separate studies, each with their own treatment (Figure 4): (1) the grazing intensity study and (2) the latrine study. While I aimed to analyse data along a grazing intensity gradient in the first study, the purpose of the latrine study was to investigate areas influenced by intense dung deposition of mesoherbivores on the one hand, and megaherbivores on the other. For the grazing intensity study, I used three treatment levels: (A) intensely grazed grazing lawn, (B) intermediately grazed tall grassland, and (C) lightly grazed tall grassland. The latrine study included two treatment levels: (E) impala latrine and (F) white rhino latrine. In order to keep abiotic and biotic factors constant, I sampled treatment levels in a block. I hereby kept unknown variation of the measurements caused by unknown factors as limited as possible by sampling treatment levels in close mutual proximity (Bolker, 2008). In the grazing intensity study, I maintained a minimum and maximum distance among different treatment plots within a block of 2.5 m and 50 m, respectively, and a minimum distance between blocks of 500 m. In the latrine study, distances between plots of level E and F ranged from approximately 50 to 150 m. I used a Garmin GPS eTrex 10 to obtain coordinates of each plot's centre and measured their geodesic distances in ArcGIS 10.6.1 (ESRI, 2011). I sampled six blocks resulting in six replicates of each treatment. As an exception, I only sampled five impala latrines because I could not find one close to the sixth block. In addition, I spread blocks across a MAR, fire frequency and soil texture gradient (Appendix A.1) which were determined from long-term park monitoring records (rainfall, soil) and satellite data (fire) derived from MODIS monthly fire-scar data.

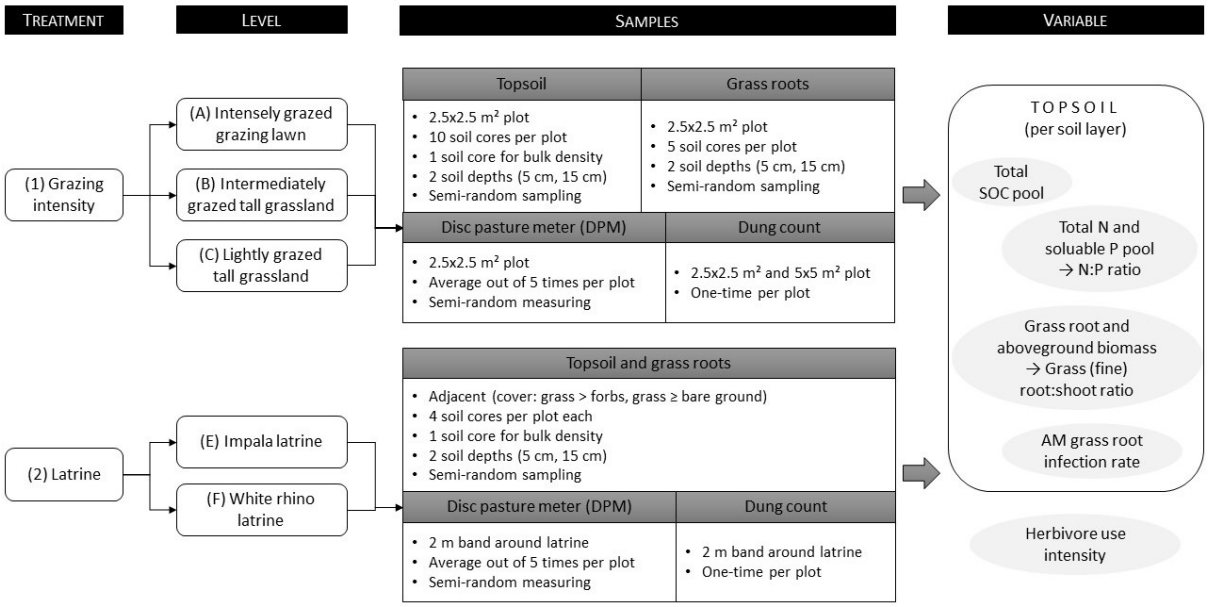

Figure 4: Overview of technical research design.

3.2.1 Grazing intensity study

In each block, I selected three 2.5x2.5 m² plots reflecting an intensely grazed plot (treatment level A), an intermediately grazed plot (level B) and a lightly grazed plot (level C). I based these differences in grazing intensity between the plots on signs of grazing and trampling, grass species composition and disc pasture meter (DPM) measurements. The DPM is a disc (plate) meter for estimating aboveground biomass as the height at which the disc settles on the grass (Harmse, Dreber, & Trollope, 2019; Figure 5F). Within the 2.5x2.5 m^2 plot, I took the average DPM of the four corners and the middle. I associated high grazing intensity plots with short-grass patches (DPM = 2.33 ±0.88 cm, Appendix A.2a) dominated by prostrate growing, often stoloniferous grass species (Waldram et al., 2008), such as *Sporobolus nitens*, *Digitaria longiflora*, *Urochloa mosambicensis*, *Eragrastis superba* and *Panicum coloratum*. On the contrary, the lightly grazed tall grassland consisted of different tussock-forming species that grow upright (DPM = 8.25 ±3.84 cm; Waldram et al., 2008), such as *Panicum maximum*, *Sporobolus pyramidalis*, *Bothriochloa insculpta*, *Cynoden dactylon* and *Themeda triandra*. The intermediately grazed patches exhibited both lawn and bunch species and had a grass biomass that was in between the intensely grazed and lightly grazed patches (DPM = 6.10 ±1.82 cm). I determined grass species with the help of a local field technician and the identification book by Oudtshoorn (2012).

As a second criterion, I selected plots with similar grass, forb, and bare ground cover, consisting of about 85-100% grass, 1-5% forbs and 5-10% bare ground (Appendix A.3). I visually assessed the percentage cover of grass, forbs, and bare ground as aerial cover for every plot. Furthermore, plots did not contain any woody plants and signs of disturbances, such as depressions on the ground, heavily eroded patches, aardvark holes or wallows. I also did not situate them on or next to termite mounds or latrines, and ideally not on a slope. If I sampled on a slope, I placed plots along the same contour, as to prevent the effects caused by potential run-off and leaching interfering with the results. Lastly, an A-horizon of at least 30 cm was present in all plots.

3.2.2 Latrine study

I selected latrines (treatment level E and F) differently than the grazing intensity plots because the availability of latrines limited the selection. I usually sampled the closest impala and white rhino latrines to the three plots of treatment level A, B and C. If there were two or three latrines in the close surrounding, I chose the one that impalas or white rhinos utilized more heavily at that moment and that exhibited the relatively highest surrounding grass cover. I measured the DPM as the average of five measurements that I took within the first two meters evenly distributed around the latrine, and used it as a proxy for the grazing intensity of treatment levels E and F.

3.3 Fieldwork

3.3.1 Topsoil and grass root samples

The thesis benefitted from being associated with the PhD study of Olli Hyvärinen. This meant that Olli already collected part of the samples for the grazing intensity study before I started my fieldwork. Therefore, the sampling period of soil samples in treatment levels A, B and C lasted from November 2019 until February 2020 whereas I took soil samples around latrines (level E and F) and grass root samples in all plots of both studies between January and March 2020.

For the drilling of soil cores, I used Beater soil samplers that allow for sampling at two different depths (0-5 cm, 5-15 cm; Figure 5G). Although the IPCC recommends a sampling depth for SOC stocks of 30 cm (Penman et al., 2003), I only sampled up to 15 cm because the soil was too hard to sample deeper. The cores had a diameter of 4 cm and were developed by the South African Sugarcane Research Institute (SASRI). For the grazing intensity study, I took 10 soil cores per plot and pooled these subsamples into one composite sample per depth per plot and treatment level. The pooled samples were analysed for nutrient and carbon content. I sampled the cores in pairs in each corner and in the middle of the plot (Figure 5B). In addition, I took five further soil cores to estimate grass root biomass and AM root infection rates (Halbritter et al., 2019). I again considered the upper two soil layers (0-5 cm, 5-15 cm), which is a common sampling depth for AM fungi (Halbritter et al., 2019), and pooled the five subsamples into one composite sample per depth per plot and treatment level. I collected one subsample in each corner and in the middle of the plot. To soften the soil and facilitate the coring of the deeper layer, I poured some water into the holes after sampling the first layer. Finally, I used one core from the middle of the plot to measure bulk density for each layer separately.

For the latrine study, I sampled nine soil cores in total (Figure 5E). I took four pairs of soil cores, consisting of one core for soil and one for grass root sampling, and pooled these subsamples into two composite samples per depth per plot and treatment level. I noticed that invasive forb species grow in and around most of the latrines. During the sampling, I considered this forb-dominated area as part of the latrine and collected samples adjacent to it. I distributed pairs as evenly as possible around the latrine, avoiding patches close to a path or dominated by forbs or bare ground. In addition, I took one further soil core to measure bulk density for each layer separately. I randomly chose its location in between two pairs of soil and grass root samples adjacent to the latrine.

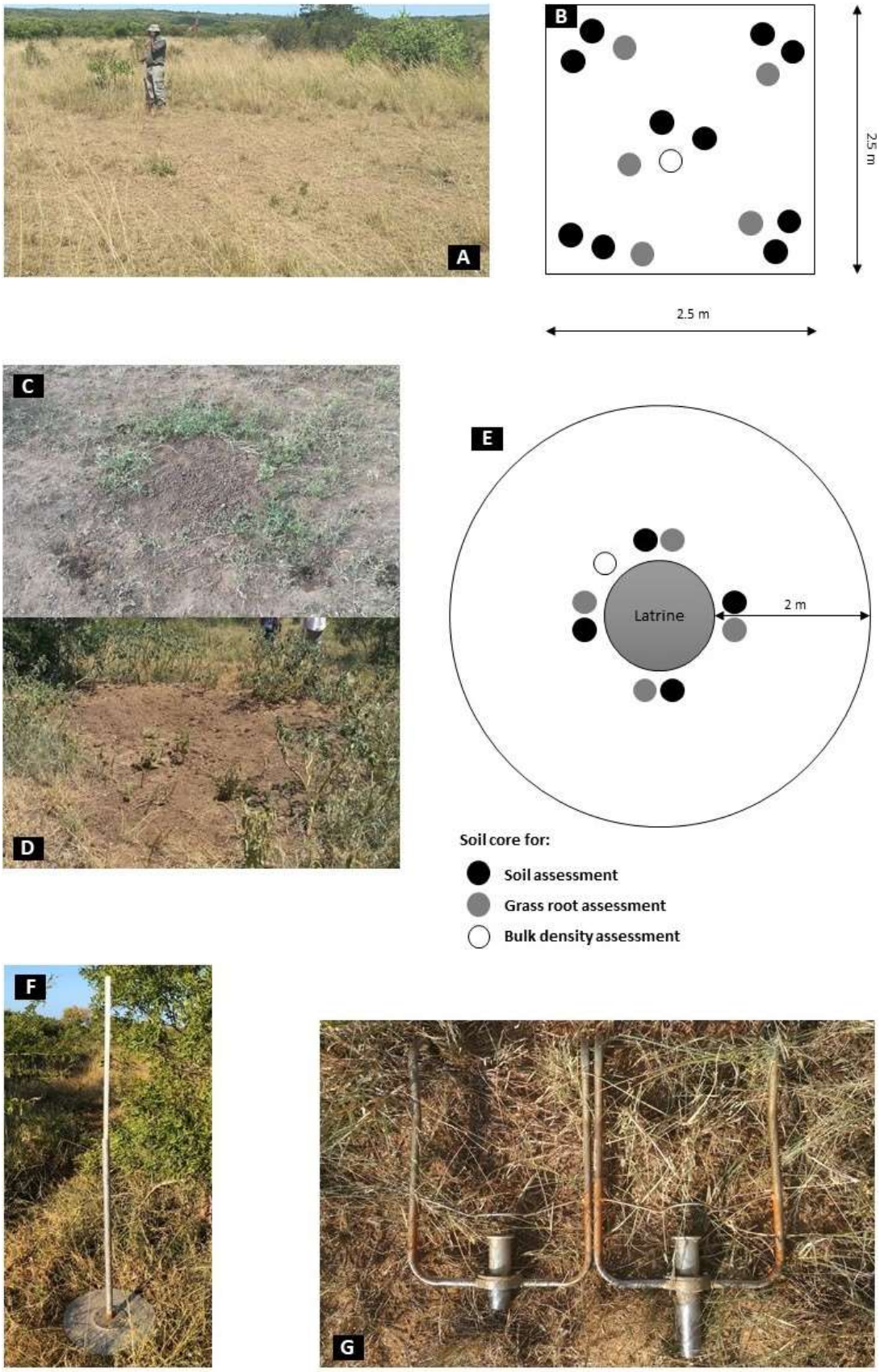

Figure 5: Fieldwork impressions. (A) Typical grazing lawn; **(B)** plot design in treatment level A, B and C; **(C)** impala latrine; **(D)** white rhino latrine; **(E)** plot design in treatment level E and F; **(F)** DPM device; **(G)** Beater soil samplers for 5 and 15 cm soil depth.

3.3.2 Dung counts

Considering that grazing is a continuous variable, grazing intensities varied within the grazing intensity treatment levels, i.e. within level A, B and C. Therefore, I used dung pellet group counts as an accepted measure of variation in plot-scale herbivore use intensity (Cromsigt, van Rensburg, Etienne, & Olff, 2009; Appendix A.2c). I counted the number of dung pellet groups per ungulate species in all treatment plots in an extended 5x5 m² plot, including and surrounding the plot where I took soil cores. Similarly, the use of latrines by white rhino and impala for defecating, and by white rhino, impala, and other grazers for grazing around the latrines, also varied among the sampled latrines (levels E and F). I thus also counted dung pellet groups within the first two meters around the latrines. I assumed that the dung pellets reflected the use of the plots over a period of weeks to months preceding my counts.

Furthermore, I reported the average diameter of latrines and used it as another proxy for the intensity at which impalas or white rhinos used the latrine (Appendix A.2b). The rationale behind it was that the area of intense dung deposition likely influenced the amount of nutrients returned to the soil and therefore the manifestation of N:P ratios.

3.4 Laboratory work

3.4.1 SOC pools and soil N:P ratios

The soil fertility laboratory at the KwaZulu-Natal Agricultural Research Laboratories, South Africa, conducted the analyses of SOC pools, and soil N and P contents following the protocol by Manson and Roberts (2011). The preparation of soil samples included air drying, the utilization of a soil crusher and sieving out material that is coarser than 1 mm after crushing (e.g. stones, gravel; Manson & Roberts, 2011). SOC, N contents, and clay fractions were measured as total percentage of solid soil material while P content was recorded as soluble fractions in mg/l. N and SOC fractions were reported up to 0.6% and 6%, respectively. I used the soil clay content as a covariate to distinguish between soils with different textures (Appendix A.1c,d). For the determination of SOC and N pools, I required knowledge of the soil bulk density. Therefore, I recorded the wet weight of the bulk density samples directly after collection in the field, dried them in the oven at 105°C for 48h, and then recorded the dry weight (Grossman & Reinsch, 2002). I divided the dry weight by the volume of the soil core to obtain the bulk density (Appendix A.4). Although usually only <2 mm soil particles are utilized for bulk density measurements (Grossman & Reinsch, 2002), I did not exclude rocks and stones because soils generally did not contain a lot of them. The multiplication of SOC and N fractions with the bulk density gave the SOC and N pool per soil layer per plot. I finally expressed soil N:P ratios as total N per litre of soil relative to soluble P per litre of water.

3.4.2 Grass (fine) root:shoot ratios

For the determination of grass root biomass, I first washed soil from grass roots following the protocol by Cook, Jastrow, and Miller (1988) with the following minor adjustments. I soaked the samples in water, then transferred them from the sampling bags to a 2 mm sieve, which I placed on a 0.2 mm sieve, and washed them under running water. I crushed remaining soil aggregates by hand and removed coarse organic matter, other than roots, in the same process. Afterwards, I transferred soil particles, that remained on the sieves, with a spoon to a plastic cup and filled it with water. The stirring water separated floating roots from descending mineral soil particles and some heavier organic particles as well as from lighter organic debris. I repeated this process several times. In the first run, I carefully removed organic matter from the water surface with a spoon, avoiding roots. In the subsequent runs (about 2 times for the 2 mm sieve and 7 times for the 0.2 mm sieve), I immediately poured the soil water root suspension over the sieve. I hereby made sure that I kept the heavy soil particles, which settled on the bottom of the cup, in the cup so that I collected roots on the sieves. I repeated this procedure until there were no floating roots left. I also repeated the transfer of particles from the sieves to cups with the subsequent separation procedure (about 2 times for the 2 mm sieve and 5 times for the 0.2 mm sieve) until particles barely deposited on the bottom of the cup.

I kept coarse roots (>2 mm diameter) and fine roots (0.2-2 mm diameter; Halbritter et al., 2019) separately, put them into two different plastic cups, and measured their wet weight. Due to clustering during the washing process, the sample of coarse roots also contained long fine roots which I treated as coarse roots. I stored 1-2 g of fine roots in a glass tube in 70% ethanol for the subsequent analysis of AM infection rates (Halbritter et al., 2019; Cook et al., 1988) and additionally selected some long fine roots from the coarse root batch. I then put the rest of the fine and coarse roots separately in glass tubes and weighted them again. Afterwards, I dried them at 70°C for 72h, recorded their dry weight (Halbritter et al., 2019), and calculated the factor between wet and dry weights. I applied it to the wet weights of the stored roots to obtain their dry weights, and to receive the total dry weights of coarse and fine roots, respectively. Their addition gave the total dry root weight. Lastly, I obtained fine root fractions by expressing dry fine root biomass as percentage of total dry root biomass.

Furthermore, I calculated the aboveground biomass per plot from DPM measurements by making use of a linear function established by Harmse et al. (2019) for the arid dune field savanna of the south-western Kalahari, Northern Cape, South Africa. Because aboveground biomass was expressed in area density and soil core volumes differed per depth, I determined the dry root biomass density per depth per plot and root size by dividing the dry weights by the volume of the soil core. Finally, I produced the two ratios of grass root:shoot and fine root:shoot by dividing the dry (fine) root biomass density by aboveground biomass density. I missed one DPM measurement in intermediately grazed patches and therefore, I had one less sample of (fine) root:shoot ratios available than in all other treatment levels.

3.4.3 Arbuscular mycorrhizal (AM) grass root infection rates

The analysis of AM root colonization required preparation of the grass roots following Phillips and Hayman (1970). I first cleared the roots from dark phenolic compounds in a water bath of 10% KOH in a glass tube at 90°C for 1h. Afterwards, I transferred them to a Petri dish filled with water to wash off the KOH solution. I then stained the roots in a second Petri dish in water, enriched by five pipette drops of trypan blue in lactophenol, for 10 min.

I applied the gridline intersect method by Giovannetti and Mosse (1980) to determine AM root infection rates. Therefore, I first drew a grid of 0.5x0.5 $inch^2$ large squares (requirement 1) on a piece of paper, placed a Petri dish on top of it, and traced the grid on the outside of the Petri dish with a permanent marker. It was important that the edges of the Petri dish ran right through the squares and overlapped as little as possible with the grid lines (requirement 2). Placing the stained roots in the Petri dish, I made sure that roots did not obscure each other and that I created as many intersects as possible between gridlines and roots. I used a microscope with x10 magnification to scan all horizontal and vertical lines for intersects with roots, recording the presence or absence of AM infection at those points (Figure 6). I first counted all horizontal lines, starting with the upper line and going from left to right. Afterwards, I scanned the vertical lines, starting with the left line and going top down. In order to realize a comparable basis of infection rates, I counted 50 intersects per sample. When I recorded 50 intersects, I stopped the count which usually happened at the last few vertical lines. Three samples of treatment level A, one of level B, two of level C, and one of level E of the upper soil layer, and one of treatment level C of the lower layer, did not provide enough root material to reach this number of intersects though. In addition, from the samples of the sixth block, I only had those of lightly grazed patches and white rhino latrines available due to the loss of the other two samples (Appendix B). According to Newman (1966), the total root length equals the number of intersect points if requirement 1 and 2 are met. Therefore, the division of the sum of intersects with locally infected roots by the total number of intersects resulted in the AM root colonization relative to root length. I used this AM root infection rate per plot and soil depth as a proxy for AM biomass.

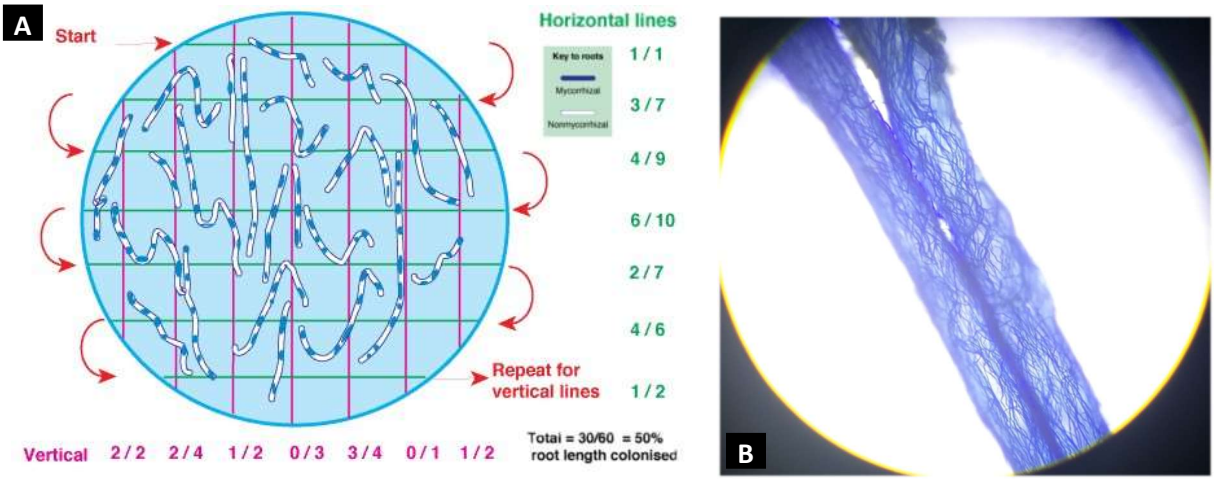

Figure 6: Determination of AM grass root infection rates. (A) Application example of gridline intersect method by Giovannetti and Mosse (1980; Brundrett, Bougher, Dell, Grove, & Malajczuk, 1996); **(B)** example of microscopic view of strongly infected root.

3.5 Statistical analysis

I used linear mixed-effect models to analyse the relationship between grazing intensity, latrine type, grass (fine) root:shoot ratios, AM grass root infection rates, soil N:P ratios and SOC pools. I analysed the data for the grazing intensity and latrine study separately, distinguishing between the upper (0-5 cm) and lower (5-15 cm) soil layers. Linear mixed-effect models are ANOVA and regression models that differentiate between fixed and random effects. While fixed effects represent predictor variables, random effects explain unknown variation due to group/block sampling (Bolker, 2008). Therefore, I needed to account for variations between the blocks by adding a random effect to the model (block effect). For the grazing intensity study, I included (fine) root:shoot ratios and AM root infection rates as response variables and covariates, and SOC pools only as a response (Appendix D). Furthermore, I added the grazing intensity treatment, as a factor with three treatment levels (A, B and C), and the dung pellet group density as a covariate, reflecting the variation in herbivore use intensity in addition to the factorial grazing intensity treatment. For the latrine study, I analysed soil N:P ratios, AM root infection rates and SOC pools as response variables and soil N:P ratios and AM root infection rates additionally as covariates (Appendix E). I perceived the produced (fine) root:shoot ratios around latrines as unreliable, as discussed later, and did not include them in the analysis. Next to the latrine treatment, as a factor with two treatment levels (E and F), and the dung pellet group density, I used the latrine size and DPM as two further covariates and proxies of grazing/herbivore use intensity. I also tested for effects of MAR, fire frequency and soil texture on the soil and grass root variables and specifically tested for interactions between these environmental variables and the grazing intensity and latrine treatment. For the grazing intensity study, I needed to apply a square root transformation of fine root:shoot ratios in the upper layer and root:shoot ratios in the lower layer, in models with the dung counts, MAR, fire frequency

or soil texture as a covariate (Appendix D.1), to fulfil the normality assumption of residuals after regression (Pierce & Kopecky, 1979). In addition, I square transformed fine root:shoot ratios in the lower layer in models with fire frequency or soil texture as a covariate. In the latrine study, I applied a logarithmic transformation of soil N:P ratios in the lower layer in models with MAR, fire frequency or soil texture as a covariate. Finally, I square root transformed soil N:P ratios in the lower layer in the model with treatment levels and soil texture (Appendix E.1).

I conducted the statistical analysis with R (R Core Team, 2018). I generated linear mixed-effect models with the lme() function from the nlme package and printed their output using anova.lme() and summary(). I determined associations between response and predictor based on p-values from the ANOVA table and a significance level of 5%. Furthermore, I obtained predictor estimates from the summary() output. For models with treatment levels, I performed Tukey all-pair comparisons (Jaccard, Becker, & Wood, 1984) using the glht() function. I evaluated the significance of the variation in the response between the different levels based on p-values from the summary() output. For all models, I made sure that residuals were normally distributed by conducting the Shapiro-Wilk test (Pierce & Gray, 1982) of residuals with shapiro.test() and a significance level of 5%. I visualized data distributions and predicted values by means of the ggplot() function from the ggplot2 package, and the scatterplot3d() function.

4 Results

4.1 Grazing intensity study

4.1.1 Associations between grazing intensity, SOC pools, (fine) root:shoot ratios, and AM root infection rates

The grazing intensity treatment did not explain the variation in neither fine root:shoot ratios nor root:shoot ratios or AM root infection rates in either of the two soil layers (Appendix D.1; Figure 7a-f). However, according to the Tukey-test, root:shoot ratios increased in intensely grazed patches compared to intermediately grazed patches in the upper soil layer, although they were similar in lightly grazed patches (Appendix D.2a,3). Furthermore, the grazing intensity treatment did not seem to influence the variation in SOC pools in the upper layer (Appendix D.1; Figure 7g). In the lower layer, SOC pools were higher in lightly grazed patches than in intermediately grazed patches, although did not differ from the intensely grazed patches (Appendix C.1,2a,3; Figure 7h). Moreover, fine root:shoot ratios, root:shoot ratios, AM root infection rates and SOC pools did not vary with dung pellet group density (Appendix C.1,4). Finally, fine root:shoot ratios, root:shoot ratios and AM root infection rates did not account for the variation in SOC pools in either of the two soil layers (Appendix D.1; Figure 8).

4.1.2 Influence of environmental drivers on associations between grazing intensity, SOC pools, (fine) root:shoot ratios, and AM root infection rates

In both soil layers, MAR, fire frequency and soil texture did not seem to affect the variation in fine root:shoot and root:shoot ratios (Appendix D.1). Likewise, MAR did not explain the variation in AM root infection rates in either of the layers. In the lower layer, AM root infection rates increased with increasing fire frequency at high grazing intensity but decreased with increasing fire frequency at lower grazing intensities (Appendix D.1,2a,5b). In addition, in the upper layer, AM root infection rates overall decreased with increasing clay content (Figure 10a) but, at intermediate grazing, they increased with increasing soil clay content (Appendix D.1,2a,5a). Furthermore, SOC pools increased with increasing MAR in the lower layer and increased with increasing soil clay content in either of the soil layers (Appendix D.1,2b; Figure 9b,e,f). The effects did not differ among grazing intensity levels. In addition, MAR, fire frequency and soil texture seemed to positively influence the variation in SOC pools in both layers when considered together with fine root:shoot and root:shoot ratios (Appendix D.1,2b,6,7). When considered together with AM root infection rates, SOC pools also increased with increasing soil clay content in the lower layer (Appendix D.1,2b,8).

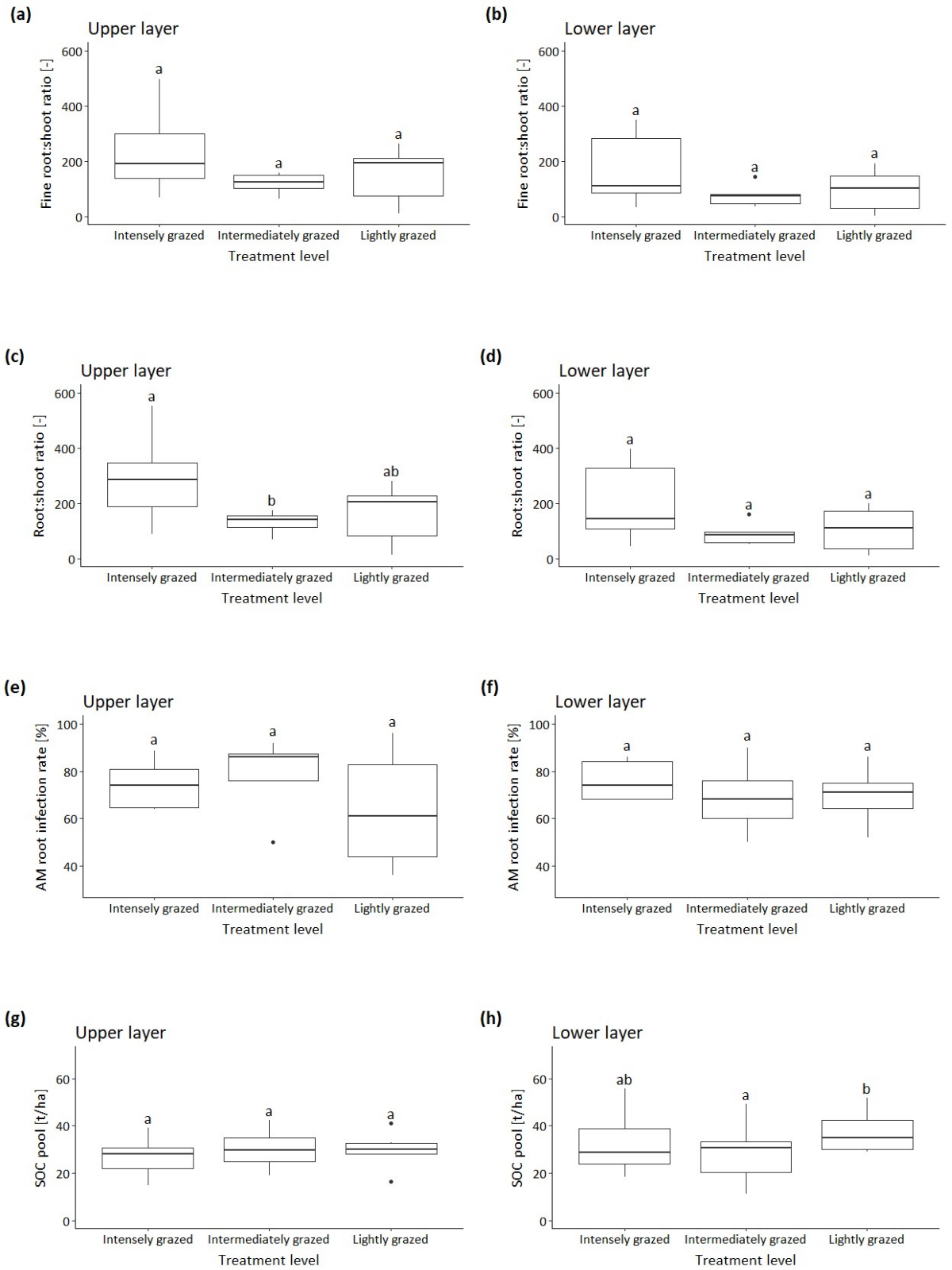

Figure 7: Results I of grazing intensity study. Associations between grazing intensity and **(a)** fine root:shoot ratios in upper (0-5 cm) soil layer, **(b)** fine root:shoot ratios in lower (5-15 cm) soil layer, **(c)** root:shoot ratios in upper soil layer, **(d)** root:shoot ratios in lower soil layer, **(e)** arbuscular mycorrhizal (AM) root infection rates in upper soil layer, **(f)** AM root infection rates in lower soil layer, **(g)** soil organic carbon (SOC) pools in upper soil layer, and **(h)** SOC pools in lower soil layer.

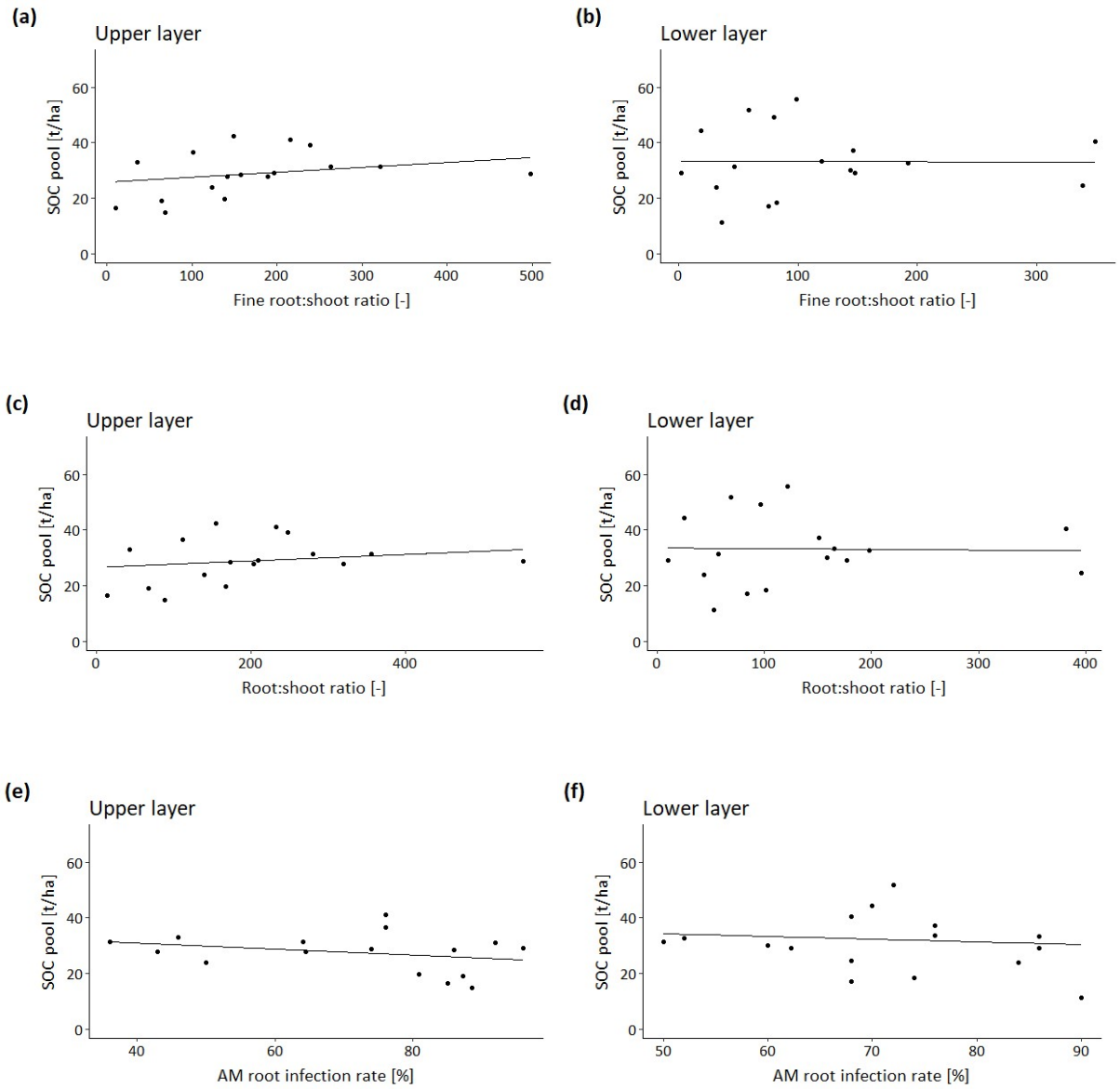

Figure 8: Results II of grazing intensity study. Associations between SOC pools and **(a)** fine root:shoot ratios in upper soil layer, **(b)** fine root:shoot ratios in lower soil layer, **(c)** root:shoot ratios in upper soil layer, **(d)** root:shoot ratios in lower soil layer, **(e)** AM root infection rates in upper soil layer, and **(f)** AM root infection rates in lower soil layer; ( ) $p > 0.05$; (*) $p < 0.05$; (**) $p < 0.01$.

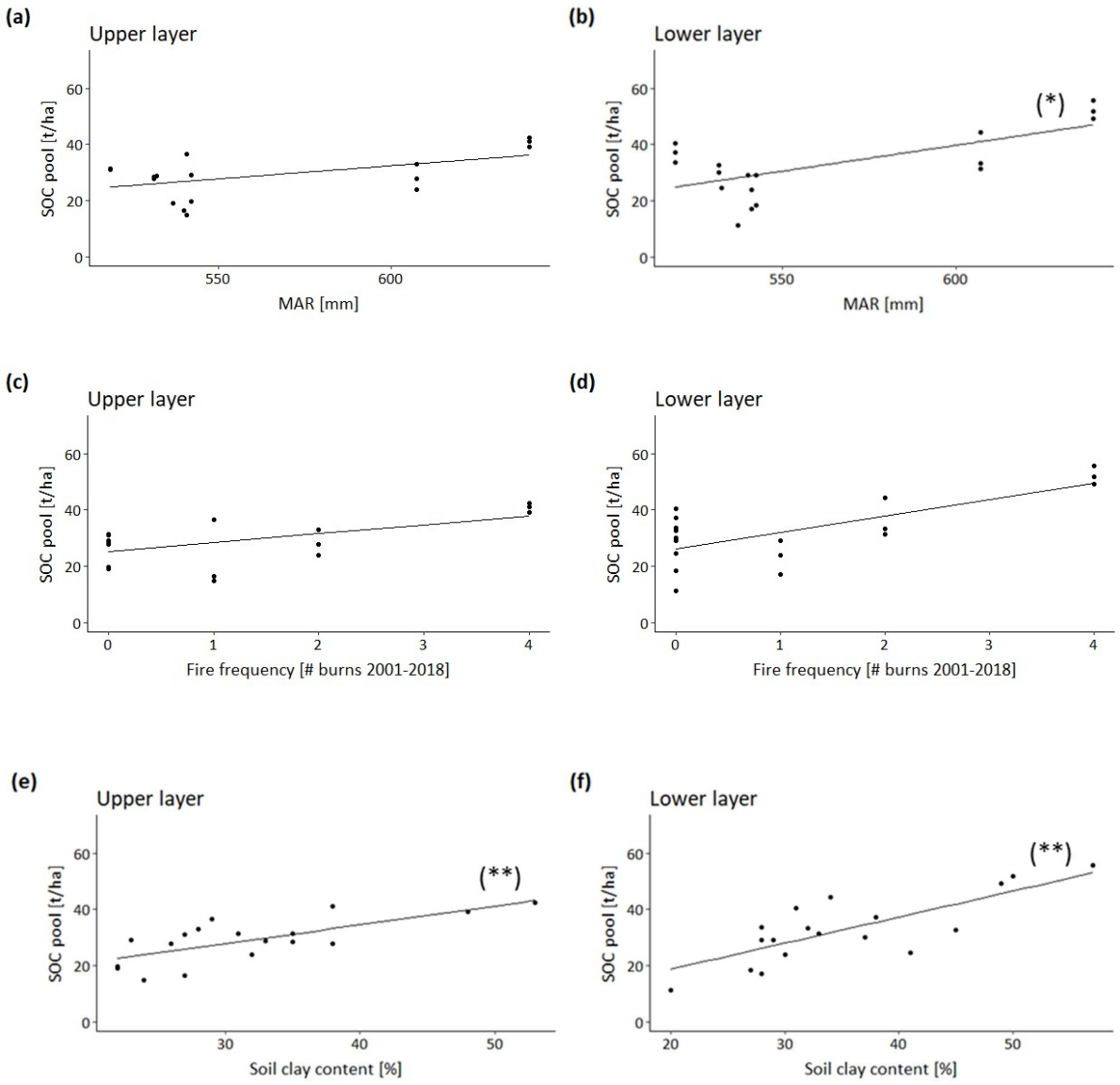

Figure 9: Results III of grazing intensity study. Associations between SOC pools and **(a)** mean annual rainfall (MAR) in upper soil layer, **(b)** MAR in lower soil layer, **(c)** fire frequency in upper soil layer, **(d)** fire frequency in lower soil layer, **(e)** soil clay content in upper soil layer, and **(f)** soil clay content in lower soil layer; ( ) $p > 0.05$; (*) $p < 0.05$; (**) $p < 0.01$.

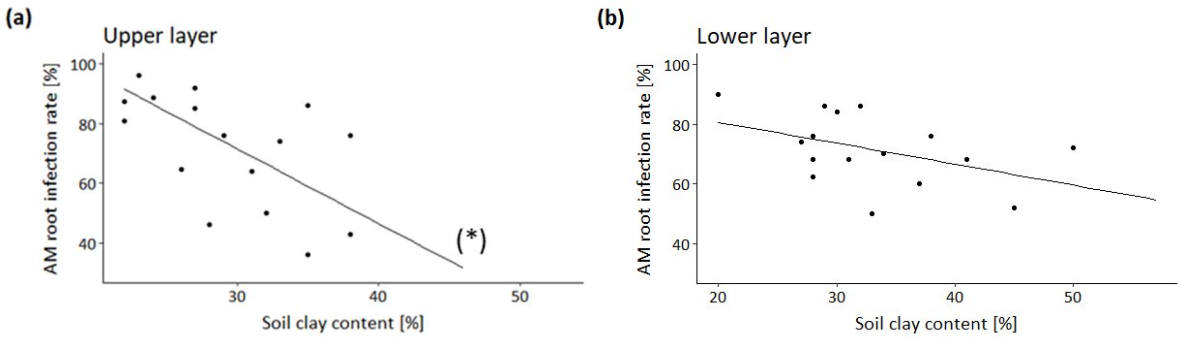

Figure 10: Results IV of grazing intensity study. Associations between AM root infection rates and soil clay content in **(a)** upper and **(b)** lower soil layer; ( ) $p > 0.05$; (*) $p < 0.05$; (**) $p < 0.01$.

4.2 Latrine study

4.2.1 Associations between latrine type, SOC pools and AM root infection rates

The latrine treatment did not account for the variation in soil N:P ratios but seemed to influence the variation in SOC pools in either of the soil layers (Appendix E.1; Figure 11a,b,e,f). SOC pools were hereby higher around white rhino than impala latrines (Appendix E.2a,3). In addition, AM root infection rates differed between latrine types in the lower layer with increased rates around impala latrines (Appendix E.1,2a; Figure 11d). Moreover, soil N:P ratios decreased with increasing dung pellet group density in both layers while SOC pools increased with increasing dung pellet group density in the lower layer, and with increasing DPM in the upper layer (Appendix E.1,2b,4a,b,6e). AM root infection rates did not vary with either dung pellet group density, latrine size or DPM (Appendix E.1,4-6). Furthermore, soil N:P ratios did not explain the variation in AM root infection rates or SOC pools in either of the soil layers (Appendix E.1; Figure 12,13a,b). In addition, SOC pools did not vary with AM root infection rates in the upper layer but decreased with increasing AM root infection rates with AM root infection rates in the lower layer (Appendix E.1,2b; Figure 13c,d).

4.2.2 Influence of environmental drivers on associations between latrine type, SOC pools and AM root infection rates

In both soil layers, MAR and fire frequency did not explain the variation in neither soil N:P ratios nor SOC pools (Appendix E.1). In addition, MAR, fire frequency and soil texture did not seem to influence the variation in AM root infection rates in either of the layers. In the upper layer, soil N:P ratios increased with increasing soil clay content (Figure 14a), just like SOC pools increased with increasing clay content, when considered together with soil N:P ratios (Appendix E.1,2b,7b). Soil N:P ratios also differed between latrine types, when considered together with soil texture, with higher ratios around impala than white rhino latrines (Appendix E.1,2a,7a). The effect of soil texture on soil N:P ratios did not differ between latrine types.

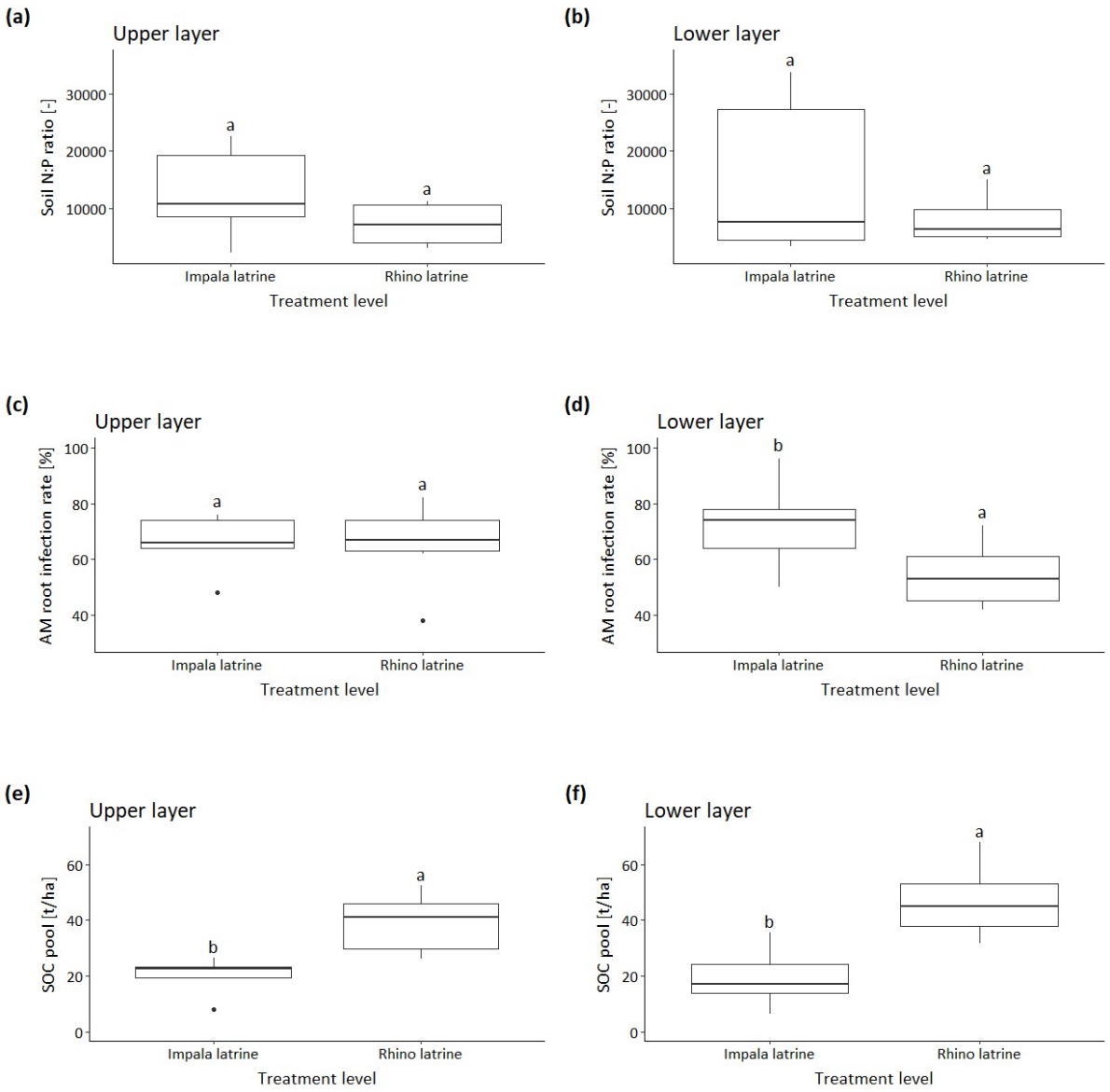

Figure 11: Results I of latrine study. Associations between latrine type and **(a)** N:P ratios in upper soil layer, **(b)** N:P ratios in lower soil layer, **(c)** AM root infection rates in upper soil layer, **(d)** AM root infection rates in lower soil layer, **(e)** SOC pools in upper soil layer, and **(f)** SOC pools in lower soil layer.

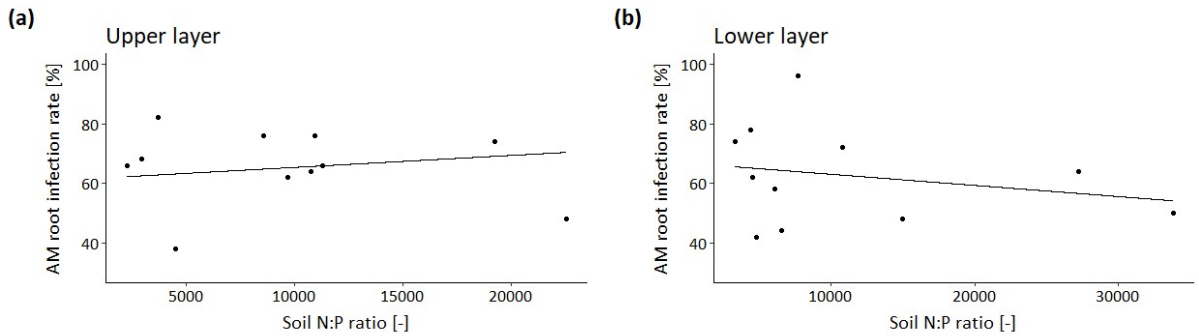

Figure 12: Results II of latrine study. Associations between AM root infection rates and soil N:P ratios in **(a)** upper and **(b)** lower soil layer; ( ) $p > 0.05$; (*) $p < 0.05$; (**) $p < 0.01$.

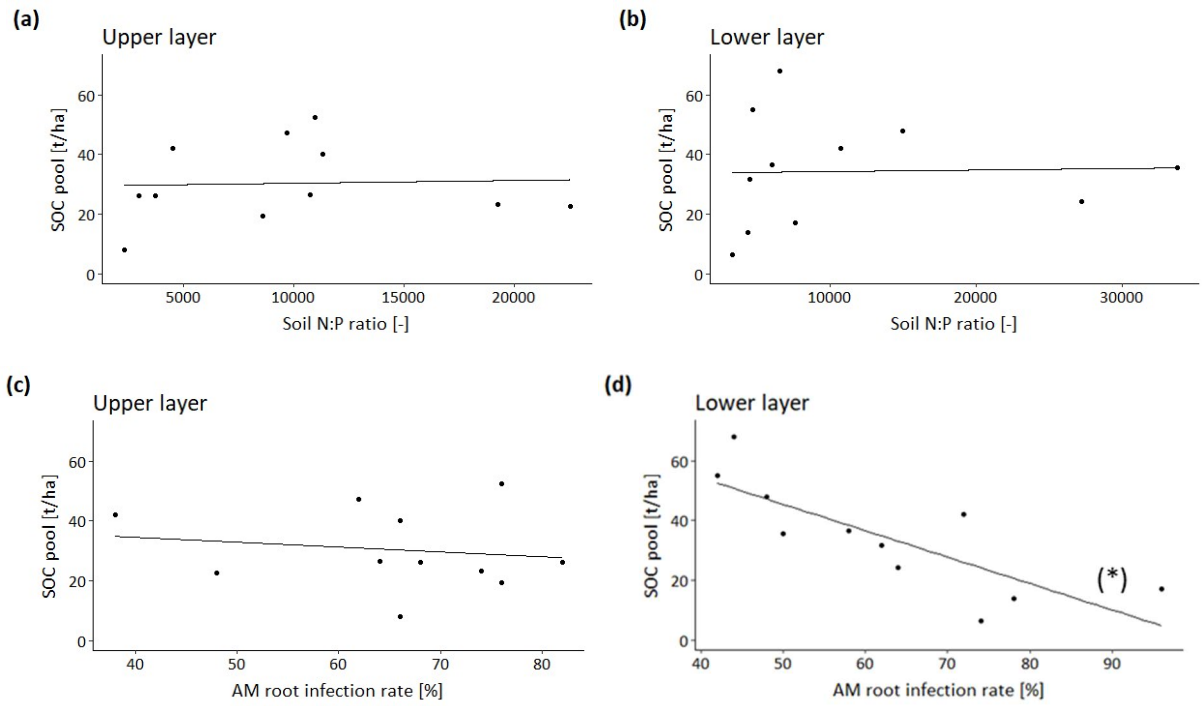

Figure 13: Results III of latrine study. Associations between SOC pools and **(a)** soil N:P ratios in upper soil layer, **(b)** soil N:P ratios in lower soil layer, **(c)** AM root infection rates in upper soil layer, and **(d)** AM root infection rates in lower soil layer; ( ) $p > 0.05$; (*) $p < 0.05$; (**) $p < 0.01$.

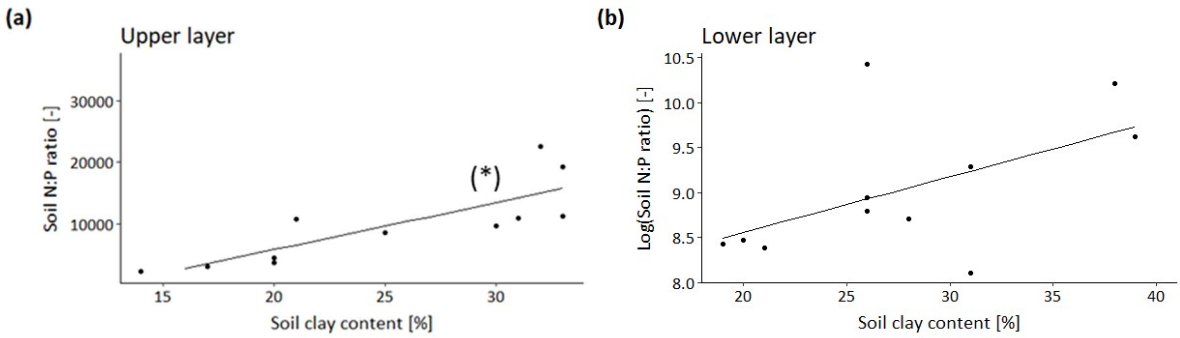

Figure 14: Results IV of latrine study. Associations between soil N:P ratios and soil clay content in **(a)** upper and **(b)** lower soil layer; ( ) $p > 0.05$; (*) $p < 0.05$; (**) $p < 0.01$.

5 Discussion

5.1 Main findings

Against my expectations (hypothesis a), grazing intensity was not associated with variation in (fine) root:shoot ratios and AM root infection rates. This could however result from a low sample size of this study because there is clear evidence that (fine) root:shoot ratios increased under intense grazing, compared to intermediate and light grazing, in either of the soil layers. In addition, AM root infection rates tended to increase in intensely versus lightly grazed patches while in the upper layer, they also tended to increase in intermediately grazed patches. Both trends would be consistent with my hypothesis (a) that grazing by wild large mammals stimulates fine root production and AM biomass in savannas whereas my findings do not support this hypothesis. Besides, my findings show similar fine root:shoot and root:shoot ratios in this study which proposes high fine root fractions of total root biomass, and a prevalent positive influence of grazing on fine root biomass across grazing intensity levels. This implies that herbivores could have even intensely grazed in the lightly grazed patches earlier in the season or during the previous season which might be reflected in a low variation and relatively high fine root fractions. Fine roots accounted for 86.4% and 80.3% of the total root biomass density in the upper and lower soil layer, respectively (Appendix A.5). Moreover, at intense grazing, my findings reveal a decrease of AM root infection rates with increasing soil clay content in the upper soil layer and an increase of AM root infection rates with increasing fire frequency in the lower one. This might show the value of AM symbioses for grasses at a reduced nutrient availability, due to soil properties or fire-driven nutrient losses.

I also rejected my hypothesis (b) on finding a contrast in soil N:P ratios between impala and white rhino latrines. Soil N:P ratios strongly tended to increase around impala latrines in either of the soil layers though. This trend would contradict my expectation (hypothesis b) that impala and white rhino latrines exhibit low and high soil N:P ratios, respectively. Both, the lack of variation and the trend, suggest dung N:P ratios to not primarily determine soil N:P ratios around impala and white rhino latrines but a more complex way of their occurrence. Moreover, my findings show increased AM root infection rates around impala latrines in the lower soil layer, although no association between soil N:P ratios and AM root infection rates. This proposes that an increasing P limitation does not necessarily promote the abundance of AM fungi through their efficiency in P acquisition for grasses (hypothesis c) but the influence of other factors. However, the observed trend in the soil N:P ratio data would explain the higher AM root infection rates around impala than white rhino latrines according to my hypothesis (c) of a positive association between AM root colonization and soil N:P ratios.

Furthermore, SOC pools did not vary with (fine) root:shoot ratios or AM root infection rates in the grazing intensity study, suggesting that (fine) roots and AM fungi do not determine and provide a SOC input in herbivore-dominated savannas (hypothesis d). In addition, I found higher SOC pools in lightly grazed patches than in intermediately grazed patches in the lower soil layer, although they did

not differ from the intensely grazed patches. On the contrary, I observed a trend of increased (fine) root:shoot ratios and AM root infection rates under intense grazing, as mentioned above, while there is also evidence in both layers that SOC pools decreased under intense grazing compared to light grazing. Therefore, other mechanisms than root and AM biomass must drive the SOC input in savannas, such as the exudation of root secretes or microbial biomass. In addition, environmental variables seemed to mainly influence SOC pools in the grazing intensity study. The increase of SOC pools with MAR and soil clay content hereby corresponds to my hypothesis (e) that increases in water and nutrient availability enhance grass productivity and thereby SOC pools. SOC pools also increased with fire frequency that might support grass productivity and/or provide carbon, that microbes incorporate into the soil, rather than promote carbon and nutrient losses.

In the latrine study, SOC pools increased around white rhino latrines compared to impala latrines in either of the soil layers. It appears straightforward to attribute this association to an increased organic matter supply through enhanced dung deposition in (impala: latrine Ø = 1.61 ±0.4 m; rhino: latrine Ø = 4.94 ±2.08 m; Appendix A.2b) and around (impala: # dung pellet groups = 6.8 ±6.42; rhino: # dung pellet groups = 13.83 ±5.04; Appendix A.2c) white rhino latrines. In addition, elevated nutrient levels could have generally increased grass productivity and therefore SOC input. The positive associations between SOC pools, dung pellet group density in the lower layer, and DPM in the upper soil layer might suggest those mechanisms, respectively. Moreover, SOC pools decreased with increasing AM root infection rates in the lower layer around latrines, which does not support my hypothesis (d) of AM fungi providing an input to SOC pools. Here, I however assume that SOC pools only weakly causally link to AM root infection rates due to the dependence of SOC pools on SOC input via dung around white rhino latrines. One might also recognize a primary influence of herbivory on white rhino latrines from the lack of variation in AM root infection rates and SOC pools with environmental drivers (hypothesis e). As an exception, increases in soil N:P ratios with increasing soil clay content might suggest a larger N storage capacity of clayey soils at increased N fluxes relative to comparatively stable soil P contents.

5.2 Comparison of findings with previous studies

5.2.1 Associations between grazing intensity and SOC pools

With one exception, grazing intensity did not determine SOC pools in this study. Besides a low sample size, one explanation would be that that the grazing intensity levels and therefore the effects of grazing on SOC pools among intensity levels were relatively similar in this thesis. Through 20-year exclosure experiments in semi-arid African savannas, Sitters, Kimuyu, Young, Claeys, and Olde Venterink (2020) and Wigley, Augustine, Coetsee, Ratnam, and Sankaran (2020), for instance, showed that SOC pools differed between grazed and not grazed areas. With contrasting results, herbivore exclusion of all types (wild meso- and megaherbivores and cattle) increased SOC pools by 20.5 t/ha in the 30 cm topsoil (Wigley et al., 2020) whereas grazing by a mix of these types also increased SOC pools compared to no

grazing or cattle grazing (Sitters et al., 2020). Those increases in SOC were, on the one hand, due to a reduced offtake and higher grass productivity enhancing the SOC input via litter and roots (Wigley et al., 2020), and on the other hand, due to megaherbivores (mainly elephants) returning carbon and nutrients to the soil rather than exporting them to paddocks (Sitters et al., 2020). In addition, the elephants competed with cattle for the nutritious grass and redirected carbon and nutrients from trees to soil by browsing and toppling. In areas only grazed by wild meso- and megaherbivores, Sitters et al. (2020) reported SOC pools in the 15 cm topsoil of 20-25 t/ha. In this project, SOC pools were 62 t/ha on average across grazing intensity levels at the same depth and therefore two and a half to three times higher. This suggests relatively high grazing intensity levels in this study and a prevalent positive effect of grazing on SOC pools in HiP across the intensity levels. Alternatively, enhanced SOC pools could have established under favourable climatic conditions promoting grass productivity. Moreover, my findings from the latrine study might similarly emphasize the importance of SOC and total nutrient input via megaherbivore dung for SOC pools, as proposed by Sitters et al. (2020). Around white rhino latrines, soils down to 15 cm contained at least 86 t/ha SOC on average whereas soils around impala latrines stored 39 t/ha SOC on average.

Since (fine) root:shoot ratios or AM root infection rates did not provide possible explanations for the variation and trend in SOC pools among grazing intensity levels, a different SOC input source must determine SOC pools among those levels. Based on the meta-analysis of livestock grazing in global C_3- and C_4-grasslands by Zhou et al. (2017), microbial biomass could represent an important SOC pool in HiP, while an intense grazing intensity could have limited microbial biomass by decreasing carbon input from litter. Importantly, this mechanism would not account for the variation in SOC pools in the lower layer with similar pools under light and intense grazing, but for SOC pools tending to increase under light versus intense grazing. Alternatively, instead of the investigated AM fungi, other types of mycorrhizal fungi could exist that play an important role in SOC sequestration. This is reasonable to assume considering the global analysis by Soudzilovskaia et al. (2019) who attributed a major influence on the variation in SOC pools to ectomycorrhizal (EcM) fungi due to higher fungal biomass and N acquisition efficiency. In grassland soils down to 1 m, SOC pools increased with biomass fractions of plants, that formed a symbiosis with EcM fungi, but decreased with AM associated plants (Soudzilovskaia et al., 2019). This finding might also explain the negative association between AM root infection rates and SOC pools in the lower soil layer around latrines.

Furthermore, the consideration of the temporal dimension could aid in explaining the similarity of (fine) root:shoot ratios between grazing intensity levels. Given that roots simultaneously grow and die off under grazing, this means that grazing might increase root turnover in HiP whereas live root biomass effectively does not change. Higher root turnover times in global pastures (Wan, 2020) give reason for this assumption. In addition, Bai et al. (2015) showed the continuous production and mortality of roots throughout the growing season in Mongolian steppe and found production and mortality peaks seasonally occurring at the same time in spring and autumn. The fine root fractions found here were 30-

35% higher compared to Ansley, Boutton, and Jacoby (2014) who reported about 50% of fine root biomass of total root biomass in a semi-arid savanna of the Great Plains. Likewise, the average AM root infection rate in a study in Kenyan grasslands grazed by wild mammals was 35% (González et al., 2018) and 30% in another study in Kruger National Park (Hartnett, Potgieter, & Wilson, 2004) which is 35-40% less than in this study. Both suggest a generally high baseline grazing intensity so that fine root production and AM root colonization were relatively high, even under light grazing, and/or an increased nutrient limitation of grasses in HiP. Besides, the sampling during the summer season might have led to overall enhanced infection rates in this study because AM root colonization may also seasonally change with the warm summer season benefitting AM fungi (Al-Karaki, McMichael, & Zak, 2004).

The insignificance of grazing intensity in explaining (fine) root:shoot ratios and AM root infection rates might also originate from assumptions made on the mechanism between these variables. I based my expectation, that grazing stimulates fine root production and AM root colonization, on the assumption that grazing/defoliation increases the nutrient demand and loss of grasses. However, if nutrients did not limit grass productivity, due to the return of nutrients through dung and urine deposition, grazing would not significantly alter grass roots or AM associations. Alternatively, a link between grazing and grass roots might not exist if grazing does not cause an increased nutrient demand but grass roots react to nutrient limitation. For instance, a study on livestock grazing in semi-arid Mexican grasslands by Medina-Roldán, Arredondo, Huber-Sannwald, Chapa-Vargas, and Olalde-Portugal (2008) showed that AM root colonization did not depend on grazing intensity but increased with N limitation and grazing intensity together. Therefore, the savanna system in HiP could have adapted to grazing so that (fine) root:shoot ratios, AM root infection rates and SOC pools do not alter with changes in e.g. species composition or bulk density. From an exclosure experiment in Kenya, it became apparent that AM fungi locally adapt their functionality to herbivory (González et al., 2018). As a response to clipping, AM associated grasses regrew faster under the grazing pressure of wild herbivores than AM associated grasses, that have not been exposed to grazing before. AM fungi facilitated the regrowth of grazing tolerant grasses by increasing their root:shoot ratio and P acquisition, and exhibited more arbuscular and less storage structures (vesicles) that increased the nutrient exchange within the symbiosis (González et al., 2018). Functional differences of AM fungi might thus also exist between grazing intensity levels whereas they might be less visible in root:shoot ratios.

Furthermore, MAR, fire frequency and soil texture seemed to greatly affect SOC pools, partially affect AM root infection rates but did not affect (fine) root:shoot ratios. It seems natural that environmental variables determined SOC pools because MAR, fire and soil properties largely drive savannas (Staver et al., 2011). Apart from the low sample size, one might also attribute some of the unexplained variation in the soil and grass root variables to other non-tested factors that influence plant productivity, such as rainfall frequency and intensity influencing water availability (d'Onofrio, Sweeney, von Hardenberg, & Baudena, 2019). Moreover, increases in fire frequency were associated with increases in AM root infection rates, and increases in soil clay content with decreases in AM root

infection rates at intense grazing. A study in Kruger National Park, South Africa, by Hartnett et al. (2004) revealed the exact opposite association between fire frequency and AM colonization. AM root infection rates hereby decreased with increasing fire frequency due to enhanced water limitation of grass growth and decreased soil N:P ratios through increased N volatilization (Hartnett et al., 2004). Fire frequencies were a lot higher than in this project though and therefore reduced photosynthetic rates might have limited the carbon transfer from grasses to AM fungi. In line with my finding, Carrenho, Trufem, Bononi, and Silva (2007) reported a strong dependence of AM root colonization on soil texture. In clayey soil, increased soil fertility and mechanical pressure on roots reduce AM root colonization. Due to a decreased pore volume, the increased contact of roots with soil particles can break the root cortex and thereby reduce colonization sites of AM fungi (Carrenho et al., 2007).

5.2.2 Associations between soil N:P stoichiometry and latrine type

A low sample size might account for the lack of variation in soil N:P ratios between the latrine types. However, the consideration of ecosystem feedbacks could also lead to explanations and would additionally suggest mechanisms that explain the trend of higher soil N:P ratios around impala than white rhino latrines. First, it seems possible that forbs, as known to commonly fixate atmospheric N (Siebert & Dreber, 2019) and exhibiting enhanced percentage cover of the sampled surrounding of impala latrines (Appendix A.3c), might have counterbalanced or reversed N limitation under mesoherbivore dominance around impala latrines. On the contrary, white rhinos provide their latrines with high dung N:P ratios which might require the here existing, different forb species to fixate no or lower amounts of N. Second, the personal observation that herbivores grazed more intensely around impala latrines (lawn species; DPM = 1.85 ±0.89 cm) than white rhino latrines (bunch species; DPM = 5.83 ±3.06 cm; Appendix A.2a) might contribute to another explanation. Because grazing alters grassland productivity (Hempson et al., 2015), grass or microbial nutrient requirements might counterbalance or reverse N:P ratios measured in soil at different dung N:P supply ratios. Ågren (2004) stated that the more productive plants are, the more N and P they need. With increasing growth rates, the requirement of P however enhances more strongly than the N requirement because plants increasingly invest into rRNA which they require to generate proteins for growth, and which represents a major pool of P in plants. Fast-growing grasses thus have low N:P ratios and a high affinity for P whereas slower-growing grasses require less P (Elser, Fagan, Kerkhoff, Swenson, & Enquist, 2010; Ågren, 2004). In this context, grasses around impala latrines, showing compensatory growth, might therefore acquire more P than grasses around white rhino latrines. Although impalas provide them with low dung N:P ratios, the P requirement might counterbalance or even reverse the supply and increase soil N:P ratios around impala latrines. Besides, abiotic factors might influence soil N:P ratios by altering N availability. Since N is more mobile in soil than P, N losses might occur e.g. through leaching or through volatilization during fire (Pellegrini et al., 2018). With a large removal of grass as fuel for fire, herbivores might reduce fire frequency around impala latrines (Archibald & Hempson, 2016). On the

contrary, more frequently burning white rhino latrines would increase N volatilization and decrease soil N:P ratios, counterbalancing or reversing the high dung N:P supply ratios. In this study, soil N:P ratios also decreased with increasing dung pellet group density and therefore with increasing herbivore use intensity around latrines, which contradicts to the theoretical approaches above. In addition, since mainly mesoherbivores and megaherbivores used the close surrounding of impala and white rhino latrines, respectively (Appendix A.2d), the variation in species, that graze around latrines, might not counterbalance or reverse soil N:P ratios associated with the latrine types either. Therefore, mechanisms behind the association between soil N:P ratios and dung pellet group density remain unclear.

While the evidence of increased soil N:P ratios around impala latrines and decreased soil N:P ratios around white rhino latrines could explain my finding of higher AM root infection rates around impala latrines in the lower soil layer, other factors might also determine AM root colonization around latrines. For instance, grazing intensity could have influenced AM root infection rates as well as SOC pools, with high grazing intensities around impala latrines possibly increasing infection rates and decreasing SOC pools, as observed from the grazing intensity study. Furthermore, AM root infection rates could have varied due to dung accumulation, as increasing the water holding capacity and therefore soil moisture of the soil through an increased organic matter input. Due to larger amounts of dung deposited in white rhino latrines, water might limit grasses around white rhino latrines to a lower extent. On the one hand, water unlimited plants can exhibit higher AM root infection rates because of an increased productivity (Al-Karaki et al., 2004). On the other hand, the value of AM symbioses can be higher for water limited plants because AM fungi facilitate the uptake of water (Davies Jr, Potter, & Linderman, 1992). The latter would explain the increased AM root infection rates around impala latrines in the lower soil layer.

5.3 Research limitations

To begin with a remark on the grazing intensity treatment levels, it is important to acknowledge that I measured the impact of wild ungulate grazing intensity on soil of the last few years (Cromsigt & Olff, 2008). I ensured this by selecting the levels based on species composition. Cromsigt and Olff (2008) experimentally showed that after two and a half years of intense grazing, stoloniferous grazing lawns can establish. Essentially, this shift from bunch to lawn species depended on the spatial scale of grazing and on nutrient availability, with an accelerated shift in larger and more fertile patches. In open and nutritious areas, lawn species have an advantage over bunch species to regrow after grazing (Cromsigt & Olff, 2008). Furthermore, Rietkerk, Dekker, de Ruiter, and van de Koppel (2004) described savannas as self-organized ecosystems that consist of vegetation patches driven by the small-scale interaction between plants and nutrient and water availability. That would mean that vegetation is constantly changing, competing for resources, and responding to disturbances, and that, for instance, stoloniferous grazing lawns might have been tall grassland in the past, and the other way around. Moreover, it is important to consider the number of dung pellet groups as a proxy for plot-scale herbivore use intensity

and not grazing intensity per se. Dung pellets gave information on the frequency of plot visitation by herbivores but did not necessarily reflect foraging intensity (Cromsigt et al., 2009) and thus not grazing intensity, as understood as a combination of foraging, trampling and excretion. Besides, a more frequent dung pellet group count over a longer period of time would estimate the use intensity of sampling plots in a more reliable manner. This was however not achievable within the timeframe of this project.

In this project, grass (fine) root:shoot ratios and AM grass root infection rates functioned as proxies for fine root production and AM biomass under grazing. I constructed (fine) root:shoot ratios by putting directly measured (fine) root biomass and from DPM measurements converted aboveground biomass into relation. This is not a usual practice, but I deployed it due to time constraints. Since species composition and environmental conditions deviate for HiP from the area assessed by Harmse et al. (2019), I therefore just roughly estimated aboveground biomass in this study. Due to the assumption of a linear increase of aboveground biomass with DPM and the interest in deviations among treatment levels, those estimates did not hamper the informative value of the results though, although the comparison to (fine) root:shoot ratios in other studies might be misleading. Therefore, (fine) root:shoot ratios represented good proxies for fine root production. Nevertheless, a direct assessment of root production (i.e. grown root biomass per time) would be more reliable. According to Halbritter et al. (2019), four methods are commonly used: sequential soil coring, in-growth cores, in-growth mesh, and root imaging. Those methods have the advantage that one could additionally calculate the turnover rate of root biomass (Halbritter et al., 2019) which gives insight into the root-derived carbon in soils. Furthermore, I used AM grass root infection rates as a proxy for AM biomass. Studies, related to SOC stocks, widely use the measurement of AM root colonization (Halbritter et al., 2019; Wilson et al., 2009; Medina-Roldan et al., 2008). Still, it is no direct measure of SOC input since e.g. high AM root infection at low root biomass probably results in a low total amount of AM biomass and litter. Indeed, van der Heyde, Bennett, Pither, and Hart (2017) showed that AM root colonization might not change under grazing even if soil hyphal length does, which would represent an alternative direct approach to determine AM biomass (Halbritter et al., 2019). Therefore, one needs to consider AM root infection rates as a proxy for AM biomass carefully in this thesis.

Next to the question of the meaningful utilization of proxies, minor practical issues of the applied laboratory methods influenced the accuracy of (fine) root:shoot ratios and AM root infection rates. As a recognized method, the technique by Cook et al. (1988), implemented to wash soil from grass roots, produced the following deficits that might be unavoidable using destructive sampling methods. They thus need to be considered during the establishment of research objectives and the interpretation of data. First, I lost similar amounts of fine roots from every sample during the washing and sieving process which thus did not influence the comparison of treatment levels. Second, I struggled to separate small organic soil particles from fine roots at the same time. This probably overestimated fine root fractions. Especially, for soil samples of white rhino latrines with a high content of fine organic matter, I perceived fine root biomass estimates as unreliable. Therefore, I did not utilize (fine) root:shoot ratios

in the latrine study. Furthermore, I learned from the assessment of AM grass root infection rates. Problems arose from the number and type of roots that I stored. Giovannetti and Mosse (1980) recommended to observe at least 100 intersects to achieve a standard error of ±4%. It turned out that I put too little fresh root material aside so that I could only count 50 intersects per sample. Therefore, I expect a standard error of more than 4% for the AM infection rates of the grass roots (Giovannetti & Mosse, 1980). AM root infection rates in intensely grazed grassland were the least robust because I counted less than 50 intersects for three of five samples (Appendix B). Moreover, I had little fine root material available for the analysis because I easily destroyed or lost it during the manual transfer of roots between vessels. Instead, I examined long fine roots contained in the coarse root sample. Although I could not avoid their mutual overlapping, I could separate those roots more easily in the Petri dish prior their observation under the microscope. Due to the availability of a relatively simple microscope, I worked with a lower magnification of x10 rather than x40, as used by Giovannetti and Mosse (1980). This led to an enlarged section, that I observed at intersect points, but I did not expect it to significantly influence the results.

Like (fine) root:shoot ratios, I could not compare soil N:P ratios in this thesis to ratios in previous studies, due to an uncustomary calculation, either. Since N was measured as fractions in soil but P was measured as fractions in solution, soil N:P ratios were generally higher than in other studies, although did not affect the comparison of treatment levels. Furthermore, N and SOC fractions of more than 0.6% and 6%, respectively, were not reported, as seen in the data of white rhino latrines. In the upper layer, one measurement of soil N:P ratios and three SOC contents were higher than the estimates used for the statistical analysis (Appendix C). In the lower layer, I underestimated one SOC pool. With the actual values, the association between latrine type and SOC pools would hence be even more significant.

Furthermore, I learned a lesson from the utilization of Beater soil samplers by SASRI to take soil and grass root samples. I experienced them as rather unsuitable for the (semi-)arid, clayey soils in HiP. Especially, the drilling from 15 cm down to 30 cm costed a lot of time and physical strength which justified the sampling down to only 15 cm, while the IPCC guidelines defined a default depth of 30 cm to measure SOC stocks (Penman et al., 2003). This suggests that northern research methods primarily inform IPCC standards so that they might be difficult to implement globally. For the use of hand augers in savannas, it might therefore help to agree on a standardized soil sampling depth of 15 cm. Alternatively, one could apply electric or hydraulic powered soil augers. Disadvantages of this approach are a higher energy consumption and lower portability that probably hinder researchers to widely use them.

5.4 Outlook

5.4.1 Implications for climate projections and herbivore management

The data and findings of this project imply a large uncertainty due to methodological shortcomings and a small number of sample replicates. Nevertheless, they suggest a prevalent positive effect of wild ungulate grazing on fine root production, the abundance of AM fungi, and SOC pools in HiP. Grazing intensities are likely to influence SOC pools in herbivore-dominated savannas, although mechanisms are unclear, and we should therefore consider them in local climate models to improve climate projections. The role of N:P stoichiometry in savannas in climate change mitigation also remains unclear whereas my findings show an importance of SOC and total nutrient input via megaherbivore dung deposition for SOC pools. An export of carbon and nutrients through cattle grazing might therefore have major implications for SOC pools in savannas.

5.4.2 Open research questions

Apart from questions remaining from this thesis due to a low sample size and limitations of the research design and methods, the same concept of N:P stoichiometry, as influenced by the relative abundance of mega- and mesoherbivores, provides a basis for one of the open questions. It is on the variation of soil N:P ratios between grazing intensity levels and/or different types of grazing lawns. Recalling that the nutrient demand by grasses conceptually links grazing intensity, fine root production and AM symbioses, nutrient limitation could have major implications for SOC pools. Indeed, le Roux et al. (in press) and le Roux, Kerley, and Cromsigt (2018) often found mesograzers, who prefer open habitat for higher visibility of predators, in large open, less risky grazing lawns whereas megaherbivores were less fear-driven and also occurred in tall grassland and lawns with low visibility (le Roux et al., in press; 2018). In addition, lawn grasses are more productive than bunch grasses and therefore probably have a high affinity for P (Elser et al., 2010; Ågren, 2004). This potential herbivore-driven N and P limitation of grasslands, based on dung N:P supply and grass N:P ratios, could be interesting to explore and relate to SOC pools. One would require an extended data analysis of soil and grass root variables between grazing intensity levels.

The consideration of other nutrient pools than total N, P and SOC within the context of herbivore-dominated savannas creates further research opportunities. For instance, Crowther et al. (2019) experimentally showed that SOC pools in global grasslands responded more strongly to potassium (K) than N and P enrichment. A combined fertilization, consisting of all three macronutrients, had the largest effect on SOC pools. Decreases in decomposition rates, that arose from water limitation of microbes in arid grasslands at increased plant productivity due to the nutrient enrichment, hereby drove increases in those pools (Crowther et al., 2019). With this suggested sensitivity of grasslands to K, it might be worthy to consider N:P:K ratios in soil as a next step, aiming to explain the variation in SOC pools, as influenced by grazing. Furthermore, in a future project, one could separate N and P pools

into plant-available/inorganic and plant-unavailable/organic quantities. The rationale behind this fractionation would be that plants' investments into fine roots and AM associations aim to make nutrients accessible in soil from unavailable sources, based on how much soils contain and plants require (Shipley & Meziane, 2002). For instance, one might expect that AM fungi, as decomposing microbes, are more abundant in soils where organic N:P ratios are high, rather than in soils with increased inorganic N:P ratios. Therefore, those pools would actively determine the allocation of carbon belowground while herbivory might influence them via dung and urine deposition (Pastor et al., 2006). Like the fractionation of N and P pools, it could be worthwhile to distinguish between labile and stable SOC compounds in the soil that can additionally be chemically or physically protected from decomposition. It would indicate the magnitude of SOC sequestration and stabilization in soil (Plaza et al., 2012). For instance, one could test variables against stable:labile SOC ratios and hypothesize that AM root colonization promotes stable:labile SOC ratios, due to the content of glomalin, a long-term binding of soil aggregates and a relatively resistant organic compound to decomposition (Wilson et al., 2009).

Finally, studies suggested a third mechanism to affect SOC pools which is microbial activity (Zhou et al., 2017; McSherry & Ritchie, 2013), which I did not investigate in this thesis. According to Griffiths, Spilles, and Bonkowski (2012) and Cleveland and Liptzin (2007), variations in soil stoichiometry do not affect microbial C:N:P ratios in grazed grasslands. This proposes that nutrients can limit microbial activity. At the same time, Manzoni, Taylor, Richter, Porporato, and Ågren (2012) found that the microbial carbon-use efficiency increases with nutrient availability. Microbes maintain their balanced body composition of carbon and other nutrients by respiring more carbon dioxide if nutrient availability is low. Any nutrient limitation would thus result in reduced microbial biomass and carbon-use efficiency, which decreases SOC sequestration, but it would also initiate lower decomposition rates, enhancing SOC storage. However, Güsewell and Gessner (2009) found that different microbial communities dominate decomposition at different N:P supply ratios. They observed that, at low N:P ratios, bacteria mostly account for decomposition of SOC whereas at high N:P supply ratios, fungi are more abundant. An increased P requirement of faster-growing bacteria to produce rRNA, compared to fungi, explains this observation (Elser et al., 2000). The latter implies a higher decomposition capacity of bacteria suggesting that SOC sequestration might depend on microbial communities, too. A combination of assessments of soil respiration and microbial populations would direct to answer research questions on microbes, as a mechanism between soil stoichiometry and SOC storage.

6 Conclusion

This research investigated the associations between (1) wild ungulate grazing intensity and SOC pools, and (2) herbivore-induced soil N:P stoichiometry and SOC pools in a game reserve in South Africa, and allowed me to answer the research question "How do grazing intensity and herbivore-induced soil N:P stoichiometry influence carbon pools in savanna soils in in Hluhluwe-iMfolozi Park?". I expected that intense dung depositions by megaherbivores (e.g. white rhino), relative to mesoherbivores (e.g. impala), increased soil N:P ratios because of an increased body P requirement. Moreover, I assessed grass (fine) root:shoot ratios and AM grass root infection rates as two mechanisms between grazing, nutrient availability and SOC pools. The statistical analysis of field data along a grazing intensity gradient and of two types of latrines, and the discussion of the findings led to the following conclusions.

a. Grass (fine) root:shoot ratios and AM grass root infection rates did not vary with grazing intensity which I attributed to a low sample size, due to a positive trend of both variables under intense versus light grazing, small differences between grazing intensity levels, or the adaptation of the savanna system to grazing.
b. Soil N:P ratios did not differ between impala and white rhino latrines, which was likely due to a low sample size because of evidently higher soil N:P ratios around impala latrines. Anyway, this suggests that e.g. variation in forb species and/or cover, or grazing intensity mainly influences soil N:P ratios around latrines.
c. Soil N:P ratios did not seem to influence AM grass root infection rates while I could not examine the association with grass (fine) root:shoot ratios. I however found increased AM root infection rates around impala latrines at a depth of 5-15 cm, either explained by the evidence of P limitation around impala latrines, or by variation in grazing intensity or soil moisture among the latrine types.
d. SOC pools did not vary with grass (fine) root:shoot ratios or AM grass root infection rates in the grazing intensity study. Along with a low sample size, this might be due to the assessment of a type of mycorrhizae, that is less strongly associated with SOC pools, or due to AM root infection rates as a misleading proxy for AM biomass. In addition, SOC pools were higher under light than intermediate grazing, although similar under intense grazing at a depth of 5-15 cm. This variation in SOC pools was not associated with (fine) root:shoot ratios or AM root infection rates, as tending to increase under intense grazing. Instead, considering the evidence of lower SOC pools under intense versus light grazing, carbon limitation of microbial biomass could have decreased SOC pools at high grazing intensity. SOC pools also increased around white rhino latrines down to 15 cm, probably because of an enhanced SOC and total nutrient supply, or due to a low grazing intensity.
e. SOC pools increased with MAR, fire frequency, and soil clay content in the grazing intensity study possibly through the support of grass productivity. In addition, while grazing mainly affected soil and grass root variables at a depth of 5-15 cm, I identified similar and further trends in both layers.

In conclusion, grazing intensity seemed to influence SOC pools in HiP, although mechanisms were unclear, whereas herbivore-induced soil N:P stoichiometry did not seem to influence SOC pools, although I only showed this for latrines. Therefore, this thesis contributed to a research field offering various open research questions on the understanding of interactions between grazing, N:P stoichiometry and climate change mitigation in savannas. However, due to clear trends in the data and a low sample size of this research, I recommend further research on this research question to then properly and holistically inform the management of herbivory and climate models.

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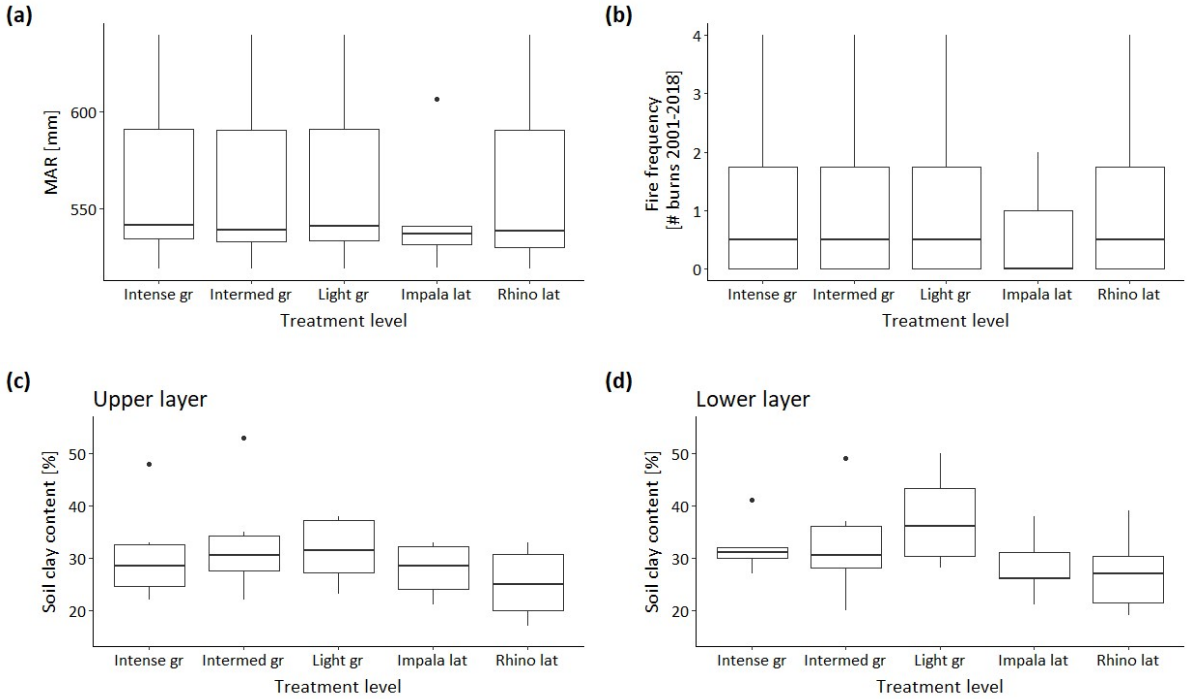
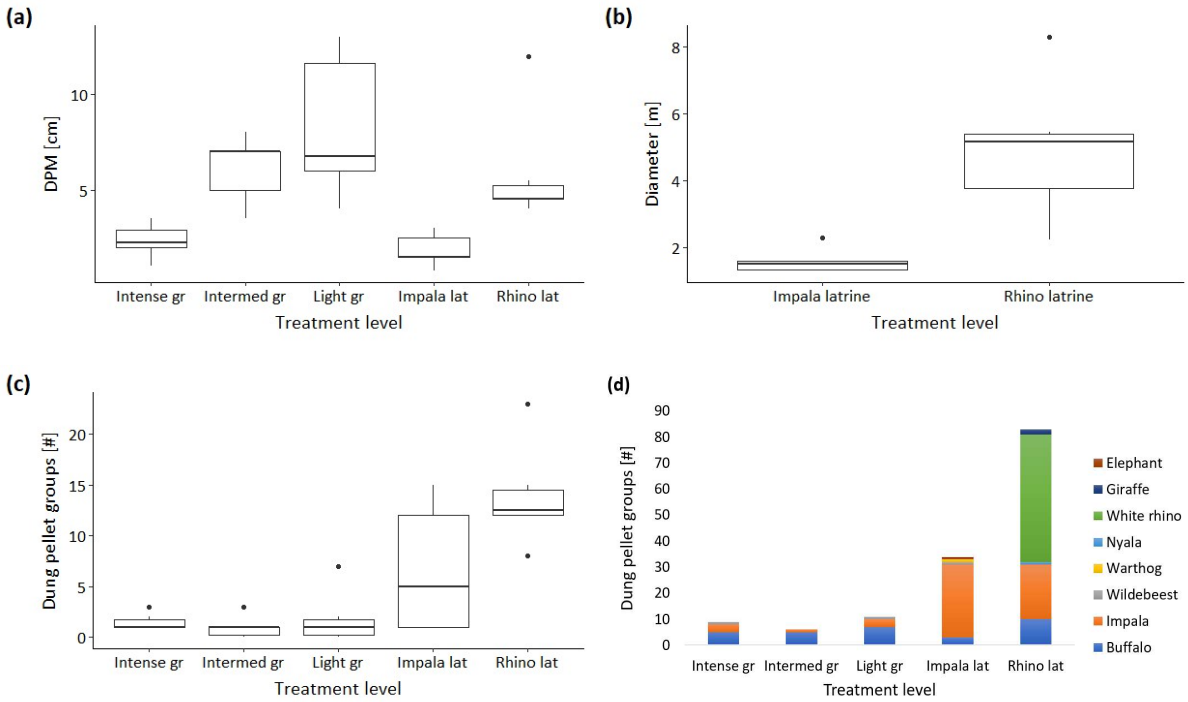
Appendix

Appendix A: Data distributions over treatment levels

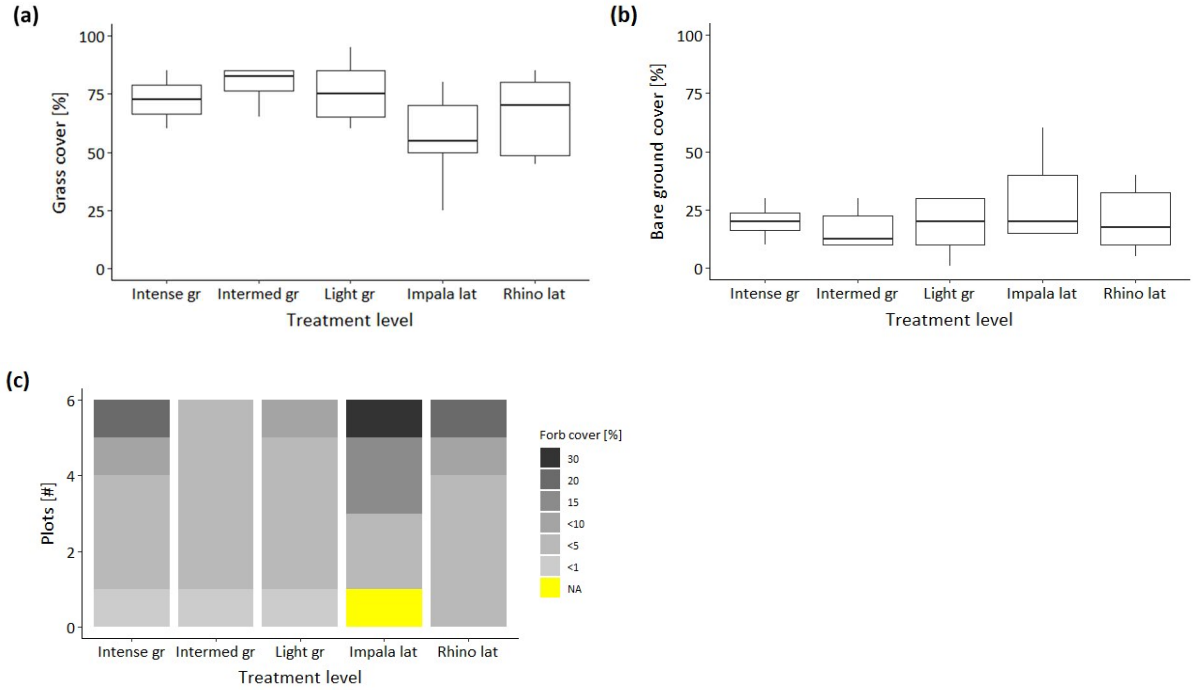
Appendix A.1: (a) MAR, (b) fire frequency, and soil clay content in (c) upper and (d) lower soil layer



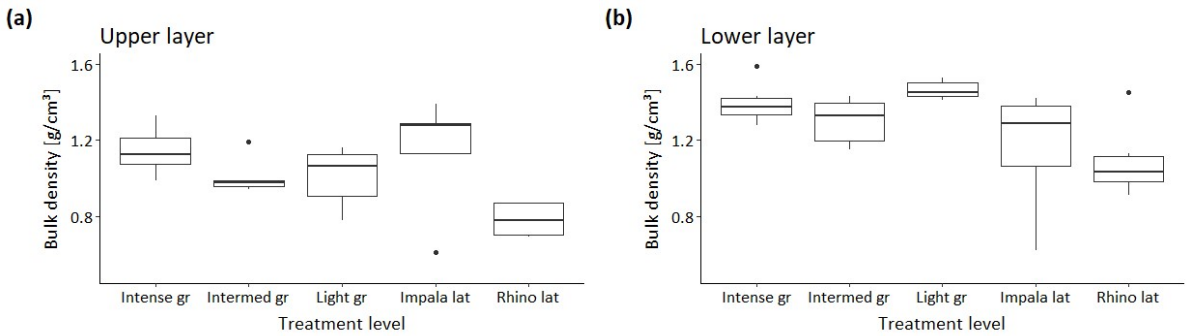
Appendix A.2: (a) DPM, (b) latrine size, (c) dung pellet group density, and (d) dung count species



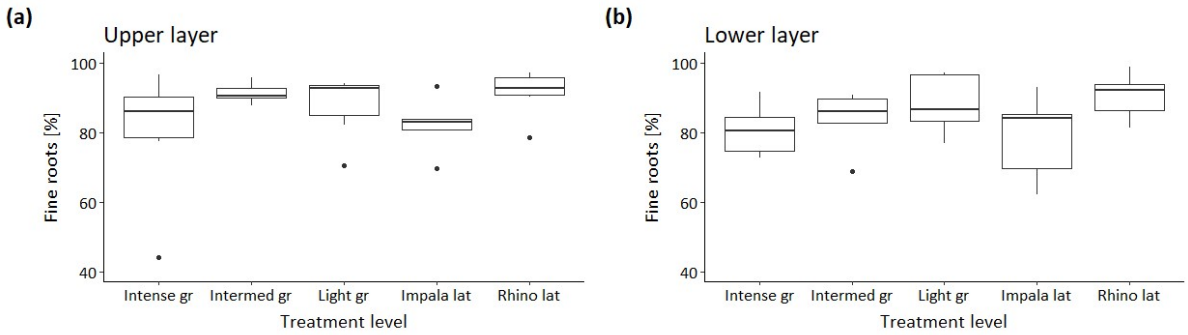
Appendix A.3: (a) Grass, (b) bare ground, and (c) forb cover



Appendix A.4: Bulk density in (a) upper and (b) lower soil layer



Appendix A.5: Fine root fractions in (a) upper and (b) lower soil layer



Appendix B: Number of counted intersects per sample for assessment of AM root infection rates

		Number of intersects	
Block	**Treatment level**	**Upper layer**	**Lower layer**
1	Intensely grazed grazing lawn	31	50
1	Intermediately grazed tall grassland	50	50
1	Lightly grazed tall grassland	50	50
1	Impala latrine	50	50
1	White rhino latrine	50	50
2	Intensely grazed grazing lawn	50	50
2	Intermediately grazed tall grassland	50	50
2	Lightly grazed tall grassland	50	50
2	Impala latrine	50	50
2	White rhino latrine	50	50
3	Intensely grazed grazing lawn	26	50
3	Intermediately grazed tall grassland	39	50
3	Lightly grazed tall grassland	50	50
3	Impala latrine	50	50
3	White rhino latrine	50	50
4	Intensely grazed grazing lawn	35	50
4	Intermediately grazed tall grassland	50	50
4	Lightly grazed tall grassland	40	37
4	Impala latrine	25	50
4	White rhino latrine	50	50
5	Intensely grazed grazing lawn	50	50
5	Intermediately grazed tall grassland	50	50
5	Lightly grazed tall grassland	28	50
5	Impala latrine	50	50
5	White rhino latrine	50	50
6	Intensely grazed grazing lawn	NA	NA
6	Intermediately grazed tall grassland	NA	NA
6	Lightly grazed tall grassland	50	50
6	Impala latrine	NA	NA
6	White rhino latrine	50	50

Appendix C: SOC and N pools per sample from white rhino latrines

		SOC pool (t/ha)		Soil N:P ratio
Block	**Treatment level**	**Upper layer**	**Lower layer**	**Upper layer**
1	White rhino latrine	>42.0	>68.0	>4519
2	White rhino latrine	>52.5	36.4	10936
3	White rhino latrine	26.3	54.9	2980
4	White rhino latrine	26.1	31.8	3702
5	White rhino latrine	40.2	47.8	11308
6	White rhino latrine	>47.1	42.1	9699

Appendix D: Grazing intensity study

Treat = treatment level; Dung = dung pellet group density; Block = block number; Fine R:Sh = fine root:shoot ratio; R:Sh = root:shoot ratio; AM = arbuscular mycorrhizal root infection rate; SOC = soil organic carbon; MAR = mean annual rainfall; Fire = fire frequency; Soil = soil texture; ( ) p > 0.05; (*) p < 0.05; (**) p < 0.01; (***) p < 0.001

Appendix D.1: ANOVA results of linear mixed-effect models

Response			**Upper layer**		**Lower layer**	
Upper layer	**Lower layer**	**Predictors**	**F-value**	**p-value**	**F-value**	**p-value**
Fine R:Sh	Fine R:Sh	= Treat + Block	2.2780	0.1583	2.7843	0.1145
Sqrt(Fine R:Sh)	Fine R:Sh	= Dung + Block	2.2228	0.1668	0.5925	0.4592
R:Sh	R:Sh	= Treat + Block	3.8639	0.0615	3.3371	0.0824
R:Sh	Sqrt(R:Sh)	= Dung + Block	1.7351	0.2171	0.8321	0.3831
AM	AM	= Treat + Block	1.3105	0.3219	0.6405	0.5520
AM	AM	= Dung + Block	0.8520	0.3801	0.1691	0.6906
SOC	SOC	= Treat + Block	0.5143	0.6129	5.9001	0.0203*
SOC	SOC	= Dung + Block	1.6919	0.2199	2.2089	0.1653
SOC	SOC	= Fine R:Sh + Block	1.1320	0.3124	0.0007	0.9798
SOC	SOC	= R:Sh + Block	0.6628	0.4345	0.0158	0.9026
SOC	SOC	= AM + Block	1.2302	0.2961	0.2882	0.6044
Sqrt(Fine R:Sh)	Fine R:Sh	= MAR + Block	0.0628	0.8072	1.5158	0.2464
Sqrt(Fine R:Sh)	Sqrt(Fine R:Sh)	= Fire + Block	0.0910	0.7779	1.0880	0.3558
Sqrt(Fine R:Sh)	Sqrt(Fine R:Sh)	= Soil + Block	0.5007	0.4953	0.4543	0.5156
R:Sh	Sqrt(R:Sh)	= MAR + Block	0.1124	0.7444	0.9416	0.3548
R:Sh	Sqrt(R:Sh)	= Fire + Block	0.1741	0.6979	1.1605	0.3420
R:Sh	Sqrt(R:Sh)	= Soil + Block	0.2134	0.6540	0.3311	0.5777
AM	AM	= MAR + Block	0.3975	0.5441	0.0185	0.8948
AM	AM	= Fire + Block	0.1576	0.7116	0.0310	0.8688
AM	AM	= Soil + Block	7.1809	0.0252*	3.5455	0.0924
SOC	SOC	= MAR + Block	3.3010	0.0966	5.0303	0.0465*
SOC	SOC	= Fire + Block	4.6431	0.0975	6.7769	0.0598
SOC	SOC	= Soil + Block	16.8541	0.0017**	14.3555	0.003**

Upper layer		Predictor 1		Predictor 2		Interaction	
Response	**Predictors**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Fine R:Sh	= Treat * MAR + Block	1.8807	0.2322	0.1818	0.6847	0.2569	0.7815
Fine R:Sh	= Treat * Fire + Block	1.9086	0.2180	0.1627	0.7073	0.3044	0.7469
Fine R:Sh	= Treat * Soil + Block	1.7624	0.2500	1.5305	0.2623	0.2063	0.8191
R:Sh	= Treat * MAR + Block	3.0639	0.1211	0.0780	0.7894	0.0846	0.9200
R:Sh	= Treat * Fire + Block	3.1646	0.1050	0.1306	0.7361	0.2041	0.8201
R:Sh	= Treat * Soil + Block	2.8440	0.1353	1.1745	0.3201	0.1444	0.8685
AM	= Treat * MAR + Block	1.2826	0.3551	0.1138	0.7495	1.5409	0.3011
AM	= Treat * Fire + Block	1.3846	0.3203	0.0012	0.9746	1.7548	0.2512
AM	= Treat * Soil + Block	11.6563	0.0131*	39.6532	0.0015**	7.3157	0.0327*
SOC	= Treat * MAR + Block	0.4341	0.6642	3.2983	0.1122	0.1462	0.8666
SOC	= Treat * Fire + Block	0.4123	0.6754	4.6431	0.0975	0.0082	0.9919
SOC	= Treat * Soil + Block	0.4533	0.6530	12.8869	0.0089**	0.1459	0.8668
SOC	= Fine R:Sh + MAR + Block	3.5410	0.0925	11.1607	0.0086**	-	-
SOC	= Fine R:Sh + Fire + Block	3.9271	0.0757	13.9043	0.0203*	-	-
SOC	= Fine R:Sh + Soil + Block	3.8773	0.0805	13.5500	0.0051**	-	-
SOC	= R:Sh + MAR + Block	2.1048	0.1808	8.4818	0.0172*	-	-
SOC	= R:Sh + Fire + Block	2.5112	0.1441	11.8526	0.0262*	-	-
SOC	= R:Sh + Soil + Block	2.8077	0.1281	14.9058	0.0038**	-	-
SOC	= AM + MAR + Block	0.7492	0.4119	1.2276	0.3001	-	-
SOC	= AM + Fire + Block	0.8800	0.3727	1.7258	0.2592	-	-
SOC	= AM + Soil + Block	1.5449	0.2491	4.5806	0.0648	-	-

Lower layer		Predictor 1		Predictor 2		Interaction	
Response	**Predictors**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Fine R:Sh	= Treat * MAR + Block	2.4287	0.1688	1.6072	0.2519	0.4424	0.6619
Fine R:Sh	= Treat * Fire + Block	2.5384	0.1483	1.6253	0.2714	0.6119	0.5690
Fine R:Sh	= Treat * Soil + Block	2.1497	0.1977	0.0272	0.8743	0.0411	0.9600
R:Sh	= Treat * MAR + Block	2.8717	0.1334	1.4719	0.2706	0.3750	0.7023
R:Sh	= Treat * Fire + Block	3.0098	0.1140	1.6023	0.2743	0.5587	0.5955
R:Sh	= Treat * Soil + Block	2.6179	0.1523	0.0190	0.8948	0.0619	0.9406
AM	= Treat * MAR + Block	1.0170	0.4260	0.0018	0.9676	3.6214	0.1066
AM	= Treat * Fire + Block	1.3845	0.3203	0.0000	0.9973	5.9831	0.0372*
AM	= Treat * Soil + Block	0.7339	0.5254	4.7935	0.0802	1.5314	0.3028
SOC	= Treat * MAR + Block	4.9631	0.0455	4.9304	0.0618	0.0768	0.9269
SOC	= Treat * Fire + Block	5.1908	0.0359*	6.7770	0.0598	0.3989	0.6837
SOC	= Treat * Soil + Block	5.6036	0.0352*	5.8413	0.0463*	1.3849	0.3113
SOC	= Fine R:Sh + MAR + Block	0.0039	0.9514	6.0688	0.036*	-	-
SOC	= Fine R:Sh + Fire + Block	0.0693	0.7977	31.4488	0.005**	-	-
SOC	= Fine R:Sh + Soil + Block	0.0074	0.9332	13.6873	0.0049**	-	-
SOC	= R:Sh + MAR + Block	0.0038	0.9521	5.1288	0.0498*	-	-
SOC	= R:Sh + Fire + Block	0.0004	0.9852	10.0620	0.0338*	-	-
SOC	= R:Sh + Soil + Block	0.0012	0.9729	13.8776	0.0047**	-	-
SOC	= AM + MAR + Block	0.3786	0.5555	3.8750	0.0845	-	-
SOC	= AM + Fire + Block	0.4324	0.5273	4.9176	0.0909	-	-
SOC	= AM + Soil + Block	0.5315	0.4868	9.0067	0.017*	-	-

Appendix D.2: Summary results of linear mixed-effect models

a) Models with treatment levels

		Upper layer				Lower layer			
	Response	Fine R:Sh	R:Sh	AM	SOC	Fine R:Sh	R:Sh	AM	SOC
	Predictors	= Treat + Block							
Intense	**Estimate**	234.1667	288.5000	75.0743	26.9000	170.0000	201.8333	76.0726	32.7000
	Std. Error	46.6306	48.4786	8.4601	3.4178	40.3465	43.0868	5.3984	4.9934
	t-value	5.0217	5.9511	8.8739	7.8705	4.2135	4.6843	14.0918	6.5486
	p-value	0.0007	0.0002	0.0000	0.0000	0.0023	0.0011	0.0000	0.0001
Intermediate	**Estimate**	130.8226	138.7416	78.9343	30.1500	93.5453	105.4039	68.8726	28.8000
	Std. Error	52.6803	59.4779	10.2118	3.5024	38.8911	45.1253	7.0210	2.4822
	t-value	-1.9617	-2.5179	0.3780	0.9279	-1.9659	-2.1369	-1.0255	-1.5712
	p-value	0.0814	0.0329	0.7153	0.3753	0.0809	0.0613	0.3351	0.1472
Light	**Estimate**	151.6667	163.6667	63.6500	29.7667	94.3333	105.0000	69.7000	37.3167
	Std. Error	49.5502	56.0797	9.9012	3.5024	36.4703	42.3743	6.7701	2.4822
	t-value	-1.6650	-2.2260	-1.1538	0.8185	-2.0748	-2.2852	-0.9413	1.8599
	p-value	0.1303	0.0530	0.2819	0.4321	0.0678	0.0482	0.3741	0.0925

Upper layer: Influence of predictor 2 at grazing intensity level	**Response**	Fine R:Sh	R:Sh	Fine R:Sh	R:Sh	Fine R:Sh	R:Sh
	Predictors	= Treat * MAR + Block		= Treat * Fire + Block		= Treat * Soil + Block	
Intense	**Estimate**	-0.842	-0.489	-25.961	-23.338	6.666	4.761
	Std. Error	1.148	1.219	34.706	36.427	5.341	5.811
	t-value	-0.734	-0.401	-0.748	-0.641	1.248	0.819
	p-value	0.491	0.702	0.496	0.557	0.259	0.444
Intermediate	**Estimate**	0.938	0.613	29.987	28.237	-3.952	-2.164
	Std. Error	1.322	1.521	38.755	44.287	6.491	7.456
	t-value	0.710	0.403	0.774	0.638	-0.609	-0.290
	p-value	0.505	0.701	0.464	0.544	0.565	0.781
Light	**Estimate**	0.522	0.167	16.948	14.481	-0.476	2.955
	Std. Error	1.235	1.426	37.038	42.405	8.754	9.973
	t-value	0.422	0.117	0.458	0.341	-0.054	0.296
	p-value	0.688	0.911	0.661	0.743	0.958	0.777

Upper layer: Influence of predictor 2 at grazing intensity level	Response	AM	SOC	AM	SOC	AM	SOC
	Predictors	= Treat * MAR + Block		= Treat * Fire + Block		= Treat * Soil + Block	
Intense	Estimate	-0.056	0.100	-0.312	3.008	-3.915	0.794
	Std. Error	0.268	0.072	10.130	2.107	1.064	0.306
	t-value	-0.207	1.387	-0.031	1.428	-3.681	2.598
	p-value	0.844	0.208	0.977	0.227	0.014	0.036
Intermediate	Estimate	-0.380	-0.031	-16.619	0.277	1.128	-0.208
	Std. Error	0.333	0.086	12.439	2.675	0.929	0.407
	t-value	-1.140	-0.361	-1.336	0.103	1.214	-0.512
	p-value	0.306	0.729	0.230	0.920	0.279	0.624
Light	Estimate	0.130	0.014	3.074	-0.036	-1.831	-0.203
	Std. Error	0.295	0.086	10.668	2.675	0.813	0.548
	t-value	0.442	0.166	0.288	-0.014	-2.251	-0.371
	p-value	0.677	0.873	0.783	0.990	0.074	0.722

Lower layer: Influence of predictor 2 at grazing intensity level	Response	Fine R:Sh	R:Sh	Fine R:Sh	R:Sh	Fine R:Sh	R:Sh
	Predictors	= Treat * MAR + Block		= Treat * Fire + Block		= Treat * Soil + Block	
Intense	Estimate	-1.342	-1.369	-40.675	-42.922	0.588	0.645
	Std. Error	0.885	0.965	26.564	28.695	4.122	4.507
	t-value	-1.517	-1.419	-1.531	-1.496	0.143	0.143
	p-value	0.180	0.206	0.201	0.209	0.891	0.891
Intermediate	Estimate	0.896	0.964	30.353	33.789	0.599	0.580
	Std. Error	0.958	1.116	27.640	32.222	4.489	5.157
	t-value	0.935	0.864	1.098	1.049	0.133	0.112
	p-value	0.386	0.421	0.309	0.329	0.898	0.914
Light	Estimate	0.471	0.479	10.727	11.831	-0.841	-1.413
	Std. Error	0.894	1.043	26.384	30.798	4.791	5.495
	t-value	0.527	0.459	0.407	0.384	-0.175	-0.257
	p-value	0.617	0.662	0.697	0.712	0.867	0.806

Lower layer: Influence of predictor 2 at grazing intensity level	Response	AM	SOC	AM	SOC	AM	SOC
	Predictors	= Treat * MAR + Block		= Treat * Fire + Block		= Treat * Soil + Block	
Intense	Estimate	0.192	0.194	9.701	6.584	-0.632	0.661
	Std. Error	0.157	0.089	5.412	2.461	0.982	0.299
	t-value	1.220	2.172	1.792	2.676	-0.643	2.209
	p-value	0.277	0.067	0.148	0.056	0.549	0.063
Intermediate	Estimate	-0.478	-0.014	-20.750	-0.740	-1.474	0.193
	Std. Error	0.181	0.061	6.007	1.809	1.273	0.270
	t-value	-2.637	-0.229	-3.454	-0.409	-1.157	0.714
	p-value	0.046	0.825	0.014	0.693	0.299	0.498
Light	Estimate	-0.169	-0.024	-9.521	-1.614	0.195	-0.317
	Std. Error	0.165	0.061	5.414	1.809	1.114	0.295
	t-value	-1.024	-0.390	-1.759	-0.892	0.175	-1.073
	p-value	0.353	0.708	0.129	0.398	0.868	0.319

b) Models with only covariates

Upper layer					
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**
Sqrt(Fine R:Sh)	= Dung + Block	-0.8911	0.5977	-1.4909	0.1668
R:Sh	= Dung + Block	-25.1224	19.0722	-1.3172	0.2171
AM	= Dung + Block	-2.5322	2.7434	-0.9230	0.3801
SOC	= Dung + Block	1.2578	0.9670	1.3007	0.2199
SOC	= Fine R:Sh + Block	0.0177	0.0167	1.0640	0.3124
SOC	= R:Sh + Block	0.0116	0.0143	0.8141	0.4345
SOC	= AM + Block	-0.1077	0.0971	-1.1092	0.2961
Sqrt(Fine R:Sh)	= MAR + Block	-0.0098	0.0391	-0.2506	0.8072
Sqrt(Fine R:Sh)	= Fire + Block	-0.3581	1.1867	-0.3017	0.7779
Sqrt(Fine R:Sh)	= Soil + Block	0.1116	0.1578	0.7076	0.4953
R:Sh	= MAR + Block	-0.3211	0.9579	-0.3352	0.7444
R:Sh	= Fire + Block	-12.0356	28.8471	-0.4172	0.6979
R:Sh	= Soil + Block	2.0220	4.3768	0.4620	0.6540
AM	= MAR + Block	-0.0934	0.1481	-0.6305	0.5441
AM	= Fire + Block	-1.9171	4.8289	-0.3970	0.7116
AM	= Soil + Block	-2.4979	0.9322	-2.6797	0.0252
SOC	= MAR + Block	0.0941	0.0518	1.8169	0.0966
SOC	= Fire + Block	3.0879	1.4330	2.1548	0.0975
SOC	= Soil + Block	0.6703	0.1633	4.1054	0.0017

Lower layer					
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**
Fine R:Sh	= Dung + Block	-0.4546	0.5906	-0.7698	0.4592
Sqrt(R:Sh)	= Dung + Block	-0.5598	0.6137	-0.9122	0.3831
AM	= Dung + Block	-0.7243	1.7616	-0.4112	0.6906
SOC	= Dung + Block	1.4792	0.9953	1.4862	0.1653
SOC	= Fine R:Sh + Block	-0.0006	0.0239	-0.0260	0.9798
SOC	= R:Sh + Block	-0.0025	0.0202	-0.1255	0.9026
SOC	= AM + Block	-0.0970	0.1806	-0.5368	0.6044
Fine R:Sh	= MAR + Block	-0.9382	0.7620	-1.2312	0.2464
Sqrt(Fine R:Sh)	= Fire + Block	-1.1607	1.1127	-1.0431	0.3558
Sqrt(Fine R:Sh)	= Soil + Block	0.1057	0.1569	0.6740	0.5156
Sqrt(R:Sh)	= MAR + Block	-0.0340	0.0350	-0.9704	0.3548
Sqrt(R:Sh)	= Fire + Block	-1.1313	1.0502	-1.0772	0.3420
Sqrt(R:Sh)	= Soil + Block	0.0893	0.1553	0.5754	0.5777
AM	= MAR + Block	-0.0128	0.0940	-0.1361	0.8948
AM	= Fire + Block	-0.5248	2.9818	-0.1760	0.8688
AM	= Soil + Block	-0.7015	0.3725	-1.8830	0.0924
SOC	= MAR + Block	0.1832	0.0817	2.2428	0.0465
SOC	= Fire + Block	5.7996	2.2278	2.6033	0.0598
SOC	= Soil + Block	0.9274	0.2448	3.7889	0.0030

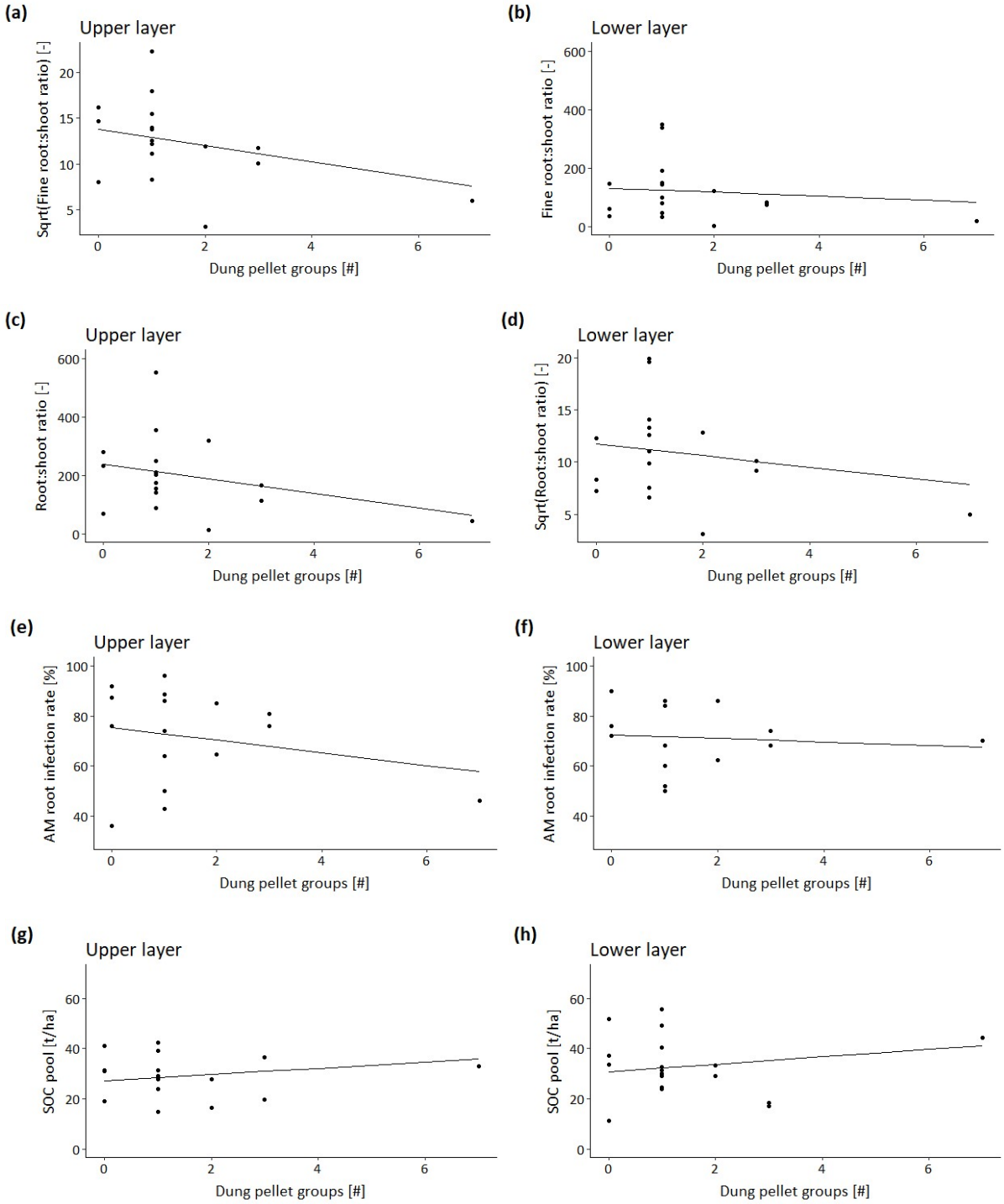
Upper layer		Predictor 1				Predictor 2			
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**	**Estimate**	**Std. Error**	**t-value**	**p-value**
SOC	= Fine R:Sh + MAR + Block	0.0312	0.0132	2.3608	0.0425	0.1136	0.0340	3.3408	0.0086
SOC	= Fine R:Sh + Fire + Block	0.0311	0.0125	2.4810	0.0325	3.6107	0.9683	3.7288	0.0203
SOC	= Fine R:Sh + Soil + Block	0.0094	0.0131	0.7172	0.4914	0.6519	0.1771	3.6810	0.0051
SOC	= R:Sh + MAR + Block	0.0218	0.0126	1.7266	0.1183	0.1074	0.0369	2.9124	0.0172
SOC	= R:Sh + Fire + Block	0.0236	0.0118	1.9899	0.0746	3.5232	1.0234	3.4428	0.0262
SOC	= R:Sh + Soil + Block	0.0092	0.0114	0.8041	0.4421	0.6620	0.1715	3.8608	0.0038
SOC	= AM + MAR + Block	-0.0656	0.1018	-0.6449	0.5371	0.0605	0.0546	1.1079	0.3001
SOC	= AM + Fire + Block	-0.0741	0.0985	-0.7519	0.4713	2.1976	1.6728	1.3137	0.2592
SOC	= AM + Soil + Block	0.0139	0.1036	0.1346	0.8963	0.7777	0.3634	2.1402	0.0648

Lower layer		Predictor 1				Predictor 2			
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**	**Estimate**	**Std. Error**	**t-value**	**p-value**
SOC	= Fine R:Sh + MAR + Block	0.0171	0.0233	0.7334	0.4820	0.1954	0.0793	2.4635	0.0360
SOC	= Fine R:Sh + Fire + Block	0.0510	0.0201	2.5361	0.0296	7.4253	1.3241	5.6079	0.0050
SOC	= Fine R:Sh + Soil + Block	-0.0046	0.0193	-0.2371	0.8179	0.9745	0.2634	3.6996	0.0049
SOC	= R:Sh + MAR + Block	0.0089	0.0199	0.4474	0.6652	0.1880	0.0830	2.2647	0.0498
SOC	= R:Sh + Fire + Block	0.0190	0.0198	0.9583	0.3605	6.3675	2.0074	3.1721	0.0338
SOC	= R:Sh + Soil + Block	-0.0048	0.0167	-0.2894	0.7788	0.9753	0.2618	3.7253	0.0047
SOC	= AM + MAR + Block	-0.0972	0.1712	-0.5678	0.5857	0.1674	0.0851	1.9685	0.0845
SOC	= AM + Fire + Block	-0.1021	0.1710	-0.5975	0.5649	5.4350	2.4509	2.2176	0.0909
SOC	= AM + Soil + Block	0.0035	0.1590	0.0220	0.9830	0.9467	0.3154	3.0011	0.0170

Appendix D.3: Tukey-test results of linear mixed-effect models

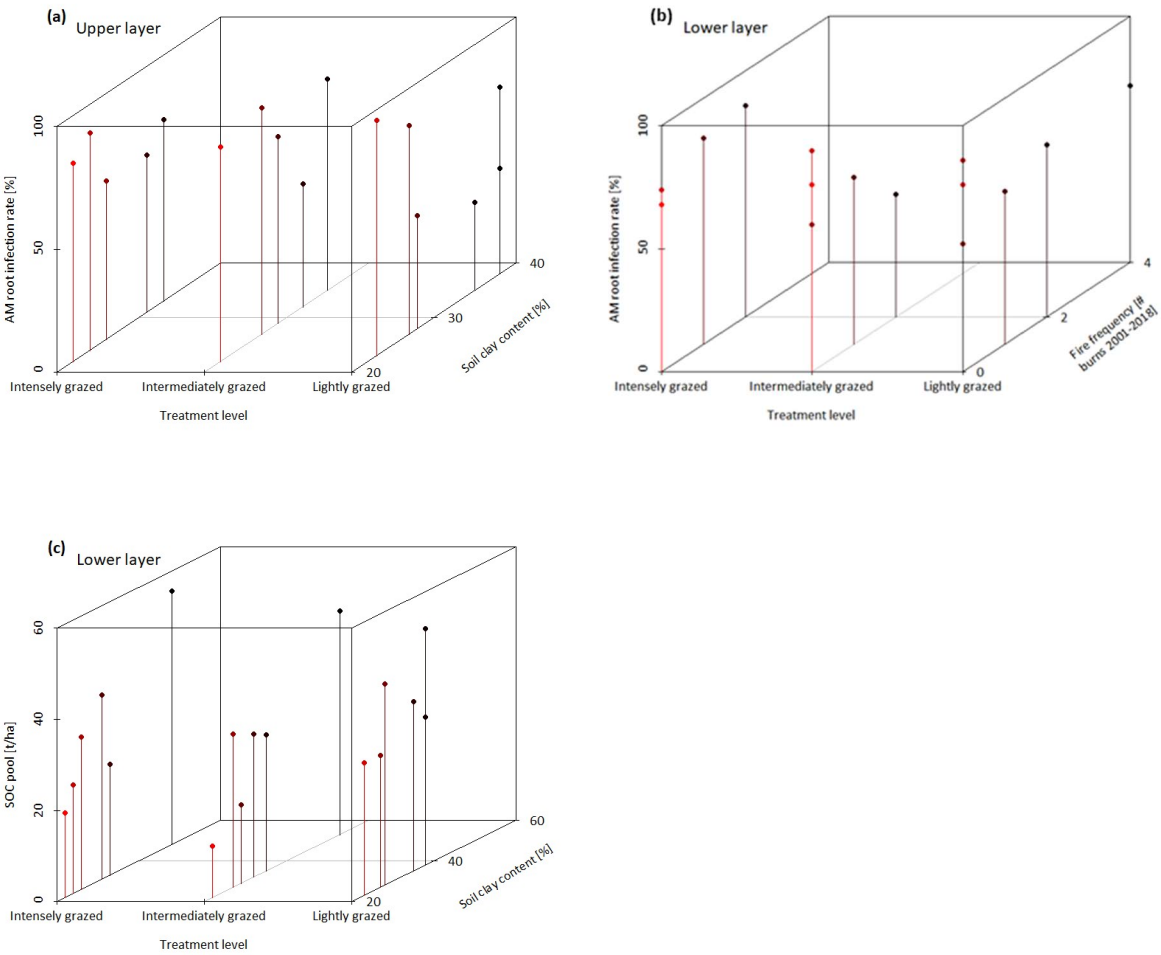
			Intense - Intermediate		Intense - Light		Intermediate - Light	
	Response	**Predictors**	**z-value**	**P-value**	**z-value**	**P-value**	**z-value**	**P-value**
Upper layer	Fine R:Sh	= Treat + Block	-1.962	0.122	-1.665	0.219	0.396	0.917
	R:Sh	= Treat + Block	-2.518	0.0317*	-2.226	0.067	0.419	0.908
	AM	= Treat + Block	0.378	0.924	-1.154	0.481	-1.544	0.270
	SOC	= Treat + Block	0.928	0.623	0.818	0.692	-0.109	0.993
Lower layer	Fine R:Sh	= Treat + Block	-1.966	0.121	-2.075	0.095	0.020	1.000
	R:Sh	= Treat + Block	-2.137	0.083	-2.285	0.058	-0.009	1.000
	AM	= Treat + Block	-1.025	0.561	-0.941	0.614	0.122	0.992
	SOC	= Treat + Block	-1.571	0.258	1.860	0.151	3.431	0.00174*

Appendix D.4: Associations between dung pellet group density and (a) fine root:shoot ratios in upper soil layer, (b) fine root:shoot ratios in lower soil layer, (c) root:shoot ratios in upper soil layer, (d) fine root:shoot ratios in lower soil layer, (e) AM root infection rates in upper soil layer, (f) AM root infection rates in lower soil layer, (g) SOC pools in upper soil layer, and (h) SOC pools in lower soil layer



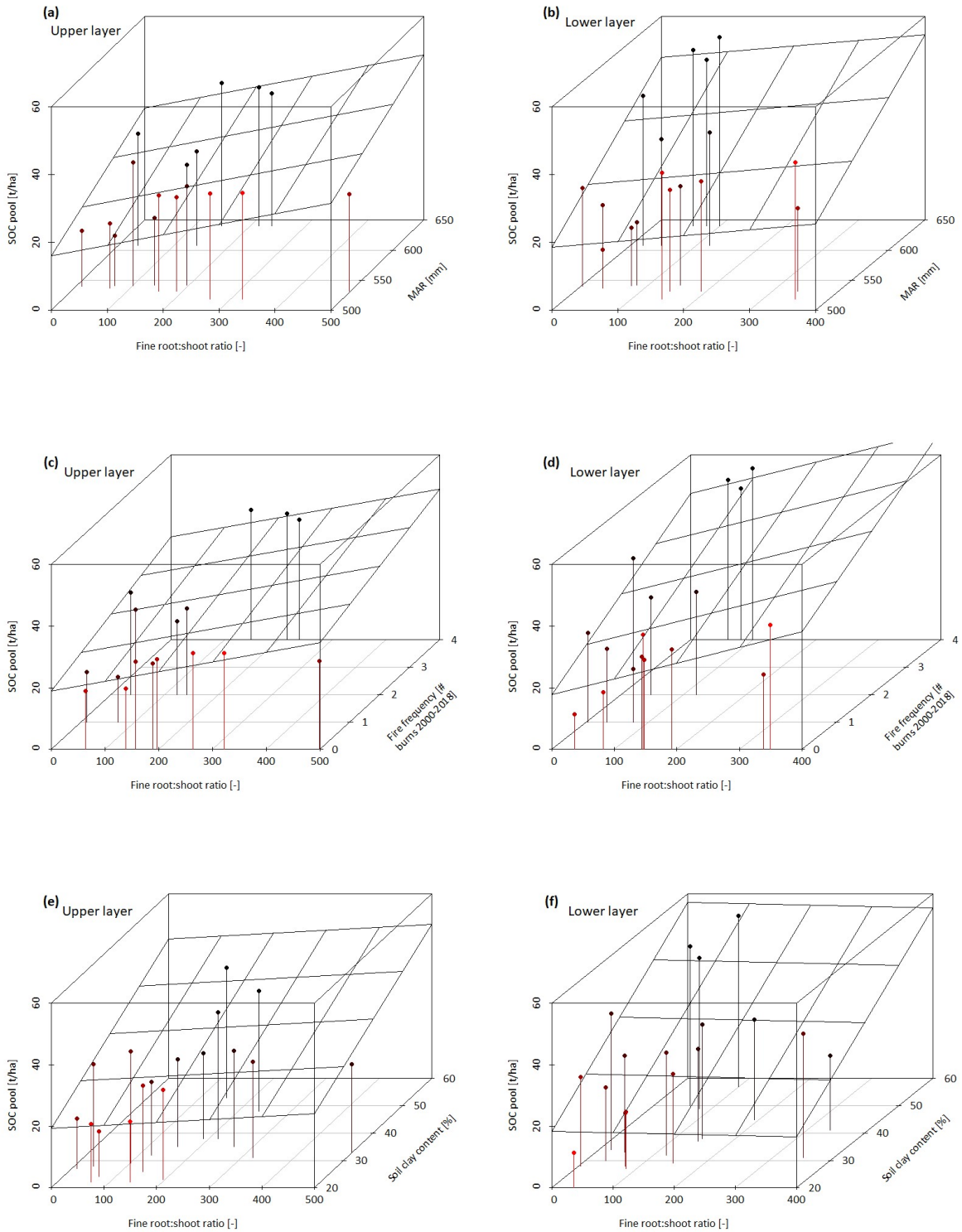
Appendix D.5: Associations between grazing intensity and (a) AM root infection rates and soil clay content in upper soil layer, (b) AM root infection rates and fire frequency in lower soil layer, and (c) SOC pools and soil clay content in lower soil layer

(a), (b) interaction between grazing intensity and environmental driver ($p < 0.05$); (c) no interaction but significant predictors ($p < 0.05$); colour: light-dark = low-high MAR/fire freq./soil clay cont.



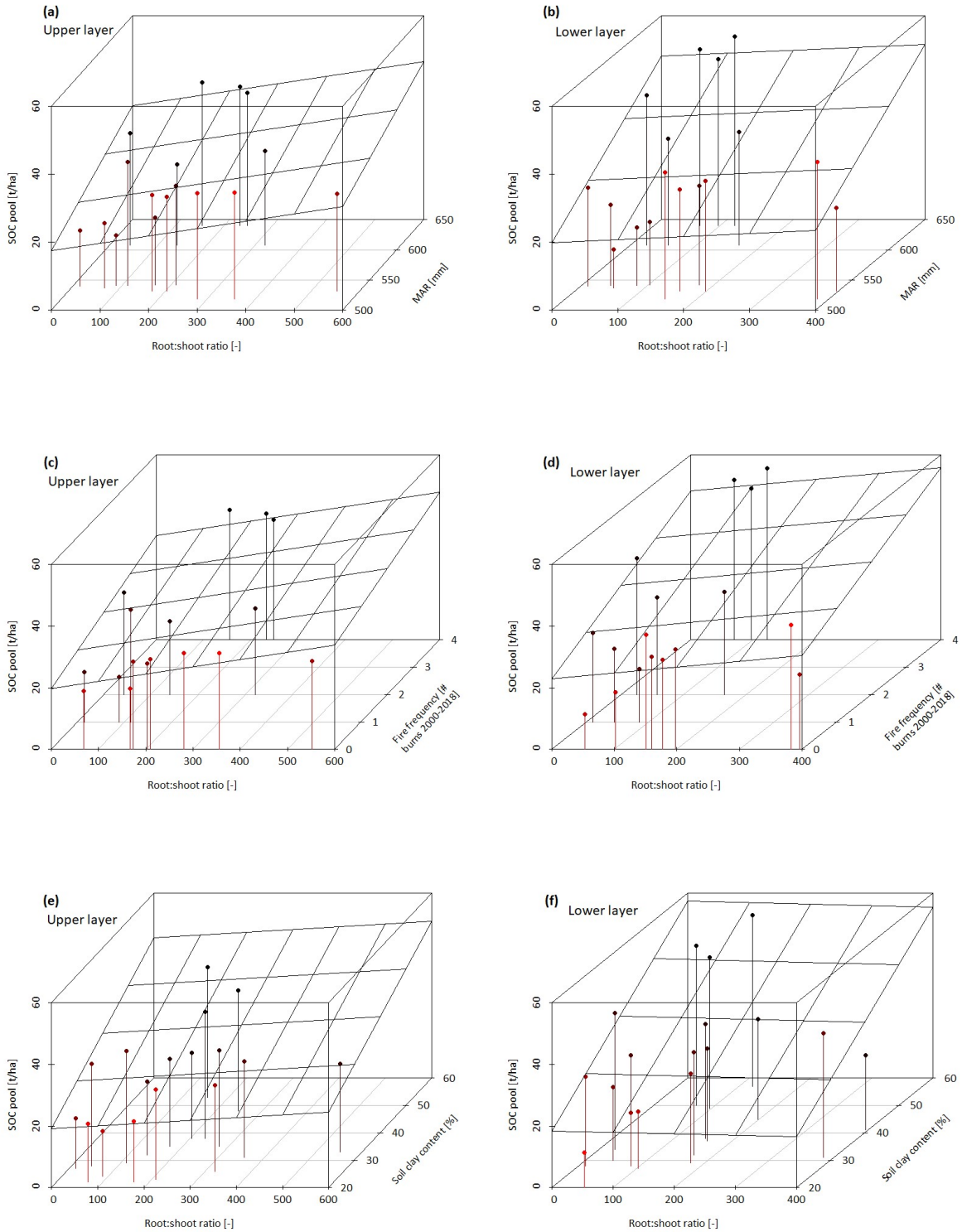
Appendix D.6: Associations between SOC pools, fine root:shoot ratios and (a) MAR in upper soil layer, (b) MAR in lower soil layer, (c) fire frequency in upper soil layer, (d) fire frequency in lower soil layer, (e) soil clay content in upper soil layer, and (f) soil clay content in lower soil layer

Significant impact of environmental variable on SOC pools (b, c: $p < 0.05$; a, d, e, f: $p < 0.01$); colour: light-dark = low-high MAR/fire freq./soil clay cont.



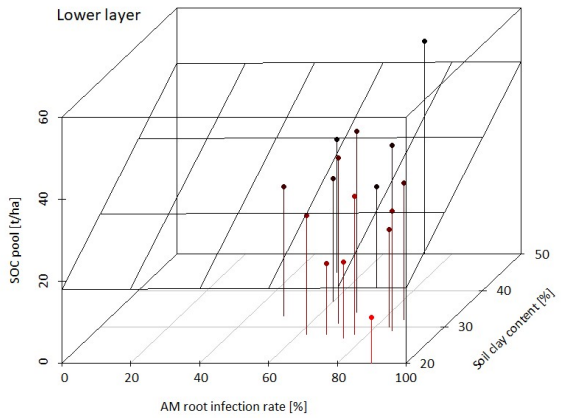
Appendix D.7: Associations between SOC pools, root:shoot ratios and (a) MAR in upper soil layer, (b) MAR in lower soil layer, (c) fire frequency in upper soil layer, (d) fire frequency in lower soil layer, (e) soil clay content in upper soil layer, and (f) soil clay content in lower soil layer

Significant impact of environmental variable on SOC pools (a, b, c, d: $p < 0.05$; e, f: $p < 0.01$); colour: light-dark = low-high MAR/fire freq./soil clay cont.



Appendix D.8: Association between SOC pools, AM root infection rates and soil clay content in lower soil layer

Significant impact of environmental variable on SOC pools ($p < 0.05$); colour: light-dark = low-high MAR/fire freq./soil clay cont.



Appendix E: Latrine study

Treat = treatment level; Dung = dung pellet group density; LSize = latrine size; DPM = DPM; Block = block number; NP = soil N:P ratio; AM = arbuscular mycorrhizal root infection rate; SOC = soil organic carbon; MAR = mean annual rainfall; Fire = fire frequency; Soil = soil texture; ( ) p > 0.05; (*) p < 0.05; (**) p < 0.01; (***) p < 0.001

Appendix E.1: ANOVA results of linear mixed-effect models

Response			**Upper layer**		**Lower layer**	
Upper layer	**Lower layer**	**Predictors**	**F-value**	**p-value**	**F-value**	**p-value**
NP	NP	= Treat + Block	3.1177	0.1522	2.2041	0.2118
NP	NP	= Dung + Block	10.5943	0.0312*	11.2086	0.0286*
NP	NP	= LSize + Block	1.8323	0.2473	1.7849	0.2525
NP	NP	= DPM + Block	1.0161	0.3705	2.2685	0.2065
AM	AM	= Treat + Block	0.0034	0.9563	9.1456	0.039*
AM	AM	= Dung + Block	0.0027	0.9611	0.0060	0.9421
AM	AM	= LSize + Block	1.3555	0.3090	2.3276	0.2018
AM	AM	= DPM + Block	1.0107	0.3716	7.1341	0.0557
SOC	SOC	= Treat + Block	34.5191	0.0042**	56.5940	0.0017**
SOC	SOC	= Dung + Block	5.5806	0.0775	18.3901	0.0128*
SOC	SOC	= LSize + Block	3.5104	0.1343	4.8024	0.0935
SOC	SOC	= DPM + Block	17.9277	0.0133*	1.5491	0.2812
AM	AM	= NP + Block	1.2547	0.3254	0.5039	0.5170
SOC	SOC	= NP + Block	0.0187	0.8978	0.0071	0.9371
SOC	SOC	= AM + Block	0.2119	0.6692	15.1097	0.0177*
NP	log(NP)	= MAR + Block	0.1567	0.7124	0.5629	0.4948
NP	log(NP)	= Fire + Block	0.0678	0.8074	0.2088	0.6714
NP	log(NP)	= Soil + Block	18.3300	0.0128*	3.5901	0.1310
AM	AM	= MAR + Block	3.1773	0.1492	0.4683	0.5313
AM	AM	= Fire + Block	1.0053	0.3728	0.0354	0.8600
AM	AM	= Soil + Block	2.9137	0.1630	0.0052	0.9462
SOC	SOC	= MAR + Block	0.7599	0.4326	2.0274	0.2276
SOC	SOC	= Fire + Block	1.1991	0.3350	0.8323	0.4132
SOC	SOC	= Soil + Block	2.5590	0.1849	0.0130	0.9148

Upper layer		Predictor 1		Predictor 2		Interaction	
Response	**Predictors**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
NP	= Treat * MAR + Block	11.1821	0.0790	0.4399	0.5754	11.1089	0.0794
NP	= Treat * Fire + Block	7.8668	0.0676	0.3602	0.5807	6.7366	0.0807
NP	= Treat * Soil + Block	23.4249	0.0401*	61.2920	0.0159*	5.5446	0.1427
AM	= Treat * MAR + Block	0.0037	0.9572	2.5090	0.2540	0.9419	0.4342
AM	= Treat * Fire + Block	0.0030	0.9601	0.9344	0.3885	0.2585	0.6462
AM	= Treat * Soil + Block	0.0071	0.9407	1.8995	0.3021	0.4181	0.5842
SOC	= Treat * MAR + Block	27.1429	0.0349*	0.4695	0.5640	0.0031	0.9609
SOC	= Treat * Fire + Block	29.0114	0.0125*	0.6294	0.4720	0.1233	0.7487
SOC	= Treat * Soil + Block	30.6368	0.0311*	5.7384	0.1389	0.6373	0.5084
AM	= NP + MAR + Block	0.9747	0.3963	2.7169	0.1979	-	-
AM	= NP + Fire + Block	1.2407	0.3278	0.9014	0.3962	-	-
AM	= NP + Soil + Block	1.3089	0.3356	0.8347	0.4283	-	-
SOC	= NP + MAR + Block	0.0758	0.8010	0.7395	0.4530	-	-
SOC	= NP + Fire + Block	0.0051	0.9464	1.0820	0.3570	-	-
SOC	= NP + Soil + Block	4.4169	0.1264	20.6271	0.02*	-	-
SOC	= AM + MAR + Block	0.1704	0.7075	0.5309	0.5189	-	-
SOC	= AM + Fire + Block	0.1805	0.6928	0.8732	0.4030	-	-
SOC	= AM + Soil + Block	0.2580	0.6465	2.4203	0.2176	-	-

Lower layer		Predictor 1		Predictor 2		Interaction	
Response	**Predictors**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
NP	= Treat * MAR + Block	5.7443	0.1388	1.0371	0.4156	8.1937	0.1035
NP	= Treat * Fire + Block	3.1214	0.1754	0.4105	0.5566	2.8270	0.1913
Sqrt(NP)	= Treat * Soil + Block	1.0289	0.4172	2.5369	0.2522	0.0378	0.8638
AM	= Treat * MAR + Block	11.4830	0.0771	0.0087	0.9341	5.8865	0.1361
AM	= Treat * Fire + Block	19.9224	0.0209*	0.5314	0.5064	7.5715	0.0706
AM	= Treat * Soil + Block	8.3992	0.1013	0.1443	0.7406	0.6388	0.5080
SOC	= Treat * MAR + Block	45.9615	0.0211*	0.6148	0.5151	0.0647	0.8230
SOC	= Treat * Fire + Block	42.3770	0.0074**	0.0343	0.8620	0.0017	0.9701
SOC	= Treat * Soil + Block	56.7229	0.0172*	0.0017	0.9707	1.2478	0.3802
AM	= NP + MAR + Block	0.4613	0.5457	0.2392	0.6583	-	-
AM	= NP + Fire + Block	0.4483	0.5398	0.0076	0.9348	-	-
AM	= NP + Soil + Block	0.4518	0.5496	0.0695	0.8091	-	-
SOC	= NP + MAR + Block	0.0078	0.9353	1.8986	0.2620	-	-
SOC	= NP + Fire + Block	0.0069	0.9380	0.7347	0.4397	-	-
SOC	= NP + Soil + Block	0.0063	0.9418	0.0259	0.8824	-	-
SOC	= AM + MAR + Block	16.3787	0.0272*	1.7559	0.2770	-	-
SOC	= AM + Fire + Block	15.9275	0.0163*	1.4872	0.2896	-	-
SOC	= AM + Soil + Block	13.5482	0.0347*	0.0699	0.8086	-	-

Appendix E.2: Summary results of linear mixed-effect models

a) Models with treatment levels

		Upper layer			Lower layer		
	Response	NP	AM	SOC	NP	AM	SOC
	Predictors	= Treat + Block					
Impala	**Estimate**	12827.663	65.0960	21.0077	15461.2740	74.0544	18.62865
	Std. Error	2731.9200	5.5955	3.9897	4394.1570	6.3491	5.1141
	t-value	4.6955	11.6337	5.2655	3.5186	11.6638	3.6426
	p-value	0.0054	0.0001	0.0033	0.0169	0.0001	0.0149
Rhino	**Estimate**	-5636.996	65.3333	18.02563	7955.8330	54.3333	28.20468
	Std. Error	3192.4910	4.0671	3.0680	5055.5040	6.5212	3.7492
	t-value	-1.7657	0.0584	5.8753	-1.4846	-3.0242	7.5229
	p-value	0.1522	0.9563	0.0042	0.2118	0.0390	0.0017

Upper layer: Influence of predictor 2 around latrines of		**Impala**				**Rhino**			
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**	**Estimate**	**Std. Error**	**t-value**	**p-value**
NP	= Treat * MAR + Block	185.1000	68.7900	2.6907	0.1148	-185.5200	55.6600	-3.3330	0.0794
NP	= Treat * Fire + Block	6545.5130	2709.3780	2.4159	0.0731	-6451.9020	2485.8150	-2.5955	0.0807
NP	= Treat * Soil + Block	978.6160	132.2380	7.4004	0.0178	-427.6630	181.6210	-2.3547	0.1427
AM	= Treat * MAR + Block	-0.0748	0.1446	-0.5172	0.6565	-0.1169	0.1204	-0.9705	0.4342
AM	= Treat * Fire + Block	-1.3749	5.8311	-0.2358	0.8252	-2.6251	5.1637	-0.5084	0.6462
AM	= Treat * Soil + Block	0.7779	0.5152	1.5100	0.2701	-0.3973	0.6145	-0.6466	0.5842
SOC	= Treat * MAR + Block	0.0556	0.1240	0.4486	0.6976	0.0060	0.1088	0.0553	0.9609
SOC	= Treat * Fire + Block	3.3745	4.3939	0.7680	0.4853	-1.4057	4.0030	-0.3512	0.7487
SOC	= Treat * Soil + Block	0.5592	0.4140	1.3507	0.3093	0.4354	0.5454	0.7983	0.5084

Lower layer: Influence of predictor 2 around latrines of		**Impala**				**Rhino**			
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**	**Estimate**	**Std. Error**	**t-value**	**p-value**
NP	= Treat * MAR + Block	300.9700	107.8100	2.7916	0.1079	-285.4000	99.7000	-2.8625	0.1035
NP	= Treat * Fire + Block	8732.5270	4947.7960	1.7649	0.1523	-8329.8120	4954.1810	-1.6814	0.1913
Sqrt(NP)	= Treat * Soil + Block	3.5929	3.1807	1.1296	0.3759	-0.7825	4.0247	-0.1944	0.8638
AM	= Treat * MAR + Block	-0.3306	0.1656	-1.9970	0.1839	0.4187	0.1726	2.4262	0.1361
AM	= Treat * Fire + Block	-10.2219	5.6010	-1.8250	0.1420	14.7154	5.3479	2.7516	0.0706
AM	= Treat * Soil + Block	-0.9383	1.1269	-0.8327	0.4926	0.9293	1.1627	0.7993	0.5080
SOC	= Treat * MAR + Block	0.0616	0.1545	0.3988	0.7286	0.0333	0.1309	0.2543	0.8230
SOC	= Treat * Fire + Block	0.8635	5.7902	0.1491	0.8887	-0.2115	5.1930	-0.0407	0.9701
SOC	= Treat * Soil + Block	0.5643	0.7453	0.7572	0.5280	-0.7231	0.6474	-1.1171	0.3802

b) Models with only covariates

Upper layer					
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**
NP	= Dung + Block	-745.1620	228.9361	-3.2549	0.0312
NP	= LSize + Block	-1169.7900	864.1860	-1.3536	0.2473
NP	= DPM + Block	-655.8230	650.6060	-1.0080	0.3705
AM	= Dung + Block	-0.0221	0.4256	-0.0519	0.9611
AM	= LSize + Block	1.1173	0.9596	1.1643	0.3090
AM	= DPM + Block	0.7037	0.7000	1.0053	0.3716
SOC	= Dung + Block	1.3155	0.5569	2.3623	0.0775
SOC	= LSize + Block	2.9234	1.5603	1.8736	0.1343
SOC	= DPM + Block	3.1041	0.7331	4.2341	0.0133
AM	= NP + Block	0.0004	0.0004	1.1201	0.3254
SOC	= NP + Block	0.0001	0.0007	0.1367	0.8978
SOC	= AM + Block	-0.1608	0.3493	-0.4603	0.6692
NP	= MAR + Block	21.4716	54.2390	0.3959	0.7124
NP	= Fire + Block	452.0970	1735.7540	0.2605	0.8074
NP	= Soil + Block	763.7300	178.3850	4.2814	0.0128
AM	= MAR + Block	-0.1697	0.0952	-1.7825	0.1492
AM	= Fire + Block	-3.5251	3.5158	-1.0026	0.3728
AM	= Soil + Block	0.6333	0.3710	1.7070	0.1630
SOC	= MAR + Block	0.0912	0.1047	0.8717	0.4326
SOC	= Fire + Block	3.5631	3.2539	1.0950	0.3350
SOC	= Soil + Block	0.9014	0.5635	1.5997	0.1849

Lower layer					
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**
NP	= Dung + Block	-1153.0210	344.4000	-3.3479	0.0286
NP	= LSize + Block	-1807.8190	1353.1510	-1.3360	0.2525
NP	= DPM + Block	-1446.4720	960.3780	-1.5061	0.2065
AM	= Dung + Block	-0.0652	0.8440	-0.0773	0.9421
AM	= LSize + Block	-3.1202	2.0451	-1.5256	0.2018
AM	= DPM + Block	-3.2821	1.2288	-2.6710	0.0557
SOC	= Dung + Block	2.6855	0.6262	4.2884	0.0128
SOC	= LSize + Block	4.6059	2.1017	2.1914	0.0935
SOC	= DPM + Block	2.2768	1.8293	1.2446	0.2812
AM	= NP + Block	-0.0004	0.0005	-0.7099	0.5170
SOC	= NP + Block	0.0001	0.0006	0.0840	0.9371
SOC	= AM + Block	-0.8859	0.2279	-3.8871	0.0177
log(NP)	= MAR + Block	0.0051	0.0068	0.7503	0.4948
log(NP)	= Fire + Block	0.0998	0.2185	0.4570	0.6714
log(NP)	= Soil + Block	0.0619	0.0327	1.8948	0.1310
AM	= MAR + Block	-0.0878	0.1283	-0.6843	0.5313
AM	= Fire + Block	-0.7957	4.2324	-0.1880	0.8600
AM	= Soil + Block	-0.0594	0.8272	-0.0718	0.9462
SOC	= MAR + Block	0.1894	0.1330	1.4239	0.2276
SOC	= Fire + Block	4.1419	4.5402	0.9123	0.4132
SOC	= Soil + Block	-0.1053	0.9252	-0.1139	0.9148

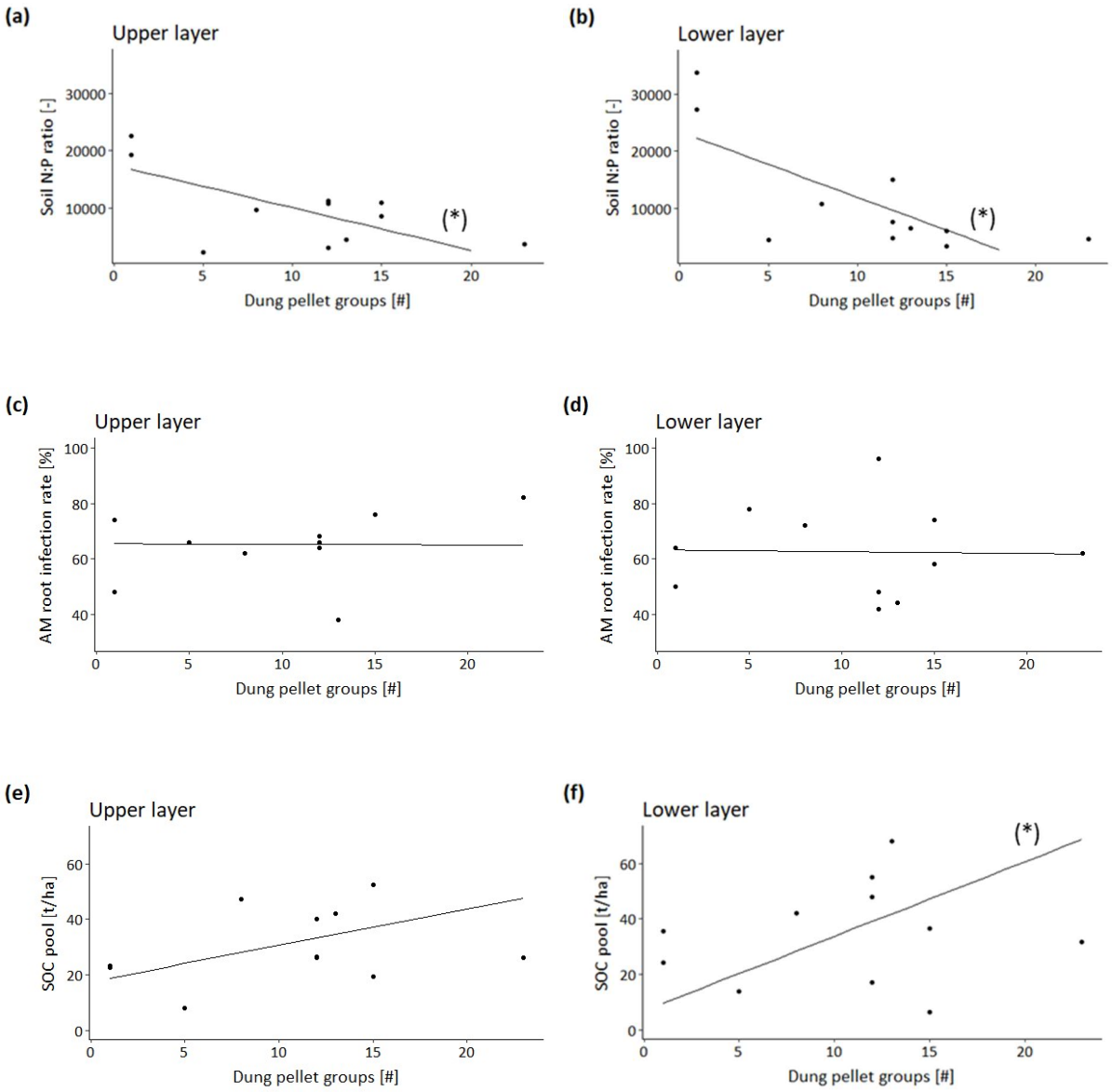
Upper layer		**Predictor 1**				**Predictor 2**			
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**	**Estimate**	**Std. Error**	**t-value**	**p-value**
AM	= NP + MAR + Block	0.0004	0.0004	1.1018	0.3510	-0.1737	0.1054	-1.6483	0.1979
AM	= NP + Fire + Block	0.0004	0.0004	1.1440	0.3164	-3.6186	3.8113	-0.9494	0.3962
AM	= NP + Soil + Block	0.0001	0.0005	0.1084	0.9205	0.5540	0.6063	0.9136	0.4283
SOC	= NP + MAR + Block	-0.0003	0.0007	-0.3807	0.7288	0.1024	0.1191	0.8600	0.4530
SOC	= NP + Fire + Block	-0.0001	0.0007	-0.1647	0.8771	3.6955	3.5528	1.0402	0.3570
SOC	= NP + Soil + Block	-0.0026	0.0005	-4.7966	0.0172	2.7034	0.5952	4.5417	0.0200
SOC	= AM + MAR + Block	0.0802	0.4972	0.1614	0.8820	0.1099	0.1508	0.7286	0.5189
SOC	= AM + Fire + Block	0.0139	0.4106	0.0338	0.9746	3.7181	3.9788	0.9345	0.4030
SOC	= AM + Soil + Block	-0.1791	0.3194	-0.5606	0.6142	0.9126	0.5866	1.5557	0.2176

Lower layer		Predictor 1				Predictor 2			
Response	**Predictors**	**Estimate**	**Std. Error**	**t-value**	**p-value**	**Estimate**	**Std. Error**	**t-value**	**p-value**
AM	= NP + MAR + Block	-0.0003	0.0006	-0.5197	0.6392	-0.0680	0.1391	-0.4890	0.6583
AM	= NP + Fire + Block	-0.0004	0.0006	-0.6503	0.5510	-0.3851	4.4203	-0.0871	0.9348
AM	= NP + Soil + Block	-0.0005	0.0006	-0.7187	0.5243	0.2516	0.9541	0.2637	0.8091
SOC	= NP + MAR + Block	-0.0002	0.0006	-0.2917	0.7895	0.2010	0.1459	1.3779	0.2620
SOC	= NP + Fire + Block	0.0000	0.0006	-0.0405	0.9696	4.1701	4.8650	0.8572	0.4397
SOC	= NP + Soil + Block	0.0001	0.0007	0.1437	0.8948	-0.1770	1.0997	-0.1610	0.8824
SOC	= AM + MAR + Block	-0.8197	0.2245	-3.6510	0.0355	0.1174	0.0886	1.3251	0.2770
SOC	= AM + Fire + Block	-0.8689	0.2224	-3.9068	0.0174	3.4505	2.8295	1.2195	0.2896
SOC	= AM + Soil + Block	-0.8874	0.2407	-3.6861	0.0346	-0.1580	0.5976	-0.2644	0.8086

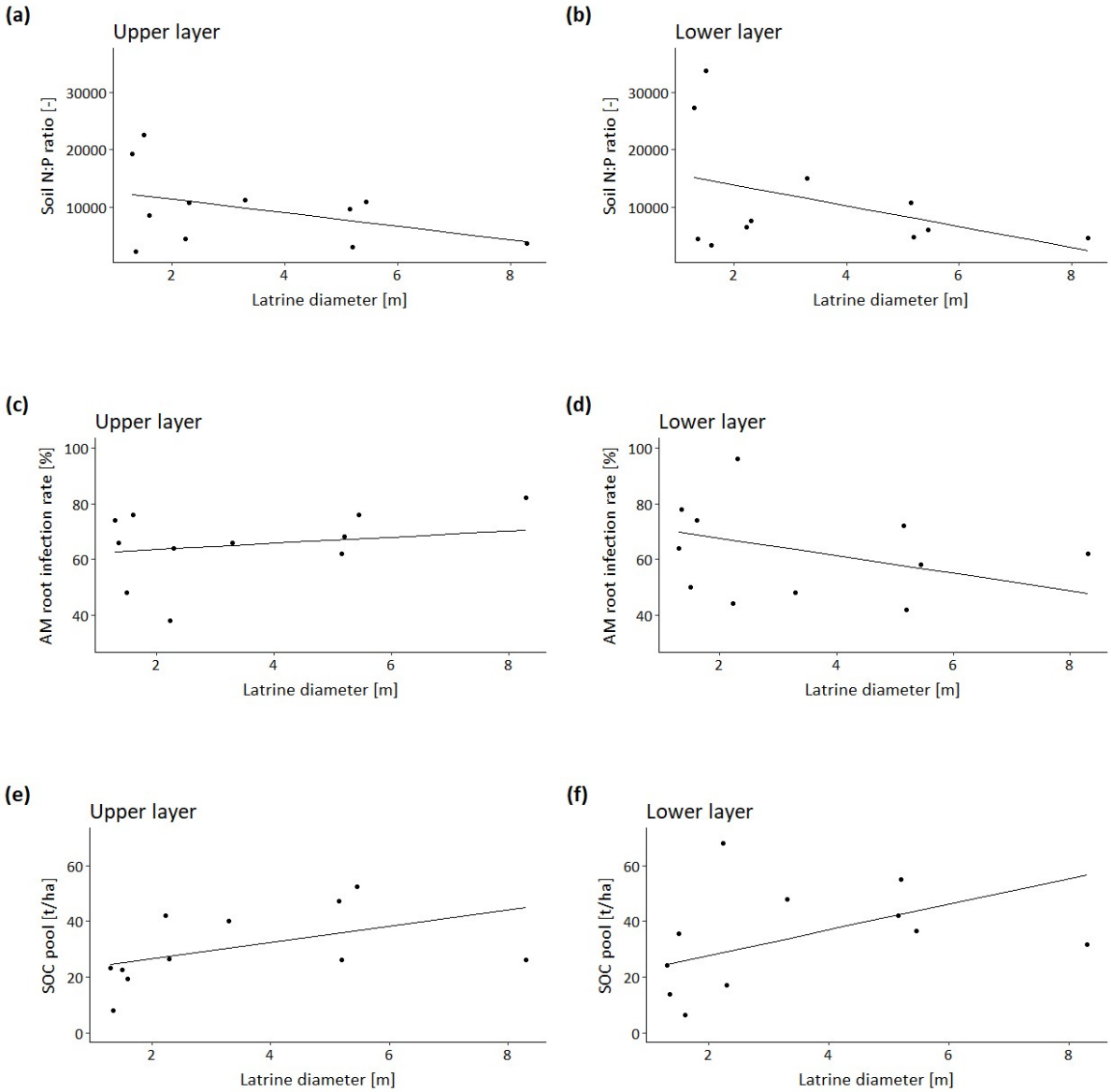
Appendix E.3: Tukey-test results of linear mixed-effect models

			Impala - Rhino	
	Response	**Predictors**	**z-value**	**P-value**
Upper layer	NP	= Treat + Block	-1.766	0.077
	AM	= Treat + Block	0.058	0.953
	SOC	= Treat + Block	5.875	4.22e-09***
Lower layer	NP	= Treat + Block	-1.485	0.138
	AM	= Treat + Block	-3.024	0.00249**
	SOC	= Treat + Block	7.523	5.35e-14***

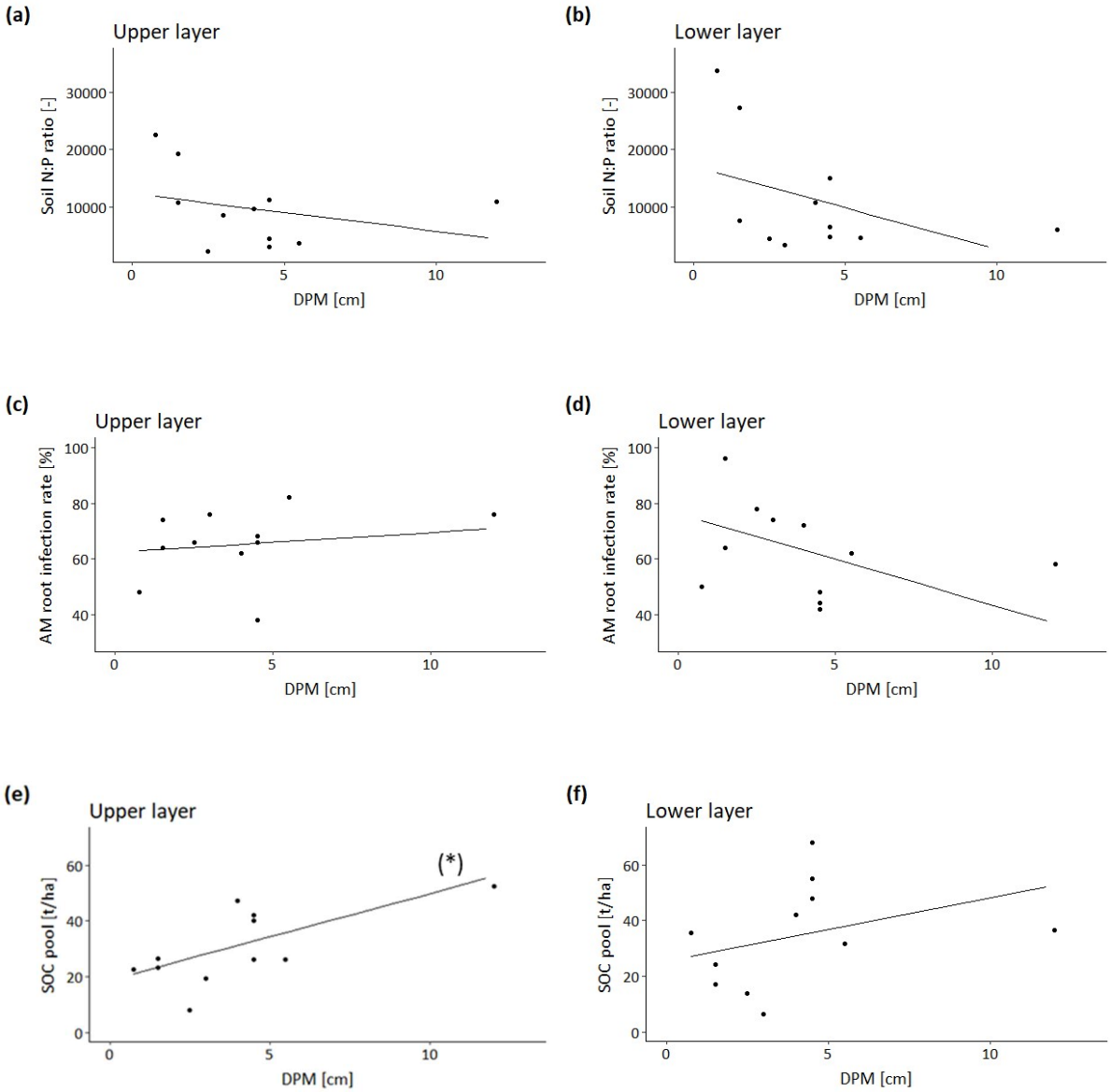
Appendix E.4: Associations between dung pellet group density and (a) N:P ratios in upper soil layer, (b) N:P ratios in lower soil layer, (c) AM root infection rates in upper soil layer, (d) AM root infection rates in lower soil layer, (e) SOC pools in upper soil layer, and (f) SOC pools in lower soil layer



Appendix E.5: Associations between latrine size and (a) N:P ratios in upper soil layer, (b) N:P ratios in lower soil layer, (c) AM root infection rates in upper soil layer, (d) AM root infection rates in lower soil layer, (e) SOC pools in upper soil layer, and (f) SOC pools in lower soil layer



Appendix E.6: Associations between DPM and (a) N:P ratios in upper soil layer, (b) N:P ratios in lower soil layer, (c) AM root infection rates in upper soil layer, (d) AM root infection rates in lower soil layer, (e) SOC pools in upper soil layer, and (f) SOC pools in lower soil layer



Appendix E.7: Associations between soil clay content and (a) latrine type and soil N:P ratios, and (b) soil N:P ratios and SOC pools in upper soil layer

(a) no interaction but significant predictors ($p < 0.05$); (b) significant impact of environmental variable on SOC pools ($p < 0.05$); colour: light-dark = low-high MAR/fire freq./soil clay cont.