Macrodetritivores, the reverse mechanism from lawn to bunch grasses

Abstract:

In grazing ecosystems, tall and short vegetation patches can shift spatially and temporally, which causes heterogeneity and a mosaic pattern of structurally discrete vegetation patches. The mechanisms that drive these vegetation patterns in grazing ecosystems are still poorly understood. A recent explanation suggests that the interplay between soil macrofauna and large herbivores and their opposing influence on the abiotic soil environment could provide the conditions that are essential to maintain heterogeneity. Soil macrodetritivore bioturbation, such as digging and tunnelling, loosen up the soil thereby alleviating plant stress. Dung is highly attractive to soil bioturbating macrodetritivores; because of the herbivore avoidance, its moisture, its high abundance of microbial bacteria and the freshly digested material. The effects on soil biophysical conditions by dung associated macrodetritivores have not been given much attention yet in the literature on vegetation mosaics. This study looked at the change in vegetation structure and at the physical changes of the soil that occurred around and underneath a dung pile in the African tropical savannas. We were especially interested in the changes induced by soil organisms in reversing the effects of large grazers. To see the effect of dung on the soil and vegetation, we set up an experiment and placed dung piles at different sites that followed a rainfall gradient. We had three different treatments; the control without dung, one with dung and where we prevented the dung beetles from tunnelling underneath the dung pile and one with dung and with the tunnelling dung beetles. Although there was no difference between the two dung treatments , the results showed an uniform significant effect, for both changes in soil structure and increased tall vegetation biomass, induced by the dung treatments across the rainfall gradient. Consequently, our study provided strong evidence that the alternation between soil fauna bioturbation and grazer biocompaction dominated states may be a key component in the heterogeneity of savannas. The understanding of this mechanism and the heterogeneity could be of conservational importance, with the current decline in nature areas through the demand for agricultural land.

Introduction:

In the African savannas, multiple processes and organisms generate and maintain heterogeneity in vegetation structure, which is an important determinant of savanna functioning (Du Toit and Cumming 1999; Pickett et al. 2003; Boers 2012). In grazing ecosystems of the tropical savannas, vegetation structure is often dominated by three main structural vegetation types: the short grazing lawns, the tall bunch grasses and the shrubs (Boers 2012, van der Plas et al 2013). These tall and short vegetation patches can shift spatially and temporally, which causes heterogeneity and a mozaic pattern of structurally discrete patches (McNaughton 1984; Belsky 1986; Looijen and Bakker 1987; McLaren and Jefferies 2004). The mechanism that causes these shifts and what drives these vegetation patterns in grazing ecosystems is still poorly understood (Anderson and Talbot 1965; Belsky 1986; HilleRisLambers 2001).

Large scale environmental gradients, e.g. rainfall, are important abiotic factors playing a role in determining vegetation communities (Anderson and Talbot 1965; Du Toit and Cumming 1999). However, aside from abiotic influences, biotic activities are also important for creating heterogeneity. Large herbivores often graze on short vegetation patches, while the tall patches are much less visited (Cromsigt et al 2009; Kleynhans et al 2011). Therefore, multiple studies suggest that large grazers are the main factor causing the vegetation shifts and patterns (McNaughton 1976; Frank et al. 1998; Mclaren and Jefferies 2004; Schrama et al. 2012; Schrama et al. 2013). The large grazers trample the soil, which causes stress such as low water availability and even low nutrient availability despite the added urine and faeces (Ruess and McNaughton 1987; Schrama et al 2012); and therefore only stress tolerant lawn grass species can survive (Milchunas et al 1988). This stress induced by frequent revisitation by large herbivores of preferred grazing patches, ensures that lawn grasses stay lawn and prevents that a transition of lawn grass to bunch grass could occur (Mikola et al 2009; Schrama 2013b; Howison et al, in prep). However, to explain the moizaic pattern and the maintenance of heterogeneity, there has to be a mechanism that converts lawn vegetation into bunch vegetation in the presence of large grazers. A recent explanation suggests that the interplay between small soil macrofauna and large herbivores and their opposing influence on the abiotic soil environment could provide the conditions that are essential to maintain functional heterogeneity (Lavelle et al 2006; Howison et al, in prep).

Large herbivores compact the soil through intensive and repeated trampling causing high plant stress (Mikola et al 2009; Schrama 2013b). In contrast, soil macrodetritivore bioturbation, such as digging and tunnelling, increase macroporosity which can promote root penetration of thicker roots, water infiltration and salt leaching, thereby alleviating plant stress (Boers 2012; Wilkinson et al 2009, Meysman 2006). There are also more nutrients available for the vegetation, because nutrients get more deeply cycled in bioturbated soils and runoff of organic matter is prevented (Wilkinson et al 2009). Tall more light competitive plants profit from this and invest their carbon resources in above ground structures and can then outcompete lawn species through shading (Milchunas et al 1988). They also get less attractive to herbivores, because of the resulting high structural compounds (lignin and cellulose), which make their leaves more difficult to digest (Iason and van Wieren 1999). Consequently macrodetritivores have an opposite impact on soil biophysical structure compared to large herbivores (Mikola et al. 2009, Wilkinson et. Al. 2009). Bioturbating macrodetritivores could therefore be an explanation for the transition from short lawn vegetation to tall bunch vegetation. The importance of bioturbation for soil processes was first realized by Charles Darwin. Darwin realized that small-scale reworking activities by small invertebrates could have dramatic consequences at larger scales, such as in the process of landscape formation (Darwin 1881). Recent investigations even provide evidence that bioturbation had a key role in the evolution of metazoan life at the end of the Precambrian Era (Meysman et al 2006). It is also recognized that bioturbation is a crucial component in sediment dynamics at coastal systems, where it was traditionally thought that the physical forces of currents and waves were the main shapers (Paarlberg et al 2005).

If a patch is dominated by large herbivores, the soft bodied macrodetritivores are trampled and killed (Andresen et al. 1990). Consequently macrodetritivores are less abundant in these highly trampled patches and are more abundant in patches that are less used by large herbivores (Andresen et al. 1990; Iason and van Wieren 1999; Schrama et al. 2013b). Therefore macrodetritivores can only convert a lawn patch to a bunch patch if it is abandoned or avoided and thus under low grazing pressure. Seasonal migration causes herbivores to abandon lawn patches. These lawn patches can then grow and provide shading, litter and a more moist soil for the macrodetritivores (Hartvigsen and McNaughton 1995; Augustine and McNaughton 1998).
Another reason for large herbivores to avoid a patch in the grazing area is dung (Weeda 1967; Fincher 1981; Ruess and McNaughton 1987). Selective foraging, or preferentially foraging away from dung, may offer protection from the transfer of parasites or disease (Hart 1990; Michel 1995). Large herbivores in savanna systems, such as the white rhinoceros, create small avoided nutrient hotspots by concentrating their faeces into middens (Waldram et al 2008; Boers 2012). Dung is highly attractive to soil bioturbating macrodetritivores; because of the herbivore avoidance, its moisture, its high abundance of microbial bacteria and the freely available and freshly digested material. (Ruess and McNaughton 1987, Mikola et al 2009).

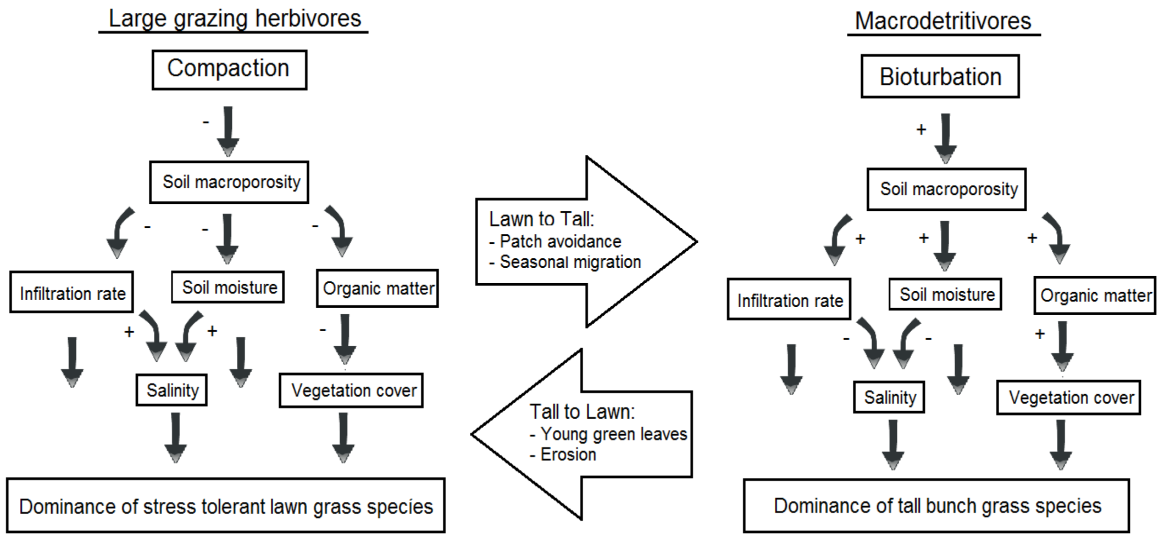

Figure 1: Large grazers and marcodetritivores have contrasting influences on the physical soil condition and the vegetation structure. A patch with a dominance of large grazers may shift to a macrodetritivore dominated path by patch avoidance and seasonal migration, causing lawn grasses to convert to bunch grasses. A patch with a dominance of macrodetritivores may shift to a large grazer dominated path by erosion and attraction to fresh regrowth, causing bunch grasses to convert in lawn grasses.

Dung beetles (Coleoptera: *Scarabaeidae*) are macrodetritivores that are attracted to dung and feed on this animal dung as both adults and larvae (Nichols 2008; Chao 2013). Dung beetles use the dung material to produce a ball were they brood their larvae (Halffter and Matthews 1966; Nichols 2008). There are three types of dung beetle strategies/functional groups: Paracoprid (tunneller) species that bury brood balls in vertical chambers close and underneath the dungpile; Telocoprid (roller) species that roll away balls some horizontal distance away, before burial beneath the soil surface; and Endocoprid (dweller) species who brood their young directly inside the dung pile (Halffter and Edmonds 1982; Nichols 2008; Chao 2013).
By this burying of their brood balls, dung beetles play a role in bioturbation through moving large quantities of earth to the soil surface during nesting (Mittal 1993; Slade et al 2007).
Other macrodetritivores, specifically termites and earthworms, also use dung and its microbial bacteria as a food source and thereby create tunnels and cause bioturbation (Gittings et al 1994; Holter 1977, 1979; Groffman et al 2004; Nichols 2008). The dung and the bioturbating attracted macrodetritivores improve soil conditions underneath the dung, like water availability, nutrients and salinity (Ruess and McNaughton 1987), and could therefore be a component in the transition from short lawn vegetation to long bunch vegetation.

The effects on vegetation mosaics by dung associated macrodetritivores have not been given much attention yet in the literature, but could have wide ranging consequences on these vegetation types. This study looks at the change in vegetation structure and at the physical changes of the soil that occur around and underneath a dung pile in the African tropical savannas. We are especially interested in the changes induced by soil organisms in reversing the effects of large grazers. This leads to the following **main question:** Is dung a key mechanism whereby lawn may convert into bunch vegetation at the tropical savannas in South Africa? We answer this question with the following **sub questions:**

- What soil properties are changed by the soil macrofauna and in what quantity?
- Does bunch grass expand in the presence of dung?
- Is there a difference in quantity between macro fauna that enter the dung true the soil (termites and earthworms) and macrofauna that enter the dung from above (dung beetles)?
- Does rainfall has an effect on the quantity of the changes?

We expect that due to the bioturbation soil macroporosity will increase which will increase the water infiltration and soil moisture and decreases the soil bulkdensity. Because of the bioturbation we expect to find a higher amount of organic matter underneath the dung, where soil fauna and microbes can convert them into nutrients (Wilkinson et al 2009). Tall more light competitive plants profit from this which leads to an increase in bunch biomass and an increase in bunch cover pertaining to lawn cover. The main players in the transition of lawn to bunch vegetation are expected to be the macrofauna that come from above which are the tunnelling dung beetles, by burying their brood balls and because of their relative large size and thus larger tunnels, they have a big influence on the soil conditions. Moreover, we expect the difference between the treatments to be bigger at the dry sites and more similar at the wet sites. Plants at a low rainfall patch will have more water stress, therefore the effect will be bigger when water infiltration is increased in these sites. Because of the attracted macrodetrivores, dung could be the mechanistic process that explains forwards and backwards shifts in vegetation mosaics, while large grazers are present.

To test these hypotheses dung piles were placed and the changes that occurred in the soil and vegetation structure over time were measured. The physical soil conditions measured are; soil macroporosity, infiltration rate, soil moisture, bulk density and salinity. Next to the internal biotic factors, an external factor, rainfall, is also included. Therefore, we will study the effects of the rainfall on soil biophysical structure changes and its effect on the abundance and distribution of macrodetritivores as well. Besides the changes that occur underneath a dung pile, another interesting question was which organisms induced these changes. The main organisms that used and were attracted to a dung pile were termites, earthworms and dung beetles. With our treatments we could separate the effect from macrodetritivores that reach the dung from above from the macrodetritivores that reach the dung through the soil.

Methods:

Research area:

This Research was performed at Hluhluwe-iMfolozi Park (HiP) in northern KwaZulu Natal, South Africa. The park consists of ca. 90 000-ha mesic savanna (Bonnet 2010;Stock 2010) and has a high diversity of grazers and mixed feeders (Stock 2010). The most common large species are buffalo, impala, nyala, zebra, white rhino, waterbuck, warthog and wildebeest. The park follows a rainfall gradient, with low rainfall of 550 mm in the South to higher rainfall of 900 mm in the North.

Site Location

In this research 5 different sites in Hluluwe-iMfolozi park were used which lay along a rainfall gradient. Site 1 Nomageja, 2 Nombali, 5 Maquanda, 17 Nseleni, 19 Madlozi, these sites all contained lawn (Sprobolus nitens, Paspalum notatum, Digitaria longiflora, Cynodon dactylon) and bunch vegetation (Themeda triandra, Sporobolus pyramidalis).

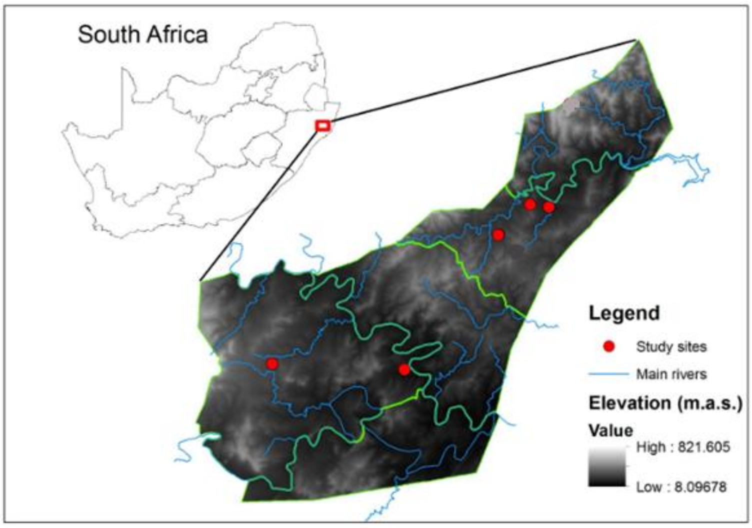

Figure 2: Map of the Hluluwe-iMfolozi park, with the 5 study sites (red).

Treatments:

The effects of termites and earthworms could not be excluded, because they come from underneath the soil and therefore bioturbate the soil even though they could not reach the dung. However, additional dung beetles could be stopped from tunnelling the dung balls under the pile. Therefore we designed three treatments, to test the effects of animals entering the dung from above (and tunnelling down) and the effects from the ones that arrive through the soil and enter the dung from below. The first treatment is the control: no dung, vegetation plot placed in the same orientation as the experimental treatments. Second the fine mesh treatment: 20kg of white rhino dung placed on a double sheet of fine mesh (mesh diameter of ca. 1mm) preventing tunnelling dung beetles from penetrating the soil below the dung pile. This is to ensure that we can separate between the effects of tunnelling dung beetles and soil fauna that may access the dungpile from below ground e.g. termites and earthworms. And third the chicken mesh treatment: 20kg of white rhino dung placed on a sheet of chicken mesh (with a mesh diameter of 2cm) to allow tunnelling dung beetles to penetrate the soil.

Figure 3: The three different treatment plots

Within each site three replicates (blocks) were set up with the treatments. The 5 different sites could be compared and therewith see if rainfall plays a role in the changing soil conditions due to dung exposure. The dung was collected as fresh as possible, i.e. has been deposited by a rhino within the previous 12 hours and is mixed before placing. The mesh package of the 2 mesh treatments were of an 1m x 1m x 25cm size.

All plots were orientated along the main downslope gradient, which allows run on of ambient rainfall which is expected to flow through the dung pile and runoff downslope from the dung pile. Permanent 40x80cm vegetation monitoring plots were set up right beside the dungpile and on its downslope side to monitor shifts in structural vegetation type dominance as a result of the presence of the dung and attractiveness to various bioturbating soil fauna. Plots were placed in a mixed bunch/lawn plot where a minimum of 20% of either lawn or bunch could be located within the same position.

Figure 4: Hammering in the poles for the permanent vegetation plot.

Vegetation measurements

The vegetation measurements were performed at the start and end of the experiment.
To identify and map the vegetation cover we divided the 80x40 cm vegetation plot into smaller $10cm^2$ blocks (4x8 blocks). Each block was subdivided into quarters and the cover of lawn vegetation (stolons and leaf cover), bunch vegetation (basal cover), dead (litter), ground (bare soil) and forb were assessed on the subdivided block and given a cover score (see table 1).
Besides noting the cover per species, we also measured the height for the lawn vegetation by dropping a small disc pasture meter (weighing 68,534 g diameter 115 mm) from 50cm above ground. We repeated this three times. For the bunch vegetation we recorded the number of tussocks, counted the number of individual rametes within each tussock and measured the tallest leaf of 10 randomly selected rametes.

We also made a biomass calibration to convert the cover and measurements into biomass without clipping the plots. For the biomass calibration a representative plot was chosen near the treatments in a block consisting of a mixture of bunch and lawn. One biomass calibration plot was taken for each block (i.e. it is repeated 3x within each site).The vegetation cover was recorded the same as the vegetation plots and also the measurements (height, rametes, etc.) for lawn and bunch were recorded the same. Then all biomass was collected, separating between different species for lawn and bunch. Forbs were put together in one bag, since we did not have a good idea of the species. At the lab all biomass samples were dried at 70^{o}C until constant weight (24 hours), weighted and used to (non-destructively) estimate the biomass within the control and treatment vegetation plots. The bunch biomass was estimated with the function: # rametes x avg height = grams. The lawn biomass was estimated with the function: cover % x height = grams.

Figure 5: Showing the vegetation monitoring quadrat

Table 1: Cover scores within the subdevided blocks of the vegetation monitoring quadrat.

Cover score	Meaning
0	not present
+	present but not enough to fill up a quarter block
1	one quarter filled (25% of block)
2	two quarters filled (50% of block)
3	three quarters filled (75% of block)
4	four quarters filled (100% of block)

Physical soil measurements:

The physical soil conditions were measured at the start, before placing the dung in all 3 replica blocks. After 10 weeks the soil conditions were measured again under the dung for the fine and chicken treatments and near the vegetation plot for the control. The initial start measurement is to control for environmental influences.
Soil macroporosity: Soil porosity was measured by the soil penetration depth. At every plot the penetration depth was measured with a custom made device called ‘the dentometer’, using the measuring index of the device in centimeters.

Dentometer (compactor): A 10cm height x 5cm diameter soil sample is drilled out of the ground and placed in 1.10m high pipe sealed at one end. A block is placed on top of the soil to prevent uneven compaction. A dentometer (a large metal pole 12kg) is dropped from a height of 1m x 10 times. The resulting compaction is recorded as the difference in height after 10 x compacting the soil sample.

***Infiltration rate**:* At every plot, the water infiltration rate has been measured using a double-ring infiltrometer. The time to let the water infiltrate from 5 mm up to 5 cm was measured using the measuring index in the inner ring. The infiltration rate is in mm/sec.

Double ring system: Outer ring diameter 206mm, Inner ring diameter 95mm. The outer and inner rings were hammered into the soil until a depth of 2cm. The outer ring is filled with water first, and checked for leaking, following that the inner ring is filled. Water in the outer ring should be kept at the same level as the inner ring, therefore may require refilling. The stop watch is started and the time it takes for the water to drop 5mm is recorded. The infiltration has been recorded for at least 45 minutes, to get the start and final infiltration rate.

***Soil moisture**:* For every plot the soil moisture was calculated from the fresh and dry weight of a soil sample. A fresh soil sample has been taken from each plot with a 100cm^3 volumetric metal ring. The fresh soil was weighed and dried in the oven (70 ˚C for 48 hours until constant weight). After drying, the dry weight has been measured. The weight loss after drying in the oven is the amount of water that was present in the soil. The soil moisture was calculated as the percentage of weight loss after drying the soil, from the total fresh weight.

***Bulk density**:* The same soil sample was also used for the bulkdensity. We dried the sample in the oven (70 °C for 48 hours until constant weight) and weighed it afterwards. The bulk density of the soil was calculated by dividing the dry weight by volume (g/cm^3).

***Salinity**:* Soil salinity was measured as electrical conductivity (EC) in units of microsiemens (µS/cm^3). C.a. 50cc soil was washed with 150ml of demi water, left to stand for ½ hour, mixed again and infiltrated. uS/cm^3 was measured using an electrical conductivity meter and used as a proxy for the total dissolved ions contained within the soil.

Volumetric metal ring: A metal ring of 100cc soil was taken at every site. Three soil samples at the beginning and nine at the end of the experiment. The metal ring was hammered into the ground after removing the vegetation, then emptied into a bag. In the lab the soil samples were divided into 2 halves; 1 half was used for salinity and the other half for moisture and bulk density.

Soil organic matter: In addition, the soil organic matter was also estimated with the dry soil samples, which were taken with us back to Rijksuniversiteit Groningen. Soil organic matter was estimated using the loss on ignition method by ashing the samples for 16 hours at 420 degrees (Stock et al 2010). Afterwards the samples were weighted again. The percentage of organic matter= (start (g) – end (g)/start (g)) x 100

Macrodetritivore distribution:

It is expected over time that termites and earthworms will become attracted to the dung pile and tunnel toward it over the study period. Therefore we checked for termite sheeting and earthworm cast underneath the dungpiles at the end of the experiment. We used two times a 40 x40 cm quadrat, one on the center (where there is maximum moisture) and one on the edge(where the transition between very wet to dry begins), to assess the % presence. The 40 x 40cm quadrat was divided into blocks of 10 x 10 cm which were further subdivided into blocks of 4 and a cover score of termite sheeting and earthworm cast per sub-square was given, using the same scale as the vegetation plots (table 1). Aside from the earthworm cast cover, earthworm hole diameters were measured when found and cast size distribution approximated. When possible, termites and earthworms were captured for identification to genus level.

For determining the dung beetle distribution all sites were being visited within 1 week of placement. The dung that was lying on top of the chicken mesh or fine mesh was lifted up and the numbers of dung beetles holes were counted.Once the dung wasplaced it was expected that tunnelling dung beetles will utilize the dung heap within a few hours (Stronkhorst 1997), that means that for the dung beetles abundance and diversity a week was too late. Therefore to study which dungbeetle species and their abundance colonized, on each of the sites a dungbeetle colonization experiment was set up. For each site 3 dungpiles on a sheet of chicken mesh were placed at 7 am. The dungpiles were being sampled after 3, 5, 8 and 26 hours (Stronkhorst 1997). At each time interval and at each of the 3 piles we removed a fixed proportion (1/4) of the dung pile and replaced this in a 5L bowl. We counted all the beetles, noted the species and measured the pronotum, which is the thickest part of the thorax of the beetle. Thereafter the removed portion of dung was replaced. At the next time interval we took a different section of the dungpile (again 1/4) and again sorted for diversity, size and abundance. During the 8h & 26h time intervals we also took a flotation measure below the dung piles, to float up the tunnelers. For this flotation an infiltration ring was placed in the centre of where the dung pile was and the ring was filled up to 5cm. Again the floated dung beetles were counted, measured and identified. All beetles were released after measuring. From the pronotum and an existing calibration we could calculate the biomass of the dung beetles.

Figure 6: Flotation with infiltration ring. Floatation is a very effective means for extracting soil dwelling organisms from below the dung pile

Statistics:

To analyze the data, the statistical program R (i386 3.0.3) was used (R Core Team 2014). To analyze the effect of treatment and rainfall on the different response variables, the field variables were analyzed individually with a mixed model with blocks as random effect factor and an ancova when block had no significant effect. To control for unforeseen effects due to site location we used block as random factor (e.g. It could be that one block is near a termite mount, while another is near a really big tree). Site was not included as random but as fixed factor, because we chose those sites based on their rainfall.

To ensure the right rainfall was used as a predictor, a model with the short term rainfall was tested against a model with the long term rainfall. Only with the organic matter and the infiltration it proved to be better to use the long term rainfall (annual rainfall), for the other response variables the short term rainfall (11 weeks, rainfall during the experiment) appeared to be better. The multcomp package was used to see if the fine and chicken mesh treatments also differed from each other (Hothorn et al 2008). The interaction term for each test was not significant unless reported in the text. The normality and the homogeneitity of the residuals were tested, with both residual plots and the shapiro and bartlett tests. Data transformations were used when necessary to ensure that the data conformed to the assumptions of each statistical model. A significance level of 0.05 was used for all statistical tests. All values in the graphs are presented as the mean +/- 1 SD.

Besides the univariate analysis, an RDA was used to perform a multivariate analysis, using the vegan package (Oksanen et al 2013). Redundancy analysis (RDA) combines multiple regression with classical ordination (PCA or CA). This method seeks, in successive order, a series of linear combinations of the explanatory variables that best explain the variation of the response matrix (Borcard et al 2011). RDA calculations were based on correlation matrices in order to standardize the variables of varying scales and magnitudes.

Results:

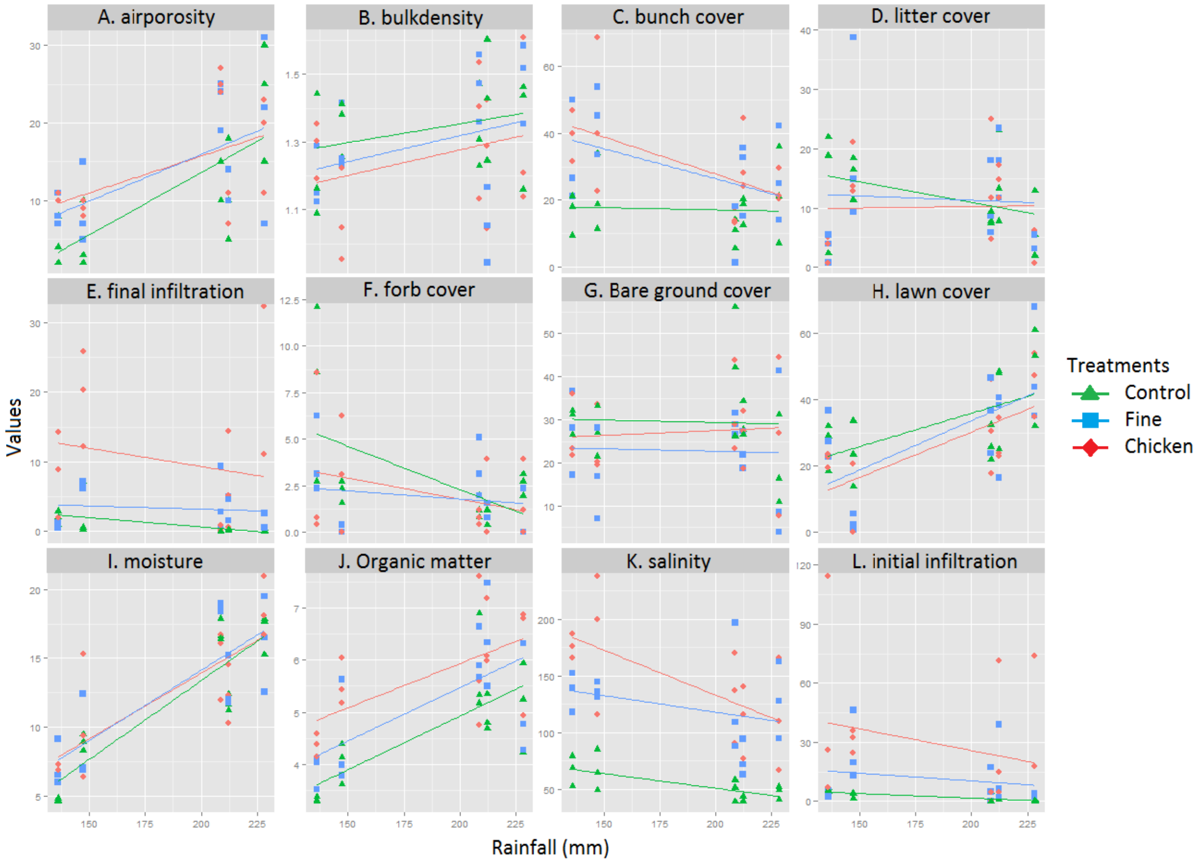

Figure 7: Each y axis represents a different response variable against the continuous predictor, the short term rainfall. The lines represent the three treatments; control (green), fine (blue) and chicken(red). All measurements were performed at 5 sites which follow the rainfall gradient. There are three sites with a higher rainfall which are also geographically apart from the two sites with the lower rainfall. At every site each treatment had three replicates, which means nine data points per site.

Treatment has an effect on multiple response variables (Organic matter, salinity, infiltration, bunch biomass and bunch % cover) (Fig 7), the chicken mesh treatment (i.e. where all soil fauna are permitted to enter the dung and soil) has an even stronger effect than fine treatment (Fig 7; CEJKL). Fig. 7 shows that rainfall has an effect at almost all response variables and that this effect seems to be lower at higher rainfall. Graph A of figure 7 displays the macro-porosity, although this graph shows a possible effect of the treatments, this was not significant when we tested it separately. Graph B shows the bulkdensity, which also seems to be effected by the treatments. When tested individually only rainfall proved to be significant, p=0.0448. The same is true for the moisture graph I, where only rainfall ($p<0.001$) was significant as well. With the dead(litter), ground (bare soil) and forb cover a trend can be seen in the data where treatment has an influence which decreases with higher rainfall, however this was not significant in the univariate analysis. Organic matter, salinity, infiltration, bunch biomass and cover do show a significant treatment effect.

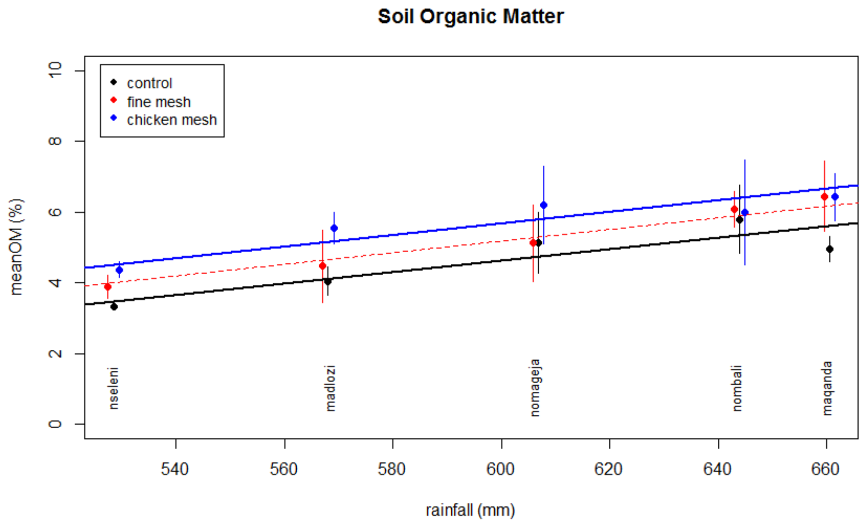

Figure 8: The Organic matter content after an 11 weeks time period at the 5 sites along the long term rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. The graph shows the means +/- SD. For each site the treatments had three replicates, giving a total of nine measurements per site.

Soil organic matter was significantly higher for the chicken mesh treament ($p<0.001$, Fig. 8). Fine treatment is not significant different from the control and the chicken treatment, but shows a higher organic matter content than the control ($p=0.0556$, Fig. 8). Rainfall also has a significant effect, organic matter content increases with higher rainfall ($p=1.84e08$). The model without a random factor proved to better (Ancova $F_{(3,41)}=20.99$, $R^2=0.6057$, $p<0.001$).

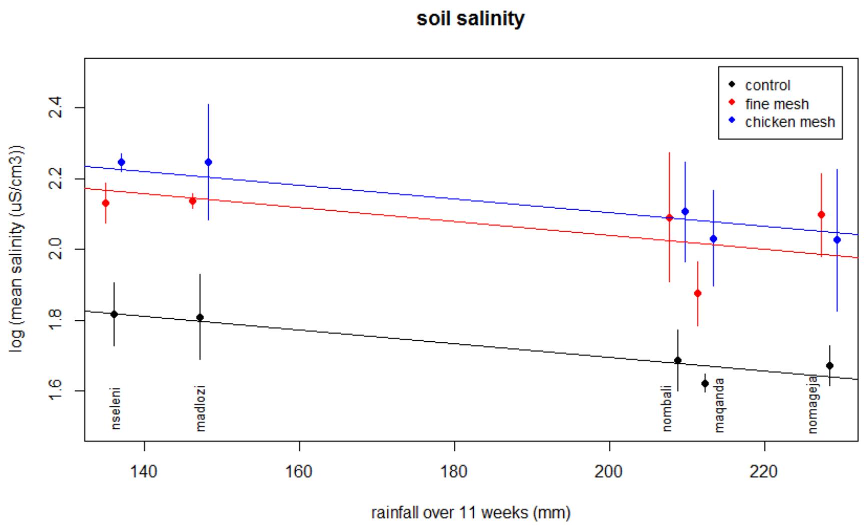

Figure 9: The salinity after an 11 weeks time period at the 5 sites along the long term rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. The graph shows the means +/- SD. For each site the treatments had three replicates, giving a total of nine measurements per site.

Soil salinity was significantly higher for both dung treatments ($p<0.001$, Fig. 9). Both the fine ($p<0.001$) and the chicken ($p<0.001$) treatments are significantly different from control. Chicken mesh shows to have a higher salinity than the fine mesh, but according to the post hoc test this is not significant ($p=0.276$). Rainfall also has a significant effect ($p<0.001$), the salinity is lower with higher rainfall. The model without a random factor proved to be better than the model with block as random factor (AnCova: $F_{(3,41)}$ =43.16, $R^2=0.7595$, $p<0.001$).

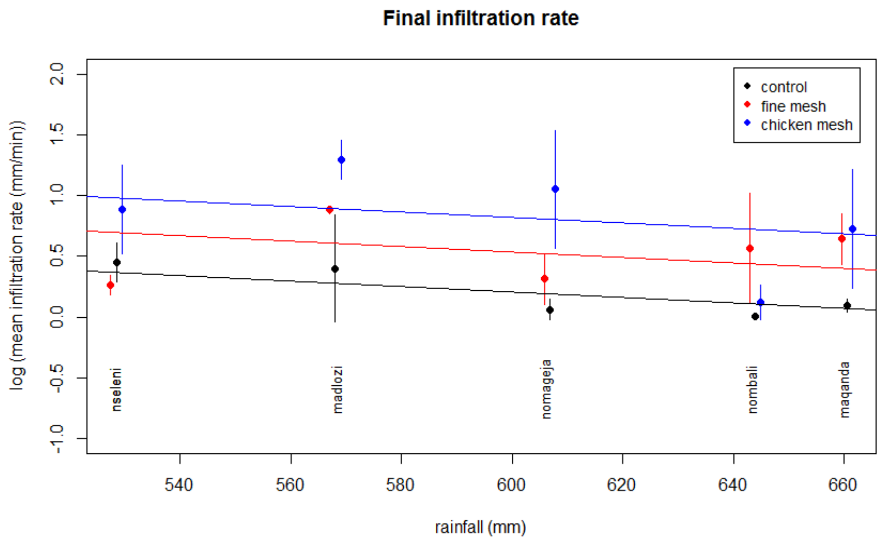

Figure 10: The final infiltration rate after an 11 weeks time period at the 5 sites along the long term rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. The final infiltration rate is the rate wherein the infiltration is constant, or the end rate after 45 min when it did not got constant. The graph shows the means +/- SD.

The final infiltration rate is significantly higher for both treatment ($p<0.001$, Fig. 10). Rainfall ($p=0.050$) has a significant effect on the infiltration rate as well. The fine ($p=0.0169$) and the chicken treatment ($p<0.001$) are different from the control. The model without block as random factor showed to be better (AnCova:$F_{(3,41)}=8.467$, $R^2=0.3826$, $p<0.001$).

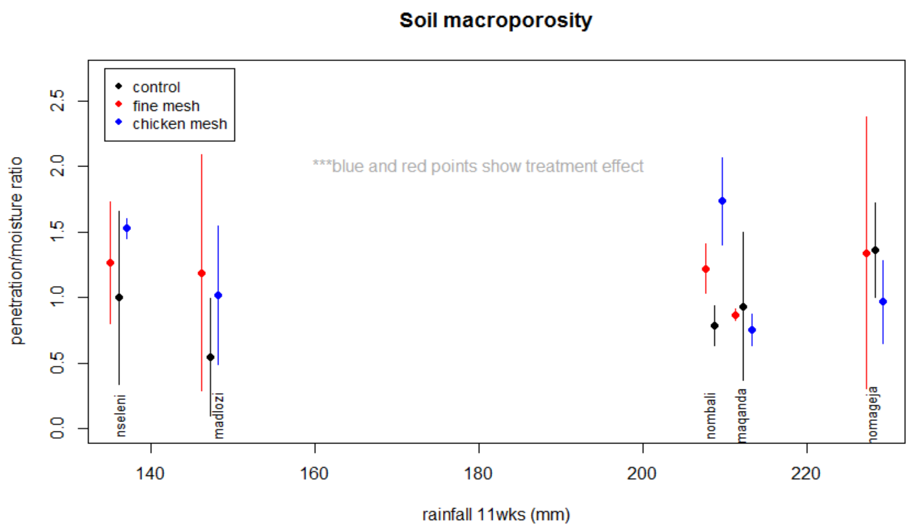

Figure 11: The penetration/moisture ratio after an 11 weeks time period at the 5 sites along the long term rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. The graph shows the means +/- SD.

The treatments and rainfall do not have a significant effect on the soil macroporosity (Fig. 11). Only the 2 with the highest rainfall do not show a clear treatment effect, but with the other three sites the soil macroporosity is higher with the dung treatments.

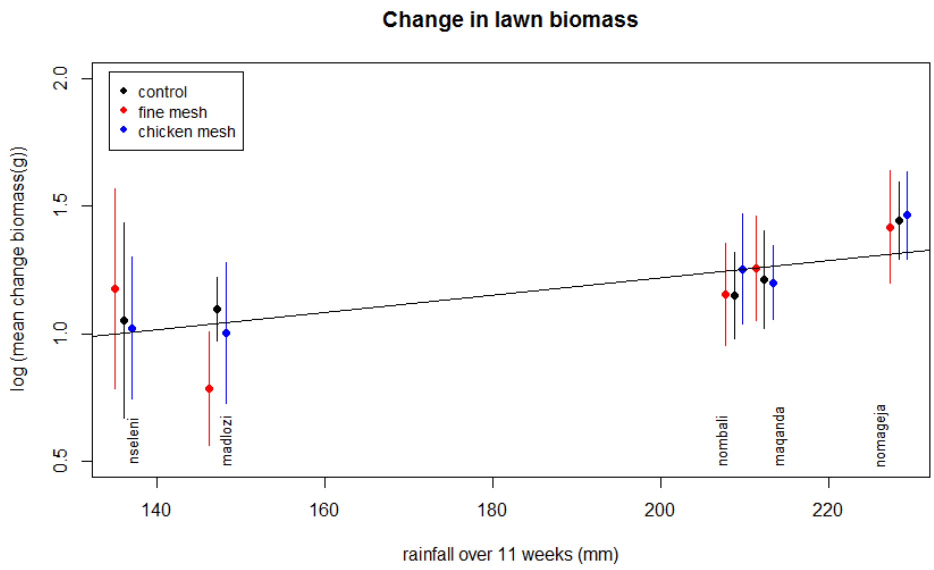

Figure 12 Change in lawn biomass of 5 different sites along the 11 weeks rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. Change is the difference between start and end conditions. The graph shows the means +/- SD.

There is no significant effect of treatments in the lawn biomass change (Fig. 12). It also does not show a clear trend, so lawn does not grow faster with a dung treatment. Rainfall does have an effect on the change in lawn biomass, the change is larger at higher rainfall (Mixed model: $F_{(3,60)}$ =3.717, adj R^2=0.1145, p<0.001).

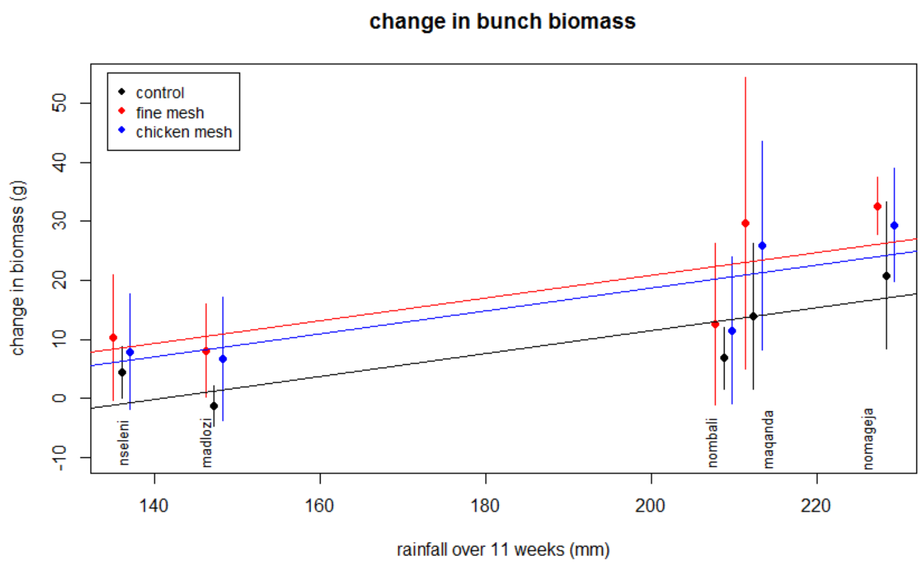

Figure 13: The change in bunch biomass over an 11 weeks time period at the 5 sites along the 11 weeks rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. Change is the difference between start and end conditions. The graph shows the means +/- SD.

Both treatment (p=0.02303) and rainfall (p<0.001) have a significant effect on bunch biomass(AnCova: $F_{(3,60)}$ =10.62, R^2=0.3469 , p<0.001; Fig. 13). Both the fine mesh (p=0.0112) and the chicken mesh treatment (p=0.0478) are significantly different from control, but they are not significantly different from each other. Bunch grasses grow faster with the dung treatments, but it makes no significant difference if tunnelling dung beetles are included. Bunch biomass changes faster at a higher rainfall than at low rainfall.

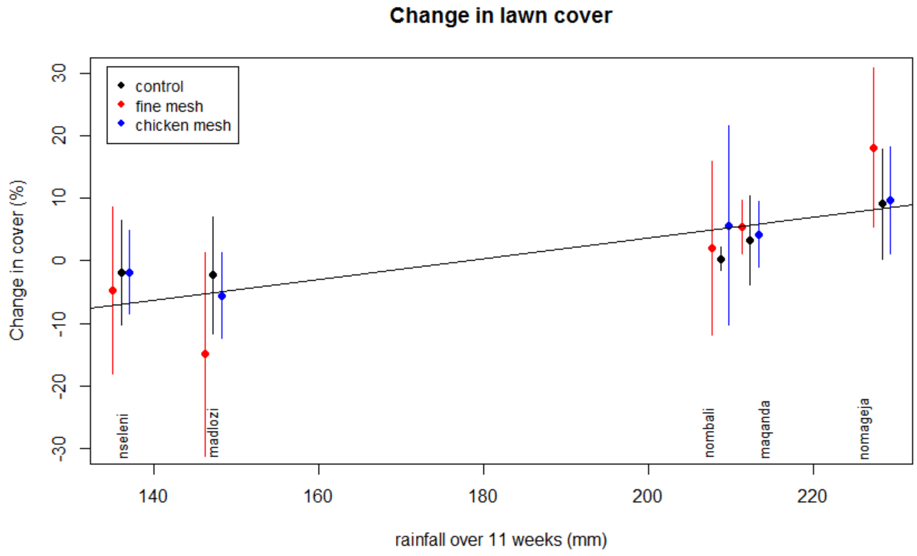

Figure 14: Change in lawn cover of 5 different sites along the 11 weeks rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. Change is the difference between start and end conditions. The graph shows the means +/- SD.

There is no significant effect of treatments for lawn cover (Fig. 14). Rainfall does have a significant effect on the change in lawn cover, the change is larger at higher rainfall (Mixed model: $F_{(3,60)}$ =3.717, adj R^2=0.1145, p<0.01).

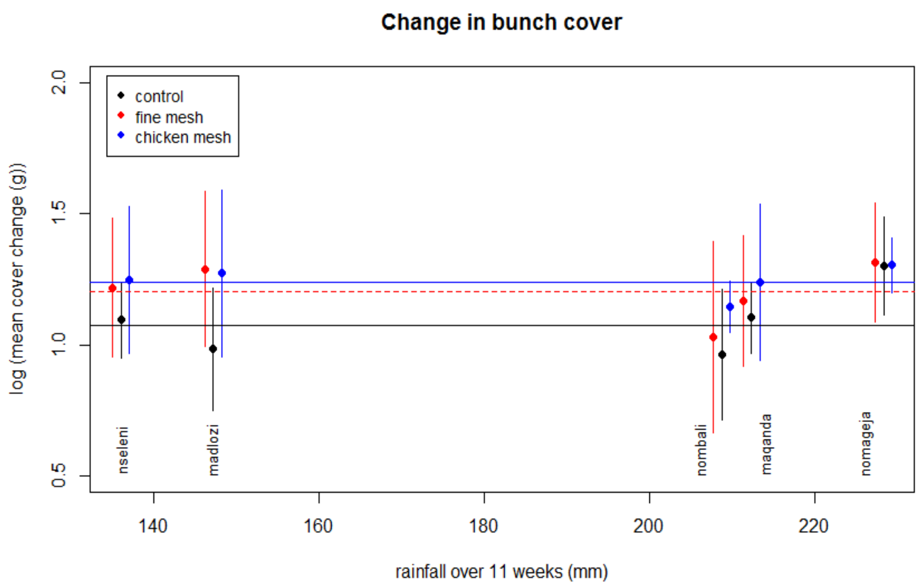

Figure 15: The change in bunch cover over an 11 weeks time period at the 5 sites along the 11 weeks rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. Change is the difference between start and end conditions. The graph shows the means +/- SD.

The bunch cover with the chicken mesh treatment deferred significantly from the control (p= p=0.0253, Fig 15).The bunch cover with the fine mesh is higher than the control, but did not differ significantly (p=0.0813). There is no significant difference between the fine mesh and the chicken mesh treatments. There is no effect of rainfall on the bunch cover. The model proved to be better without the random factor block (AnCova: $F_{(2,63)}$ =2.887, R^2=0.08397 , p=0.06312).

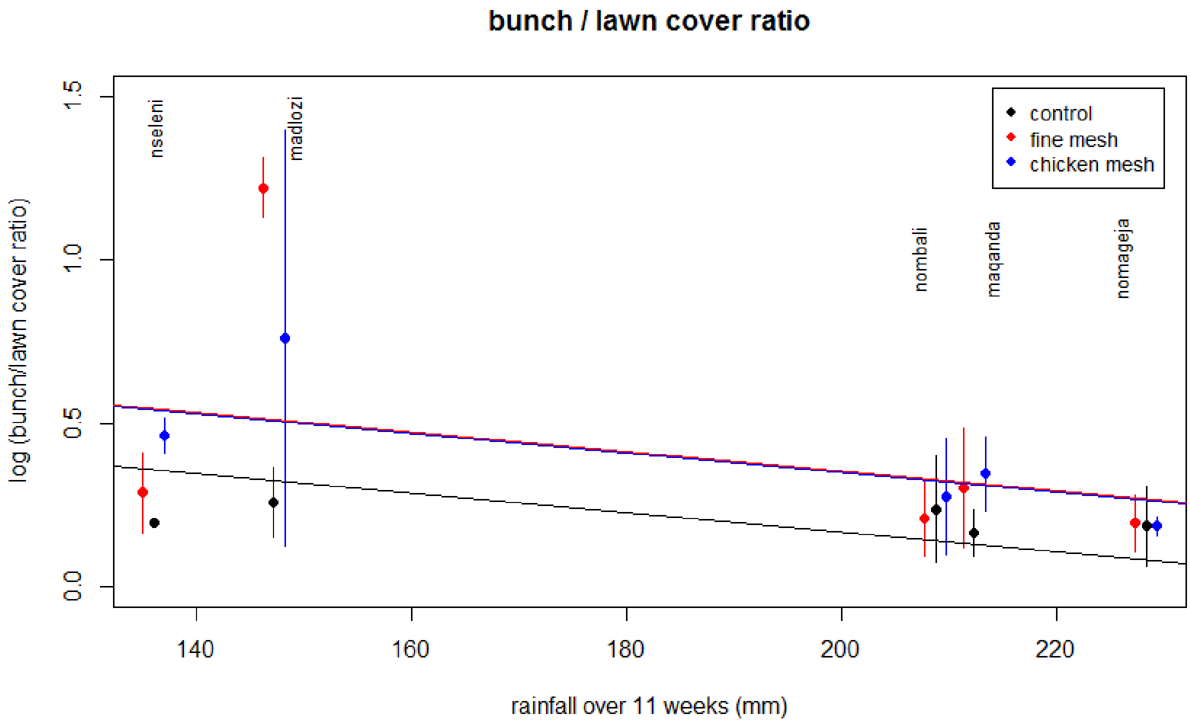

Figure 16: The bunch/lawn cover ratio over an 11 weeks time period at the 5 sites along the 11 weeks rainfall gradient, for the control (black), fine mesh (red) and chicken mesh (blue) treatments. The graph shows the means +/- SD and is log transformed. For each site the treatments had three replicates, giving a total of nine measurements per site.

The treatments have a significant effect (p=0.0017) on the bunch/lawn ratio(Fig. 16). Both the fine mesh (p<0.01) and the chicken mesh (p<0.01) are significantly different from the control. The bunch/lawn cover ratio is higher for the dung treatments, which means more bunch cover when dung is added. Bunch replaces lawn better with the dung treatments. The fine and the chicken treatments did not differ from each other. Rainfall is also significant, it appears that there is more lawn at higher rainfall (p<0.001). The model without a random factor proved to better than the model with block as random factor (AnCova: $F_{(3,39)}$= 4.586, R2=0.2608 , p<0.01).

Table 2: Correlation and P values of the RDA

```
Call:corr.test(x = Y.sc.sites, y = Y)
Correlation matrix
     lawn bunch  dead ground  forb moist bulkD salinity air_por start_infil end_infil    OM
RDA1 0.76 -0.63 -0.25   0.05 -0.21  0.82  0.45    -0.40    0.69       -0.46     -0.45  0.43
RDA2 0.13 -0.46  0.03   0.28  0.44 -0.37  0.09    -0.63   -0.33       -0.54     -0.62 -0.59
Sample Size
[1] 45
Probability values  adjusted for multiple tests.
     lawn bunch dead ground forb moist bulkD salinity air_por start_infil end_infil   OM
RDA1    0  0.00 0.61   1.00 0.81  0.00  0.03     0.07    0.00        0.03      0.03 0.04
RDA2    1  0.03 1.00   0.46 0.03  0.12  1.00     0.00    0.22        0.00      0.00 0.00

 To see confidence intervals of the correlations, print with the short=FALSE option
```

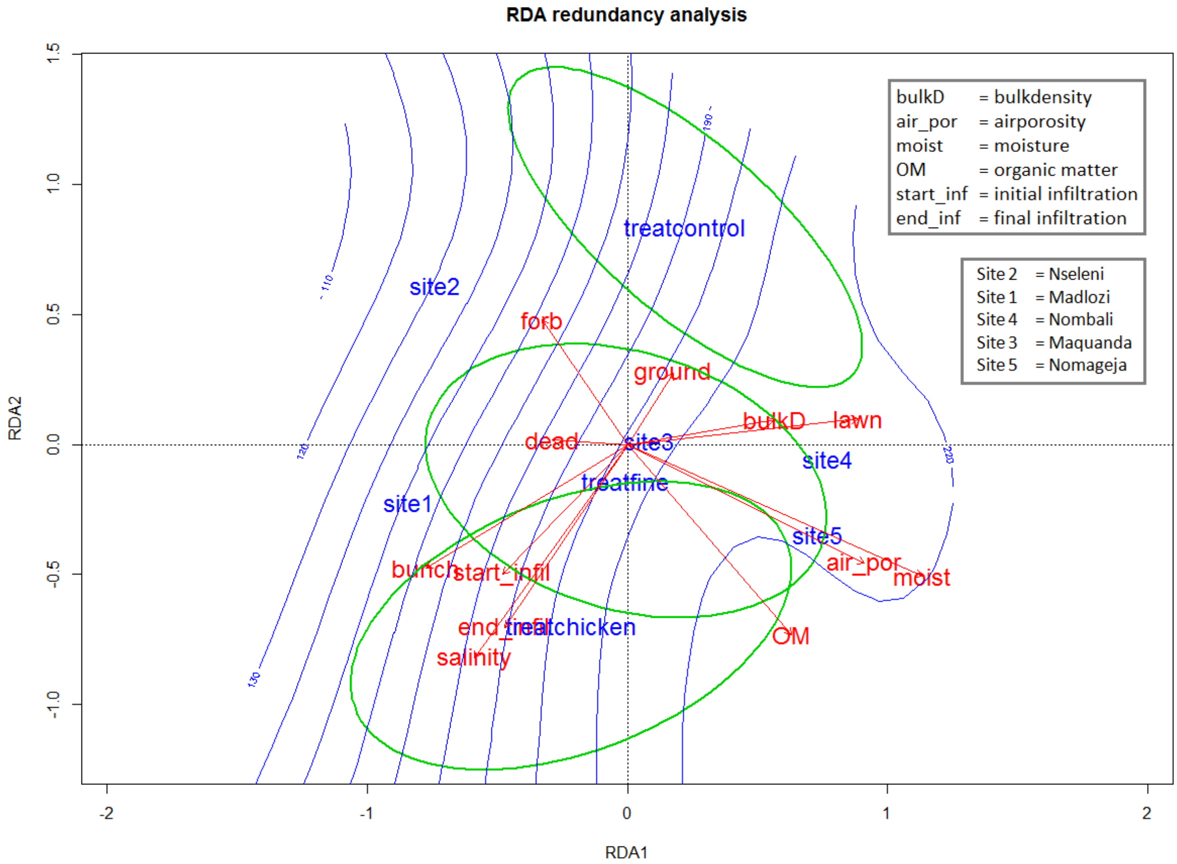

Figure 17: The RDA scores for the predictors (blue) and response variables (red) are plotted in this figure. The response variables are drawn as standardized vectors that indicate the direction in the ordination plane to which their values increase. The angle between the vectors is inversely proportional to the correlation between the variables. Using the ordiellipsefunction to draw the centroid of the treatments (circled in green) and with the ordisurf function the rainfall contour surface was added (blue lines).

The RDA analysis shows that both treatments (p=0.001) and rainfall (p=0.001) have a significant effect. Two main axes of explanation were found (Fig. 17). Along the first ordination axis we found that lawn cover, bunch cover, moisture, bulkdensity, organic matter, airporosity and infiltration were significantly correlated (Table 2). Along axis 2 bunch grass cover, forb cover, salinity, organic matter and infiltration were significantly correlated (Table 2). Rainfall variation was strongly correlated to axis 1 and the three different treatments separated along axis 2. We observe from this analysis that the control treatment (without dung) clearly separated from the experimental dung treatments showing that treatment had a strongly significant effect, with especially the chicken plots associated with higher values OM, infiltration, bunch grass cover and salinity than the control plots. Additionally the effect of treatment was independent of the rainfall gradient and of equal magnitude.

Macrodetritivores

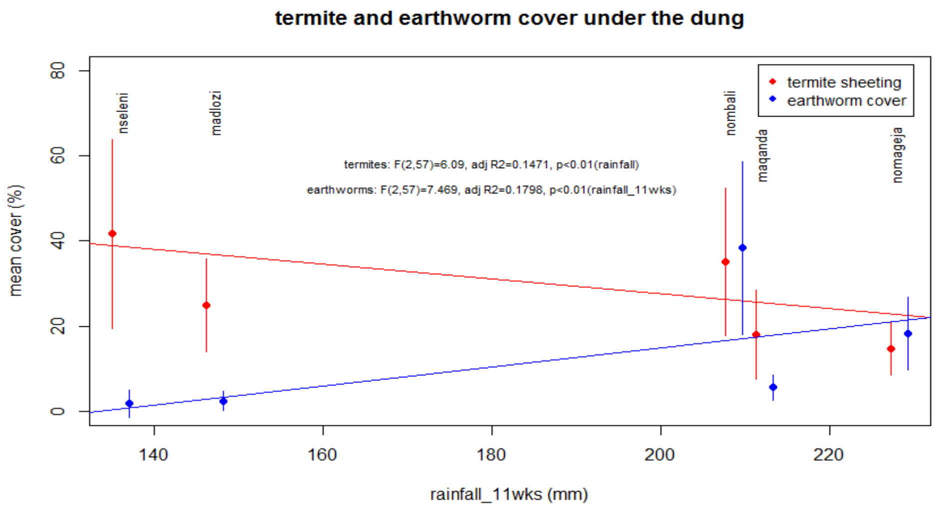

Figure 18: The cover of termite sheeting (red) and earthworm cast (blue) under the dung treatments at the 5 sites over the rainfall gradient. The graphs shows the mean +/- SD.

Figure 18 shows the cover of termites sheets and earthworm cast under the dung treatments. There were no differences between the fine mesh and chicken mesh treatment for the termite and earthworm cover, therefore we merged the data together (Fig. 18). For both the termites ($F_{(2,57)}$ =6.09, adj R^2=0.1471, p<0.01) and the earthworms ($F_{(2,57)}$ =7.469, adj R^2=0.1798, p<0.01) rainfall had a significant effect.

Table 3: Dungbeetle abundences at the 5 sites

Site	roller	dweller	tunneler
Madlozi	4	44	88
Nseleni	2	20	20
Maquanda	1	182	83
Nombali	8	47	41
Nomageja	4	108	18

Table 3 shows the number of dung beetles at the 5 different sites divided into three classes; rollers, dwellers and tunnelers. Dweller dung beetles where the most abundant at all sites, except in Madlozi. In Madlozi the tunnelers where the most abundant. At all the sites roller where not much present.

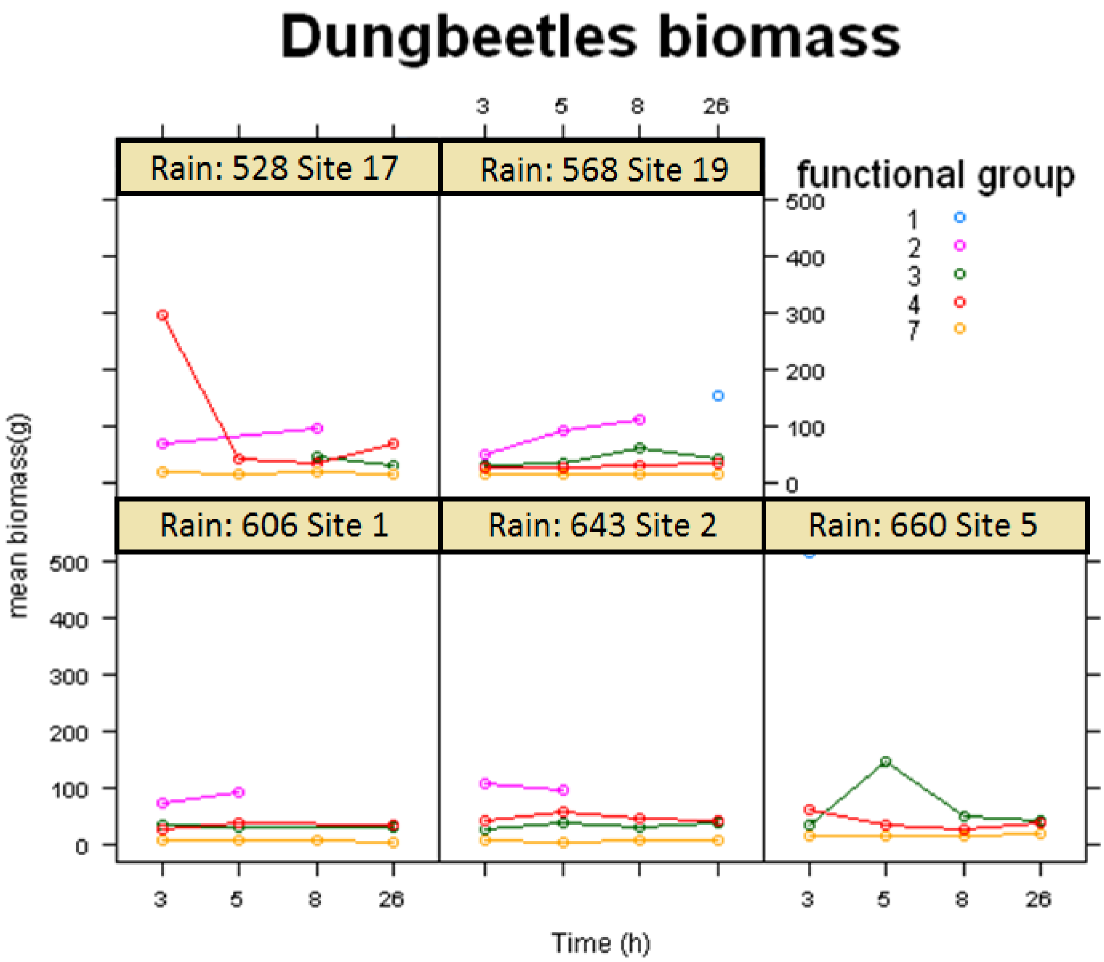

Figure 19: The dung beetle biomass at the 4 time points of the 5 different sites divided into 5 functional groups. FG1: large rollers (blue); FG2: small rollers (pink); FG3: large fast tunnelers (green); FG4: small to medium sized slow tunnelers (red); FG7: dwellers (yellow). The graphs shows the means.

Figure 19 shows mean biomass of the dung beetles present at the 4 different time point for each of the 5 sites. The rollers are much heavier than the other groups and are there only at one time point. The dwellers are constant over time. The tunnelers differ in their biomass among the sites.

Discussion:

With this research we suggest that the interplay between soil macrofauna and large herbivores and their opposing influence on the abiotic soil environment could provide the conditions that are essential to maintain structural vegetation heterogeneity. We wanted to know if dung is a key mechanism whereby lawn may convert into bunch vegetation at the tropical savannas in South Africa. Therefore we looked at the change in vegetation structure and at the physical changes of the soil that occur around and underneath a dung pile. We found significant effects of the treatments in infiltration rate, salinity, organic matter content and in the bunch biomass and cover, with a trend detected in the macroporosity. Soil macrodetritivore bioturbation loosened up the soil and thereby alleviated plant stress. Tall and more light competitive bunch grasses profited from this and outcompeted lawn species. So we can conclude that dung is a mechanism whereby lawn may convert into bunch vegetation at the tropical savannas in South Africa. In the following, I will discuss the mechanisms/relevance of these findings.

Multiple studies suggest that a higher salinity is more stressful for plants (Boland et al 1997; Mills et al 2006; Munns and Tester 2008; Mills et al 2009). Therefore we expected that the bioturbation would increase salt leaching and therewith induce a lower salinity. A lower salinity would mean less stress for the plants. However, we found that the salinity was significantly higher for the dung treatments compared to the control treatment. We also measured the salinity of the dung at the beginning and the end. The salinity of the dung was much higher at the start than after 11 weeks, which indicated that the salts leach out of the dung and into the soil. However productivity was higher next to the dung despite the higher salinity. Like Poorter and Nagel already suggested, it appears that the nutrients are more important for productivity then the stress of the salinity (Poorter and Nagel 2000).

The infiltrations under the fine and chicken treatment were significantly faster than the control infiltration. The infiltration of the chicken treatment was not significant different from the fine, but does show a higher final infiltration rate then the fine. This indicates that the dung associated bioturbating macrodetritivores increase the infiltration rate and the addition of tunnelling dung beetles increase it even more. That Madlozi shows the highest infiltration rate within the chicken treatments and also has the most tunnelling dung beetles (table 2) is proof for this statement. The rates of the infiltration become slower with higher rainfall. During our fieldwork we observed that dung beetles are less active with more rainfall, which could be an explanation for the lower infiltration rate at higher rainfall. Furthermore, the soil of the dung treatments had a higher organic matter content and the inclusion of dung beetles amplified it further. The organic matter could thus be increased due to the activities of bioturbating organisms who displace the soil through burrowing and with it they mix organic matter within the soil (Wilkinson et al 2009; Kristensen et al 2012).

With the lawn cover and lawn biomass change there is no significant effect of the dung treatments, which means that lawn does not grow faster with a dung treatment. An explanation could be that we did not exclude grazing herbivores, who could have eaten the lawn grasses and thus could have had an effect on the growth. Yet it is not expected that the grazers eat the lawn grasses of our treatments. Since it is raining season there is plenty of the lawn grasses, so they do not have to graze that close to the dung and will probably avoid it (Hart 1990; Michel 1995). This suggests that the lawn grasses do not profit from the addition of nutrients. The change lawn biomass cover is larger at higher rainfall, this means that the grass productivity is higher with increasing rainfall (Maoa et al 2014).

With the change in bunch biomass and cover there is a significant effect of treatment. The change in bunch cover and bunch biomass is larger when dung and its associated macrodetritivores are added. However it makes no significant difference if tunnelling dung beetles are included, because the change in biomass and cover did not differ between the fine and chicken treatments. As with the lawn, the bunch biomass changes faster at a higher rainfall than at low rainfall. Rainfall did not have an significant effect on the bunch cover. This could be explained by their tussock growth form, which causes them to grow more vertical than horizontal, unlike the lawn grasses that grow more horizontal. Tussocks expand in diameter over longer time periods than creeping lawn grasses, however the tussocks may quickly respond to improved growing conditions in the short term (i.e. current season) by producing a higher leaf density per tussock and longer leaves and therefore more densely connected canopies.

With the lawn/bunch cover ratio both treatments had a significant effect, although the chicken treatment shows a lower ratio. The lawn/bunch cover ratio is lower for the dung treatments, which means bunch replaces lawn better with the dung treatments. Bunch grasses are more affected by the addition of dung and the attracted macrodetritivores than the lawn grasses. An explanation for the increasing bunch cover and biomass could be that because of the bioturbating macrodetritivores the macroporosity increases, and therefore the longer and thicker roots of the bunch grasses penetrate better (van der Plas et al. 2013), and the water infiltration increases, alleviating plant stress with benefits the bunch grasses. We found that water infiltration did improve with the treatments, which means that there was more water available for the vegetation of the dung treatments. However, contrary to our expectations the penetration/moisture ratio did not significantly differ between the treatments. The three sites with the lower rainfall do show that the penetration depth is higher with the dung treatments, which confirms our expectation that the macroporosity increases due to macrodetritivores and that this effect is bigger at higher stress levels (low rainfall). It could be that the soil is compacted again by large animals during the eleven weeks. If so, the effect will be bigger and significant when all the large animals are excluded. Wet soil could also have influenced our results. When the soil is dry there are airspaces and a rigid structure in the soil that are not compressed by the compactor. When the soil is wetted up, then this hard "latent" structure comes undone and you can compress more porosity out of the soil than when it is dry. In addition, the increase in organic matter could also have an influence on the vegetation. It is shown that biomass allocation is significantly affected by nutrients and less so by other abiotic factors (Poorter and Nagel 2000). So due to the bioturbation there are more nutrients and water available for the vegetation, which we can see in the expansion of the bunch grasses with respect to lawn grasses in our treatments. It could be that the bunch grasses profit more from the added nutrient than the lawn grasses and could therefore outgrow/outshade the short lawn grasses.

Though we expected the effect to be bigger with the chicken treatment, because the larger dung beetles should have a bigger bioturbating effect, we did not explicitly find this back in our results. This could be explained by the raining season, which means there is enough rain available and water is therefore not limiting. Because there is almost no water stress, the effect of including dung beetles is minimal. It would be interesting to see the effects in a drier growing season, maybe then bioturbation has a bigger effect and the fine treatment will be significantly lower than the chicken treatment. The raining season could also explain that we did not find the difference between the treatments to be bigger at the drier sites and more similar at the wet sites. It appears that due to raining season, water is not a limiting factor for the plant growth, therefore the addition of nutrients will be the main factor causing the expansion of the bunch grasses. It could be that it shifts in the dry season to a state were the water infiltration will be the main factor.

Although the time period of this study is only eleven weeks, it is highly promising that we already measured results that point in the right direction. However during winter the termites are attracted to the dead dry dung and continue the bioturbating effects of the soil (Freymann et al 2008; Freymann et al 2010). Therefore we expect the biophysical changes to the soil to futher increase, since the bioturbation process within that short time period was not yet complete. Consequently it is suggested that more longer term measures are taken, to take a full season into account, which then accounts for the temporally different activities of different macrodetritivores groups.
Thus the separation between the treatments (and thus macrodetritivores entering the dung from either above or below ground) may yet be less important than the fundamental changes to the soil structure over longer time periods due to the presence of dung and the temporally changing attractiveness of dung materials to different groups of soil fauna.
The overall changes to the biophysical structure of the soil are important and if we can show that this continues through the dry season (i.e. winter) then we have stronger evidence that this is not only a short term switching mechanisms but also a permanent switching mechanism.

In summary, there is evidence for a reversal mechanism, bunch profited from the dung and soil fauna and outcompeted the lawn grasses. Literature shows that termites and earthworms prefer living in the loser soil of the bunch grasses (Tilman 1988; Andresen et al. 1990; Schrama et al. 2013b). So it seems that they concentrate their activities on creating optimal conditions for their own growth and are therefore ecosystem engineers. The framework of an ecosystem engineer has four components: 1. An engineer species causes structural change in the abiotic environment; 2. Structural change causes abiotic change; 3. Structural and abiotic change cause biotic change; 4. Structural, abiotic and biotic change can feedback to the engineer (Jones et al 2010). The macrodetritivores bioturbate the soil (1), which changes the soil physical conditions (2), these changes lead to an increase in bunch grass (3) and this increase in bunch grass will promote their own abundances for they prefer the loser soil underneath the bunch grasses (4).

Large grazers have an influence on their own abundances as well. Frequent, intensive grazing selects for stress resistance, small- leaved, short lawn grasses, which leads to a higher biomass concentration. The higher biomass concentration represents a potentially higher food yield to herbivores per bite of food (Stobbs 1973a, 1973b; McNaughton 1984; McNaughton 1985). Large grazers therefore produce grazing lawns of high quality, during periods of high utilization, increasing their own foraging efficiency (McNaughton 1984; Ruess & McNaughton 1987; Frank et al 1998). Large herbivore initiate small changes to plant-soil systems that trigger positive feedbacks. Their improved condition improves reproductive success which therefore allows their increased abundance (Jefferies et al 2006), macrodetritivores do the same thing but in the opposite direction. In soils and sediments, the bioturbation activities have a key role in the structure and functioning of the subsurface ecosystem (Meysman et al 2006). These interactions between macrodetrtivores and the soil are even considered to be at least as important as the trophic interactions classically studied by ecologists (Reise 2002; Meysman et al 2006). Removal of the keystone bioturbators could induce large changes in the structure of the habitat as a result of reduced ecosystem engineering, with cascading impacts on local biodiversity, and soil and sediment ecosystem functioning (Coleman and Williams 2002).

Earthworms, termites and dung beetles show to be important soil engineers. In modifying the distribution and availability of soil nutrients, soil engineers influence ecosystem services such as maintenance of biodiversity, stability, nutrient cycling and biomass production and they are all directly linked to heterogeneity (Lavelle et al 1997; Jourquet et al 2006).
Our RDA analysis showed that the internal biotically generated effect of macrofauna on landscape heterogeneity is independent and of equal magnitude to the strong external abiotic rainfall gradient. So the biotically generated heterogeneity and the internal mechanisms that drive vegetation from one state to another overrides the effects of the external abiotic forcing rainfall. This means that the long-term stability of the mosaic could depend on the positive feedback from both the compacters and the bioturbators.

An important focus of current ecological studies is on positive species interactions, but this focus is mostly on plant-plant interactions like the stress-gradient hypothesis (SGH)(He and Bertness 2014). In our study we found cross trophic positive interactions, where soil fauna are positively associated with tall shady vegetation, importantly this positive interaction is mutual because the activities of the soil fauna further promote the competitive advantage of tall vegetation (through looser soil and more nutrient availability). As Darwin already realized, bioturbation is of great importance for soil processes and even has consequences at larger scales (Darwin 1881). This outcome could push ecologists to recognize that positive interactions are present and critical in natural communities.

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