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Department of Wildlife, Fish, and Environmental Studies

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Laura van Veenhuisen

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Laura van Veenhuisen

Supervisor:	Joris Cromsigt, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Assistant supervisor:	Elizabeth Le Roux, Nelson Mandela University,, Department of Zoology
Assistant supervisor:	Marie José Duchateau Utrecht University, Department of Animal Ecology
Examiner:	Petter Axelsson, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies

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Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Wildlife, Fish, and Environmental Studies

Abstract

African megaherbivores are ecosystem engineers, which are under threat of extinction caused by, among others, poaching and climate change. Their current rates of loss means that there's a need to better analyse their impact on the environment, in order to predict the consequences of losing this group. One of the ways herbivores are influencing their habitat is by defecating in a certain spot, altering the nitrogen to phosphorus (N:P) ratio of the soil and therefore changing the nutrient availability to different plant species, which could change the structure and/or the composition of the vegetation. Therefore, the main objective of this thesis is to determine how body mass, feeding strategy and digestive type of various mammalian herbivores influences the spatial distribution of dung, nitrogen and phosphorus. I focused on two aspects in which species influence nutrient dynamics differently: (1) the variation among species in terms of dung nutrient content and (2) the way species differ in distributing dung and thus overall faecal nutrients.

From January to April 2018 I collected dung from all abundant mammalian herbivore species in Hluhluwe-Imfolozi Park (HiP). The nitrogen and phosphorus concentration in the dung samples were determined. I found that the N:P ratio in dung increases with body mass as a result of a decrease in the concentration of phosphorus. The N:P ratio in browser and mixed-feeder dung is significantly higher than the ratio in grazer dung, driven by higher concentrations of nitrogen in browser dung versus grazer dung. Also, the results showed that, even though the average N:P ratio in dung of ruminants and non-ruminants did not differ significantly, the concentration of nitrogen and phosphorus were significantly higher in ruminant dung.

In order to find the pattern of dung distribution through HiP, I combined my qualitative data with quantitative data from a long term study where herbivore dung was counted along 24 line transects.

The impact of herbivores on the distribution of nitrogen and phosphorus is found to be highly complex. Differences between species in body mass, feeding strategy and digestive type all contribute to the concentrations of nitrogen and phosphorus in dung and therefore the distribution of these nutrients over an area. This leads to the conclusion that the effect of megaherbivore extinction will differ per area depending on the identity of the megaherbivores living in that area. Possible consequences for nature reserves are changes in abundance of smaller herbivore and vegetation structures.

In HiP the expected result of megaherbivore extinction, when looking at the nutrient distribution, will be a decrease in the amount of phosphorus distributed through herbivore dung. The nitrogen distribution through herbivore dung is expected to show minimal change.

The composition of the African herbivore community is changing and to predict the full consequences of these changes it is important to conduct additional research which combines the effects of herbivory with studies on nutrient distribution.

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1. Introduction

For millions of years megafauna (all species with a body mass over 1000kg) existed widespread around the globe. In the last centuries human influence on nature increased, and by degrading habitat, hunting and changing climate by emission of greenhouse gasses humans are causing mass extinctions in this group of animals (Dirzo *et al.,* 2014; Estes *et al.,* 2011; Ripple *et al.,* 2015). Some researchers argue that the loss of these megafauna species could be the worst consequence of human influence on nature. These researchers argue that the effects of losing this group of animals are more prevalent than previously thought (Dirzo *et al.,* 2014; Estes *et al.,* 2011). As possible effects they point out changing dynamics in diseases, fire, carbon sequestration, invasive species, and changes in the exchanges among the world's soil, atmosphere and water (Dirzo *et al.,* 2014; Estes *et al.,* 2011). However, much is still unknown regarding the effects of losing the worlds megafauna. African megaherbivores (all African herbivore species with a body mass over 1000kg) is one of the groups of megafauna species that are under constant pressure from changing dynamics caused by humans (mostly in the form of poaching), which drastically decreases the number of individuals of these species (Ripple *et al.,* 2015). The loss of these species could have major consequences, on the structure and functioning of savanna ecosystems (Asner *et al.,* 2009; Staver *et al.,* 2009). Due to their various feeding strategies, movement patterns, and nutrient excretion through dung and urine they have a constant and dominant influence on their habitat (Asner *et al.,* 2009; Smit *et al.,* 2007; Staver *et al.,* 2009; Stock *et al.,* 2010). For example: megaherbivores can change vegetation patterns, which can alter the abundance of other species (Ripple *et al.,* 2015). Most African megaherbivores are even considered to be ecosystem engineers, which are species who have disproportionately large effects on their environment relative to their abundance (Haynes, 2012; Waldram *et al.,* 2008). For example, a study of Waldram *et al.,* (2008) in Hluhluwe-Imfolozi Park showed that the megaherbivore white rhino maintains short grass ('lawn') patches in mesic areas where other grazer species are unable to maintain short grass communities when white rhinos are removed. Even though savanna megaherbivores are known to have a major influence on their habitats, little is known about the possible consequences of losing this group of species. To predict these consequences it is essential to study the current effects of mammalian savanna megaherbivores on their habitat. Researchers have mostly focussed on studying the herbivory aspect of the megaherbivores. For instance, the direct effects of different feeding strategies of different megaherbivore species on the vegetation are widely studied (Levick *et al.,* 2009; Ripple *et al.,* 2015; Waldram *et al.,* 2008). However, there is a lack of research studying the effects of megaherbivores on the nutrient distribution.

Herbivore species can influence the nutrient distribution dynamics by differences between species in terms of the relative nutrient content in their dung. Relative ratios of nutrients in dung are termed stoichiometry, which differs among animal species because of differences in their physiology and behaviour (Elser *et al.,* 1996). Dung nutrient content can influence nutrient content in soils and nutrient availability to plants. The soil suitability for different plant species depends on the composition of different nutrients and their concentration in the soil (Aerts, 1999; Koerselman & Meuleman, 1996). Two of the most important nutrients for plants are nitrogen (N) and phosphorus (P), two nutrients that are often limiting in savanna systems (Augustine, 2003). Different plant species have different grow optima by various N:P ratios in the soil (Güsewell, 2004; Koerselman & Meuleman, 1996). By defecating in a certain spot animals alter the N:P ratio of the soil and therefore change the suitability for different plant species, which changes the structure and composition of the vegetation. For example: A study of Sitters *et al* (2017) suggested that among species differences in N:P ratio's in herbivore dung are sufficient to influence competition between N_2 fixing trees and non-N_2 fixing grasses. To determine the effects of mammalian herbivores on their habitat it is therefore important to determine the differences in dung N:P ratios of various species.

Studies have shown that species with different feeding and digestion types differ in dung stoichiometry (Sitters *et al.,* 2014, Sitters *et al.,* 2017). For instance, Sitters *et al.,* (2014) showed that browsers have a relatively high dung nitrogen concentration compared to grazers. This is believed to be caused by the fact that browsers eat leaves and twigs which are relatively high in nitrogen in comparison to grass. No study has tried to link dung stoichiometry to herbivore body mass. Skeletons of mammals contain apatite ([$Ca_5(OH)(PO_4)_3$]) which elevates the concentration of phosphorus in bone and leads to a relatively low bone N:P ratio (0.8:1) compared to the whole-body N:P ratio (approximately: 9.6:1 in a 1000 kg animal) (Elser *et al.,* 1996). The contribution of certain tissues in mammals varies with body mass. A study by Prange *et al.,* (1979) showed that the relative skeleton mass increases disproportionately with body size. For example, the body mass of a shrew consist of 3.8 % skeletal mass versus 13.6% skeletal mass in elephants (Prange *et al.,* 1979). This means that the concentration of phosphorus in the mammalian body also increases disproportionately. It is therefore likely that larger herbivores extract more phosphorus from their food then smaller herbivores leading to a lower dung phosphorus concentration.

Another way in which herbivore species influence nutrient fluxes is in the way they distribute dung and therefore total faecal nutrients over the landscape. To study the ways in which herbivores are distributed over the landscape, Cromsigt *et al.,* (2009) performed a study analysing the distribution of mammalian herbivores in HiP. This study found that body mass influences diversity of habitat use of large herbivores but digestive strategy potentially modifies this relationship, because non-ruminants have a wider diet tolerance than ruminants. The same study states that large herbivore species use a higher proportion of the landscape than smaller herbivores, since a wider food quality tolerance allows them to use a higher diversity of habitat types. This means that herbivores are unevenly distributed over reserves and large herbivores spread dung (and therefore nutrients) more evenly over the landscape than smaller herbivores. Another study form Wolf *et al.,* (2013) defined a mathematical framework for quantifying lateral fluxes that large herbivores make a disproportionate contribution to lateral nutrient transfer compared to smaller herbivores. Wolf proposes that lateral nutrient diffusion is a previously unrecognized ecosystem service, provided by large herbivores, which drives productivity by taking nutrients from places of excess and depositing them in places of shortage. Both Cromsigt and Wolf expect that disruptions to nutrient cycles are possibly quite large if threatened large and mega herbivores are driven to extinction.

In this study I focused on the nutrient distribution of mammalian herbivores in the savanna system of Hluhluwe-Imfolozi Park (HiP) in South Africa. Based on the previous information I decided focus on two aspects in which species differently influence nutrient dynamics: (1) the way species differ in terms of relative nutrient content in their dung and (2) the way species differ in the spatial distribution of dung and thus overall faecal nutrients over their habitat.

The first objective of this study was to search for stoichiometric differences in dung of different herbivore species while highlighting three main mechanisms which could correlate with these differences: body mass, feeding strategy and digestion type. First I aimed to determine if the increasing amount in phosphorus in herbivores with an increasing body mass (because of the disproportional increase in skeleton) is visible in the dung of the animals. It is hypothesized that the concentration of phosphorus in dung will decrease with body mass, leading to a decrease in the N:P ratio in dung. Furthermore, I hypothesized that browsers will have a relatively low N:P ratio compared to grazers because browsers eat leaves which are relatively high in nitrogen in comparison to grass (Sitters *et al.,* 2014). Lastly, I hypothesized that the N:P ratio in ruminant dung is comparable to the N:P ratio of non-ruminant dung. However, I expect the concentrations of both nitrogen and phosphorus in ruminant dung to be lower than in non-ruminant dung. This because ruminants are expected to be more efficient in extracting nutrients from their food than non-ruminants. This would mean that ruminants will be able to extract more phosphorus and nitrogen form their food than non-ruminants, but not causing a difference in the N:P ratio. These hypothesises will be tested by comparing dung N:P ratios, concentrations of nitrogen and phosphorus in dung of herbivores with different feeding and digestive strategies, ranging from impala (51.5 kg) to African elephant (3900 kg).

The second objective of this study was to determine how body mass, feeding strategy and digestive type of various herbivores are influencing the spatial pattern of dung and faecal nitrogen and phosphorus distribution. It is hypothesized that large herbivores are spreading dung more evenly over their habitat than small herbivores. However, if the hypothesis, stating that the concentration of phosphorus in dung decreases with body mass, is confirmed, than this would mean phosphorus is distributed differently over HiP than nitrogen. The spatial pattern of nitrogen distribution will more closely resemble the spatial distribution of large animal dung, whereas the spatial pattern of phosphorus distribution will more closely follow that of small species dung distribution. This would mean that a spot shown to have a large amount of small herbivore dung will also contain a high amount of phosphorus compared to nitrogen.

Previously, I hypothesized that browser dung will contain a high concentration of nitrogen compared to grazer dung. I expected that parts of HiP which contain a high density of grazer dung will also contain a high amount of phosphorus in relation to a part of HiP containing a high density of browser dung. Finally, I hypothesised that non-ruminant dung will contain a high concentration of both phosphorus and nitrogen compared to ruminants I expected that parts of HiP showing a high density of non-ruminant dung will also show high amounts of phosphorus and nitrogen in comparison to parts of HiP showing a high density of ruminant dung.

2. Method

2.1 Study area

This study was conducted in Hluhluwe-Imfolozi Park (HiP) (South Africa) (Fig. 2.1), which is the oldest proclaimed nature reserve in Africa, dating from 1895. HiP covers an area of 960 km² and has a hilly topography where altitudes vary between 80 and 540 meters above sea level (Cromsigt *et al.,* 2017). The reserve has a sub-tropical climate and lies in a summer rainfall area, meaning that the summer corresponds with a wet season and winter with a dry season. There is a positive relationship between rainfall and altitude with mean annual rainfall of 968 mm ± 36 SE calculated from monthly rainfall collected 1933-2012 (Cromsigt *et al.,* 2017). The ranges in rainfall and elevation are causing the park to have a high habitat heterogeneity. The vegetation is ranging from savanna woodland dominated by Acacia spp, to open grasslands. Also, broad-leaved woodlands can be locally abundant (Cromsigt *et al.,* 2009).

The park is divided in two main parts, the hilly, wetter northern Hluhluwe and the less undulating, dryer southern Imfolozi (Fig. 2.1.1).The reserve has a near complete set of native ungulates, and is one of the few protected areas with functionally relevant densities of multiple megaherbivore species (Table 2.1.1). The most southern part of the park is divined as wilderness area. No humans and therefore no research is allowed in this part of HiP.

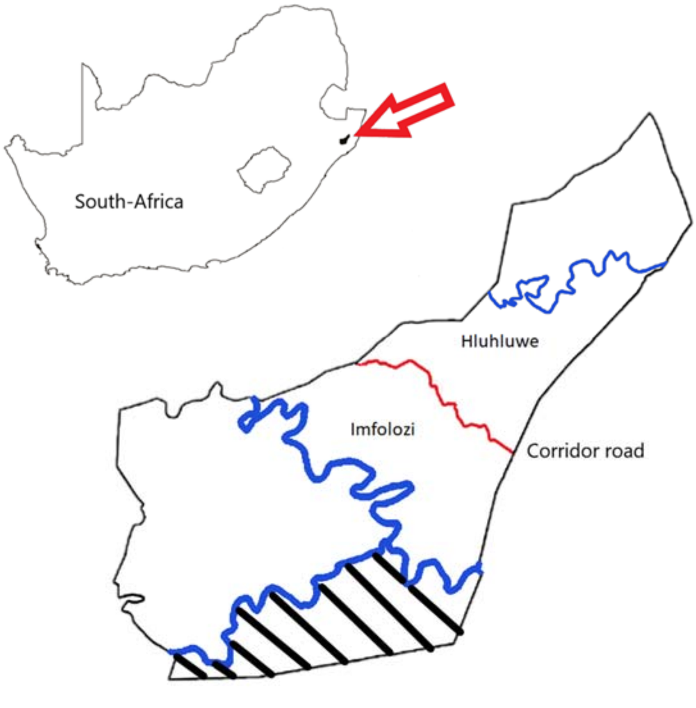


Figure 2.1.1: Map of HiP, rivers in blue, wilderness area (where no humans are allowed) is marked by black stripes (modified from: Davies et al., 2016)

Table 2.1.1: Estimated number of individuals and density in HiP per herbivore species which were included in this study (species are sorted by body mass) (HiP unpublished census reports)

Species	**Scientific name**	**Number of individuals**	**Density (km2)**	**Year**
Impala	*Aepyceros melampus*	14019	14.60	2016
Warthog	*Phacochoerus africanus*	885	0.92	2016
Nyala	*Tragelaphus angasii*	3297	3.43	2016
Blue wildebeest	*Connochaetes taurinus*	598	0.62	2016
Burchell's zebra	*Equus quagga*	986	1.03	2016
Buffalo	*Syncerus caffer*	5249	5.47	2016
Giraffe	*Giraffa camelopardalis*	367	0.38	2016
White rhinoceros	*Ceratotherium simum*	2068	2.15	2016
African elephant	*Loxodonta africana*	761	0.79	2017

2.2 Dung collection and nutrient analysis

During the period January-April 2018 I collected dung from all abundant mammalian herbivores species present in HiP (Table 2.2.1). Therefore, the study was conducted in the transition period between the rainy and dry season. However, the period in which I collected my samples was relatively wet compared with other years, meaning that at the end of my fieldwork the dry season had not yet started and I only collected data during the wet season.

The herbivores from which I collected dung have different feeding and digestion types and ranged in size from impala to African elephant (Table 2.2.1). The species were ranked in three body mass categories: small, meso and megaherbivores, these categories are commonly used in literature (Owen-Smith., 1992; Ripple *et al.,* 2015). Some of the less common species, like black-rhino, waterbuck and duiker, which do occur in HiP, were excluded, because I was unable to collect sufficient data to include them in the analysis. I searched for dung while driving a car on the roads of the park and while walking in high animal density areas, for example close to waterholes. I aimed to collect as many samples as possible per species in both Hluhluwe and Imfolozi (Fig. 2.2.1, Table 2.2.2).

Table 2.2.1: Feeding type, digestion type, average body mass and the body mass category of the species included in this study (species are sorted by body mass). The information on body mass was obtained from Owen-Smith (1992).

Species	**Feeding type**	**Digestion type**	**Average body mass (kg)**	**Body size category**
Impala	Mixed-feeder	Ruminant	51.5	Small herbivore
Warthog	Grazer	Non-ruminant	69.0	Small herbivore
Nyala	Browser	Ruminant	98.3	Small herbivore
Blue wildebeest	Grazer	Ruminant	210	Mesoherbivore
Burchell’s zebra	Grazer	Non-Ruminant	270	Mesoherbivore
Buffalo	Grazer	Ruminant	585	Mesoherbivore
Giraffe	Browser	Ruminant	1137.5	Megaherbivore
White rhinoceros	Grazer	Non-ruminant	1900	Megaherbivore
African elephant	Mixed-Feeder	Non-ruminant	3900	Megaherbivore

I identified dung with the help of local rangers and I only collected when it was estimated to be no older than one day. Dung was not collected while it was raining or when it had rained shortly before. Also, I did not collect dung from or close to tourist areas (picnic sites) and camps, because plant

nutrient content and composition on those locations are alternated by grass cutting, irrigation and fertilisation that potentially could influence the nutrient composition of the dung.
I collected the dung in paper bags, noting the habitat in which the dung was found and the weather conditions. I weighed and labelled the dung. Lastly, I classified the freshness of the dung using three categories:

1: The animal was witnessed defecating.
2: The animal or herd was witnessed in the same area as the dung within an hour before.
3: The species was not seen in the vicinity of the collected dung but it was estimated that the dung was not older than one day.

Within a few hours after I collected the dung it was put in a drying oven at 60 °C and dried for 48 hours. After the drying process the dung was weighted again, to be able to calculate the water content of the dung.
Dung samples of the same species found in the same location within a time span of 7 days were combined into composite samples. For example, multiple dung piles of one species found in the same location on the same day, most likely belong to a herd, eating from the same area and likely eating the same plant types.
When possible, I made eleven combined samples per species, of which seven combined samples originated from Hluhluwe and four samples from Imfolozi (Table 2.2.2; Appendix 1). In some cases we were unable to collect eleven samples per species. This was due to the fact that the animals are relative rare in the park (or in one of the two areas like giraffe) or that they defecated in places that are hard to reach like woody patches (Nyala).

After all dung was collected, sorted out, dried and grinded, the samples were sent to the laboratory of the Agricultural Research Council in Cedara and analysed for nitrogen and phosphorus content. To determine the total amount of nitrogen in the samples a LECO CNS 2000 Analyzer was used. For determining the total amount of phosphorus a Hunter apparatus was used.

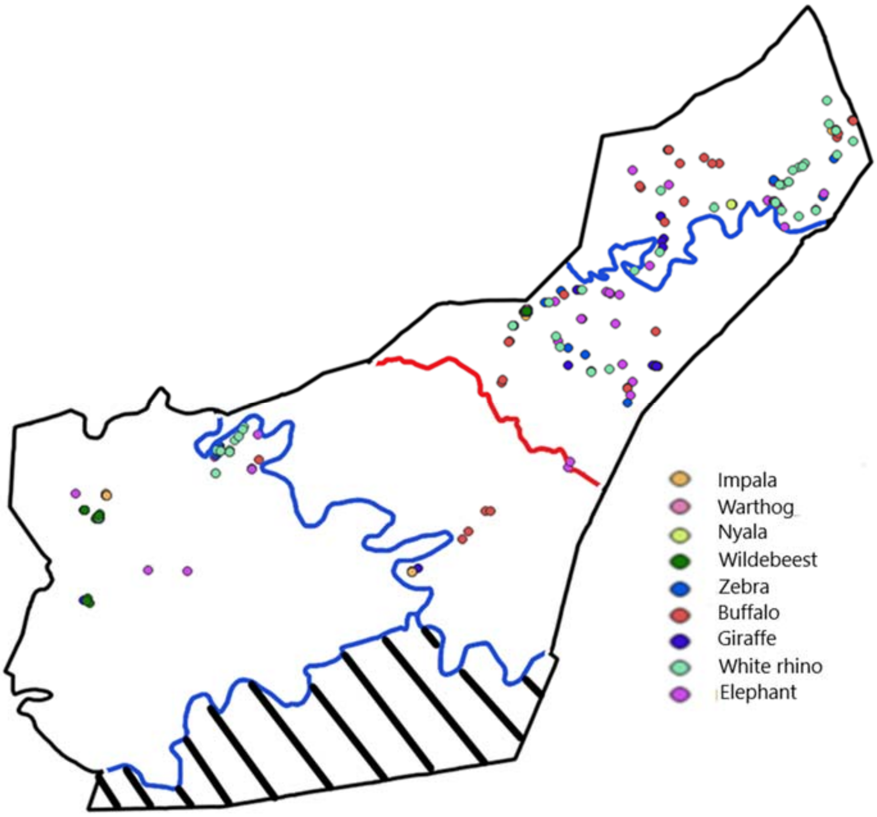


Figure 2.2.1: A map of HiP with the distribution of the dung per species used in this study, rivers in blue, wilderness area is marked by black stripes (species sorted by body mass)

Table 2.2.2: Number of samples per species per area (species are sorted by body mass)

Species	**Hluhluwe**	**Imfolozi**
Impala	6	3
Warthog	1	1
Nyala	1	0
Blue wildebeest	6	4
Burchell's zebra	7	4
Buffalo	7	3
Giraffe	7	2
White rhinoceros	7	5
Elephant	7	4
Total amount of samples	49	26
		75

2.3 Analysis of dung densities recorded along transects

To quantify the pattern of dung distribution over HiP, data from a long term study was used (Cromsigt *et al.,* 2009; HiP unpublished transect data from earth watch). During this long term study, which was also conducted in HiP, all herbivore dung was counted along 24 line transect, varying between 4 and 11 km with a total length of 190 km. This was done at the end of the dry season (August to October) in 2004 and at the start of the rainy season (October-November) in 2014. The transects were distributed evenly over the park, covering the main vegetation types, elevation levels and rainfall gradients (Figure 2.3.1). The most southern part of HiP is defined as wilderness area, no permission was granted to walk transects in this part of the park.

The transects were walked by two trained observers, which were trusted to be able to reliably identify species based on dung. The number of dung pellet groups per species were noted per five meter plot along the transect within one meter on each side of the transect. Only dung of the nine

most observed grazers in the park were recorded: impala, nyala, blue wildebeest, African buffalo, common warthog, Burchell's zebra, African elephant, giraffe and white rhino. Since white rhino's use middens to defecate, their dung distribution is more patchily distributed. To get a sufficient estimate of the distribution of this species all middens that could be seen from the transects (within 50 meters on either side of the transect were recorded instead of the 1m from the transect centre). The rhino middens were estimated to have on average 100 dung boli each.

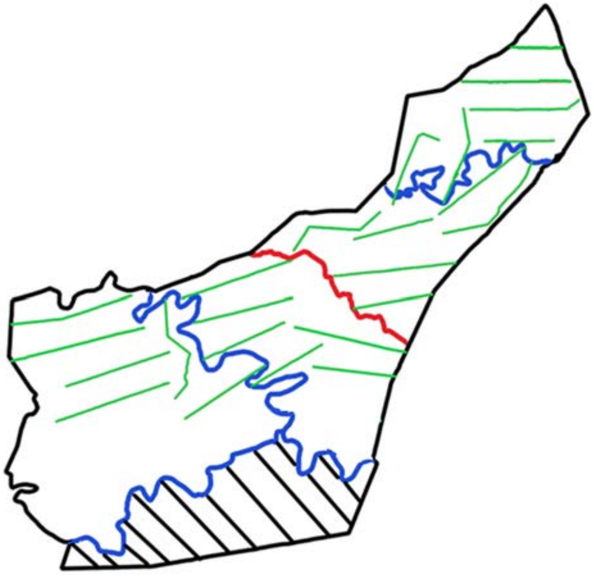


Figure 2.3.1: A map of HiP showing the location of the transects (in green) used in this study and the study of Cromsigt et al., 2009. Rivers in blue, wilderness area is marked by black stripes

2.4 Statistics and data analysis

2.4.1 Statistical analysis of the nutrient content in dung

The data collected on datasheets in the field were entered in Excel (2016). I used the program R (3.4.4 (2018-03-15)) for data analyses. I used One-Way analysis of variance (ANOVA's) followed by Post-hoc paiwise comparison tests (Tukey test) to test for differences in dung N:P ratio's, dung nitrogen concentration and dung phosphorus concentration among herbivores with different body sizes (small herbivores, mesoherbivores and megaherbivores), among feeding strategies (browser, grazer and mixed-feeders) and among digestive strategies (ruminants and non-ruminants).

If necessary, data was log-transformed to meet the assumptions of normality. When analyses were performed on species separately then nyala and warthog were excluded since these species have a very small sample (respectively 1 and 2). When all species were combined into subcategories (body size category, feeding type and digestive type), then the data of nyala and warthog were included in the analysis to increase the total sample size per category.

No significant differences were found in the nutrient content of dung originating from the Hluhluwe and Imfolozi sections of HiP (One-way ANOVA: df=1, F=<0.001, p= 0.9802. It therefor was not necessary to correct for the two parts of the parks by implementing a random term into the models.

2.4.2 Data analysis of the distribution of dung across HiP

I combined all dung per 500m transect segment per species per year and multiplied this value by the average dung pile weight (kg) per species (Appendix 2). To achieve the amount of dry weight (kg) per 500m transect per species per year I used the following calculation: (1-(average percentage of water per species/100) (Appendix 2).

This amount of dry weight per species per 500m transect per year was multiplied by the average percentage of nitrogen and phosphorus (obtained in this study, and tabled in Appendix 2) per species and divided by 100 to determine the total input of nitrogen and phosphorus per 500m transect per species per year. Then the average amount of dry weight dung per species was calculated over both years.

Three groups of heatmaps with three subgroups were produced in QGIS to show the impact of body mass, feeding strategy and digestive type on the distribution of dry weight dung, faecal nitrogen and faecal phosphorus. The three main groups and their subgroups are described below:

I made three subsets of heat maps (Fig. 4.1 to 4.3) to show how herbivore species of different body size, feeding strategy and digestive strategy influence the spatial distribution of dung, faecal nitrogen and faecal phosphorus. The maps showing all species combined are repeated in each figure (panel 1) for comparison. The table below (Table 2.4.1) summarises the categories and the map number

Table: 2.4.1: Overview of the heatmaps made to visualize the distribution of dung, nitrogen and phosphorus over HiP

	Figure 4.1: Body size		**Figure 4.2:** Feeding strategy			**Figure 4.3:** Digestive strategy	
Panel 1: All herbivores	**Panel 2:** Meso-herbivores	**Panel 3:** Mega-herbivores	**Panel 2:** Browsers	**Panel 3:** Grazers	**Panel 4:** Mixed feeders	**Panel 2:** Ruminants	**Panel 3:** Non-ruminants
a. Dung b. N c. P	a. Dung b. N c. P	a. Dung b. N c. P	a. Dung b. N c. P	a. Dung b. N c. P	a. Dung b. N c. P	a. Dung b. N c. P	a. Dung b. N c. P

3. Results

3.1 Results of the nutrient content in dung

3.1.1 N:P ratio and the concentrations of nitrogen and phosphorus in dung in relation to bodysize

The results show a significant positive linear relationship between N:P ratio in dung and the bodymass of the herbivore (one-way ANOVA: df=1, F=63.134, p=<0.001). An increase in bodymass leads to a increase in the dung N:P ratio (Fig. 3.1.1.1). To see if these differences were caused by a specific body size category, I split the data into small, meso and megaherbivores (Table 2.2.1). I found significant differences in the average N:P ratio in the three different categories (one-way ANOVA: df=2, F= 21.097, P=<0.001). A post-hoc paiwise comparison (Tukey test) showed that the average N:P ratio in megaherbivore dung is significantly higher than the N:P ratio in small and mesoherbivore dung (Fig. 3.1.1.2), but that the N:P ratios between small and meso herbivores were comparable. Futher splitting of the data into species showed that N:P ratios also differed significantly between species (one-way-ANOVA: df=6, F= 20.875, p=<0.001). See figure 3.1.1.3 for these differences.

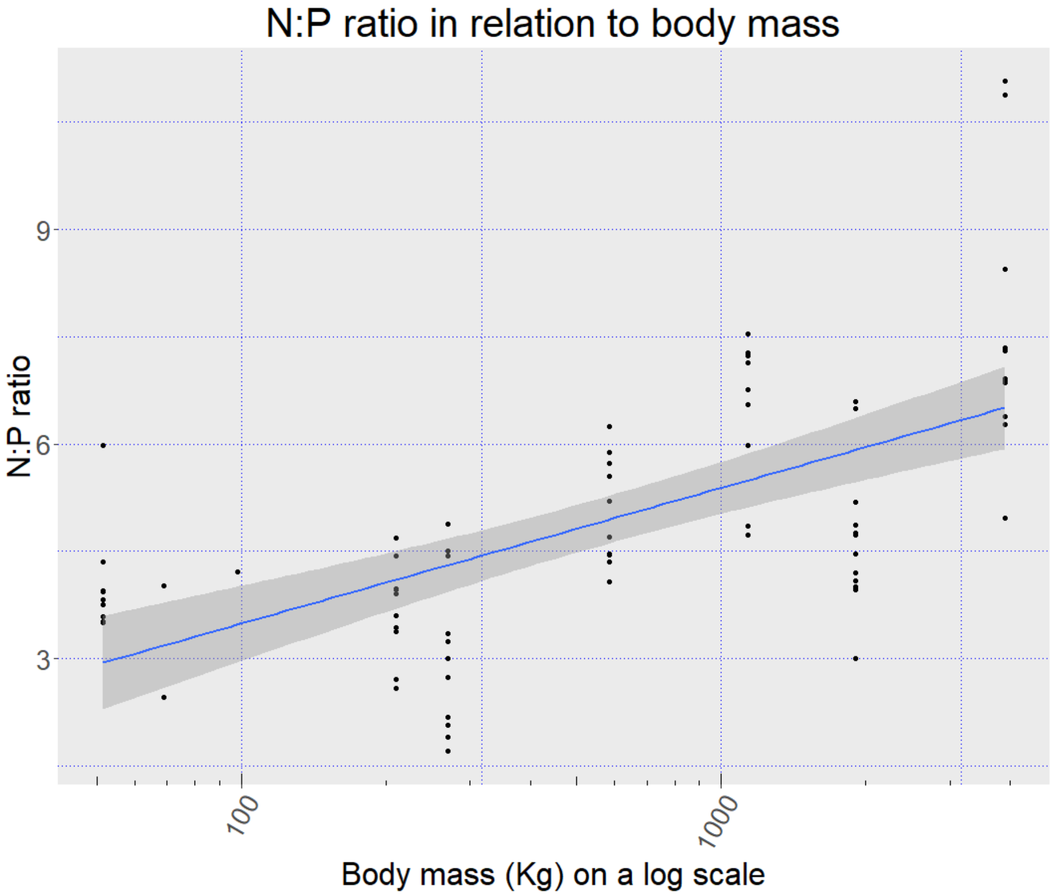


Figure 3.1.1.1: The N:P ratio of dung from nine different herbivore species present in HiP in relation to body mass. Body mass is plotted on a logaritmic scale

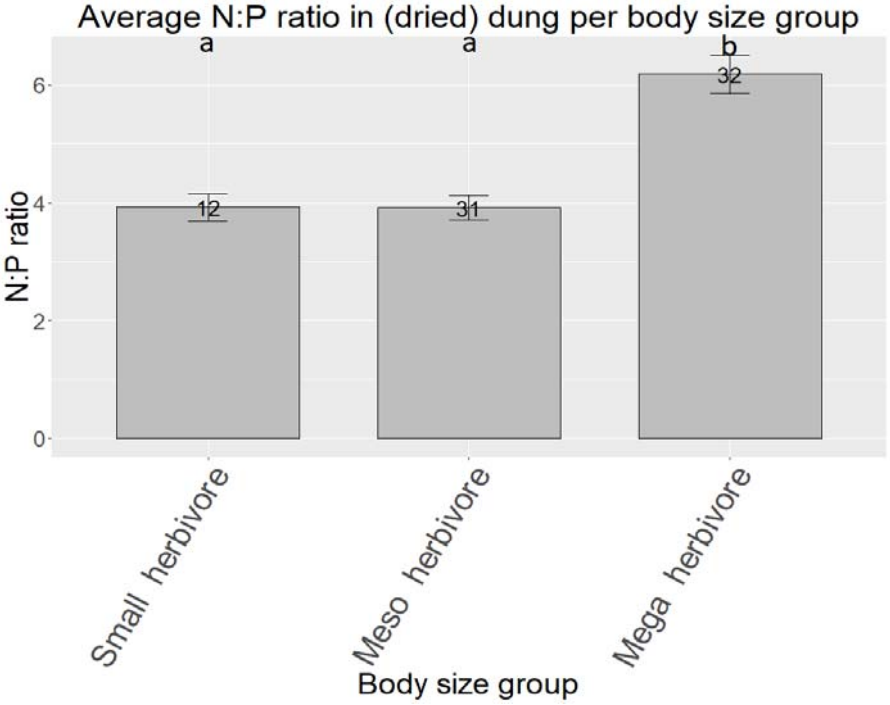


Figure 3.1.1.2: The average N:P ratio of herbivore dung plus standard error per bodysize group, different letters indicate significant differences between the different body size categories (α=0.05). Numbers inside the barplots are representing the sample size of each species.

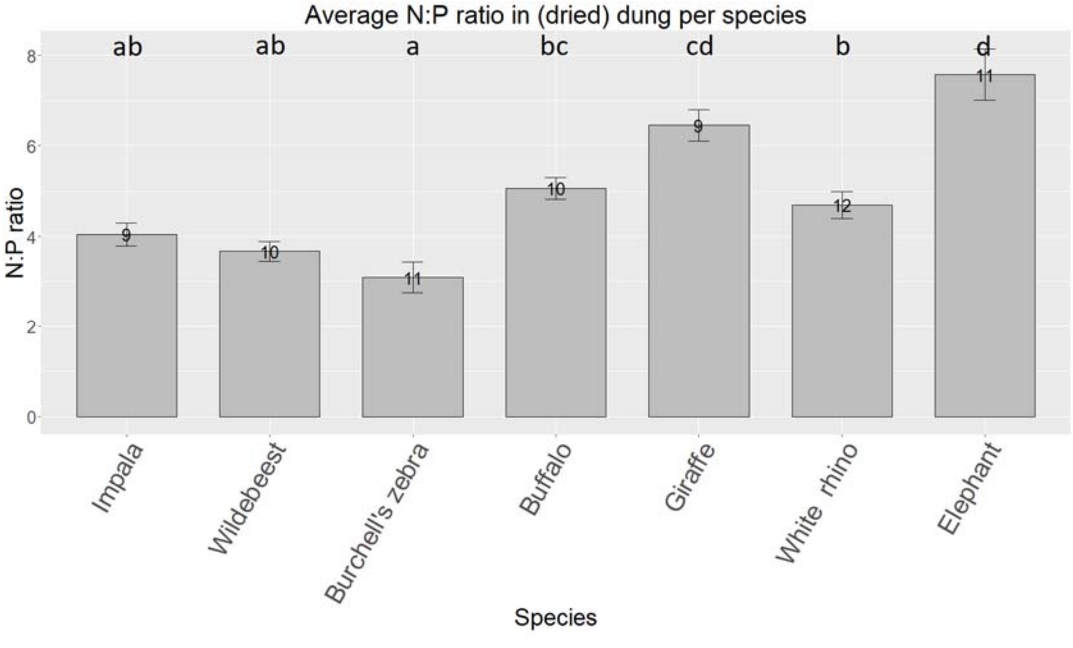


Figure *3.1.1.3: The average N:P ratio of herbivore dung plus standard error per species. Species are sorted by bodymass (lowest to highest), different letters indicate significant differences between the different species (α=0.05). Numbers inside the barplots are representing the number of combined dung samples per of each species. Nyala and warthog are excluded due to low sample size.*

No significant relationship was found between the average percentage of nitrogen in dung and the bodymass of the herbivores (one-way-ANOVA: df=1, F=0.9431, P=0.3347) (Fig. 3.1.2.1). Visible is that giraffe has an average percentage of nitrogen in its dung which deviates strongly from all other species (Fig 3.1.2.2).

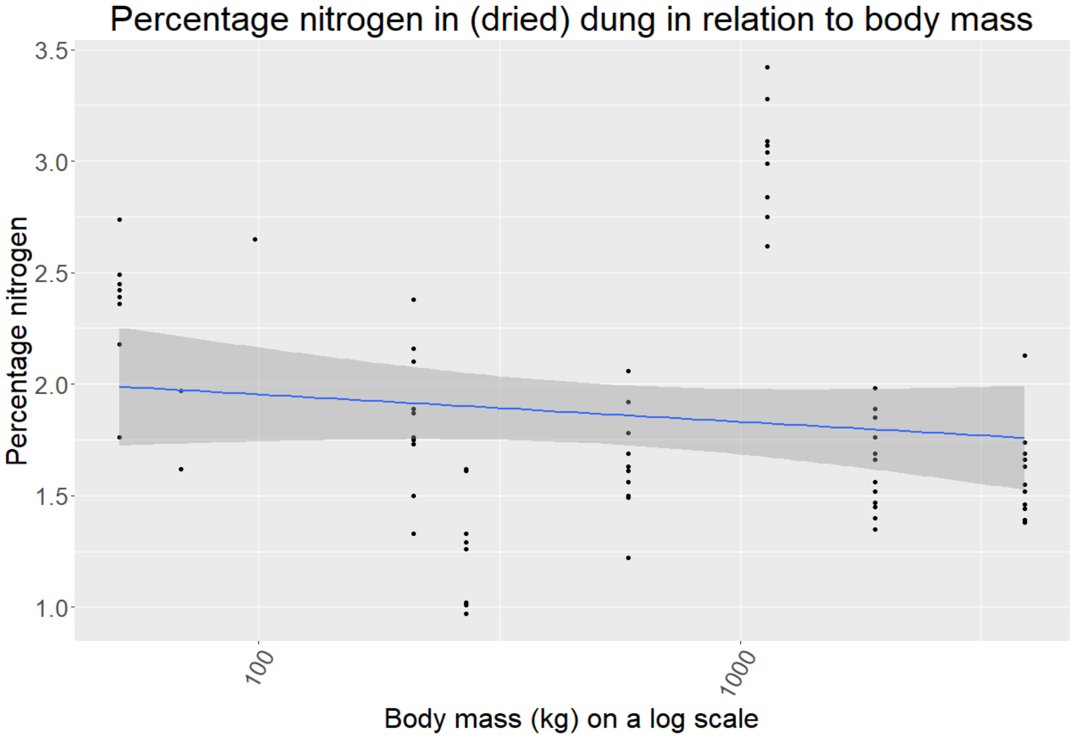


Figure 3.1.2.1: The percentage of nitrogen in (dried) dung of nine herbivore species present in HiP in relation to body mass. Body mass is plotted on a logaritmic scale

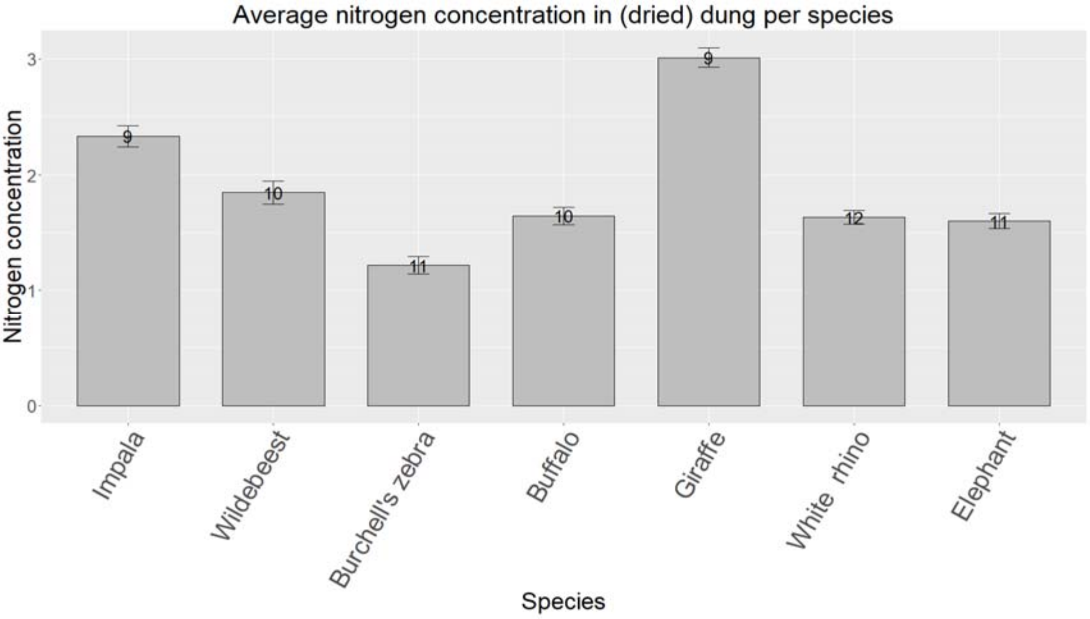


Figure 3.1.2.2: The average percentage of nitrogen plus standard error in (dried) herbivore dung of seven speices present in HiP (species are ordered by body mass). Numbers inside the barplots are representing the number of combined dung samples per of each species.

A strong negative linear relationship was found between body mass and the average percentage of phosphorus in herbivore dung (one-way-ANOVA: df=1, F= 46.776, p=<0.001) (Fig. 3.1.3.1). After categorizing the species into the body mass categories it became clear that there are significant differences between the average percentage of phosphorus in the categories (One-Way-ANOVA: df=2, F=13.772, p=<0.001). A post-hoc pairwise comparison shows that all three categories differ significantly from each other (Fig. 3.1.3.2). Further splitting of the data into species shows that there are significant differences between species (one-way-ANOVA: df=6, =18.608, p=<0.001). A post-hoc pairwise comparison determined were these differences lie (Fig. 3.1.3.3).

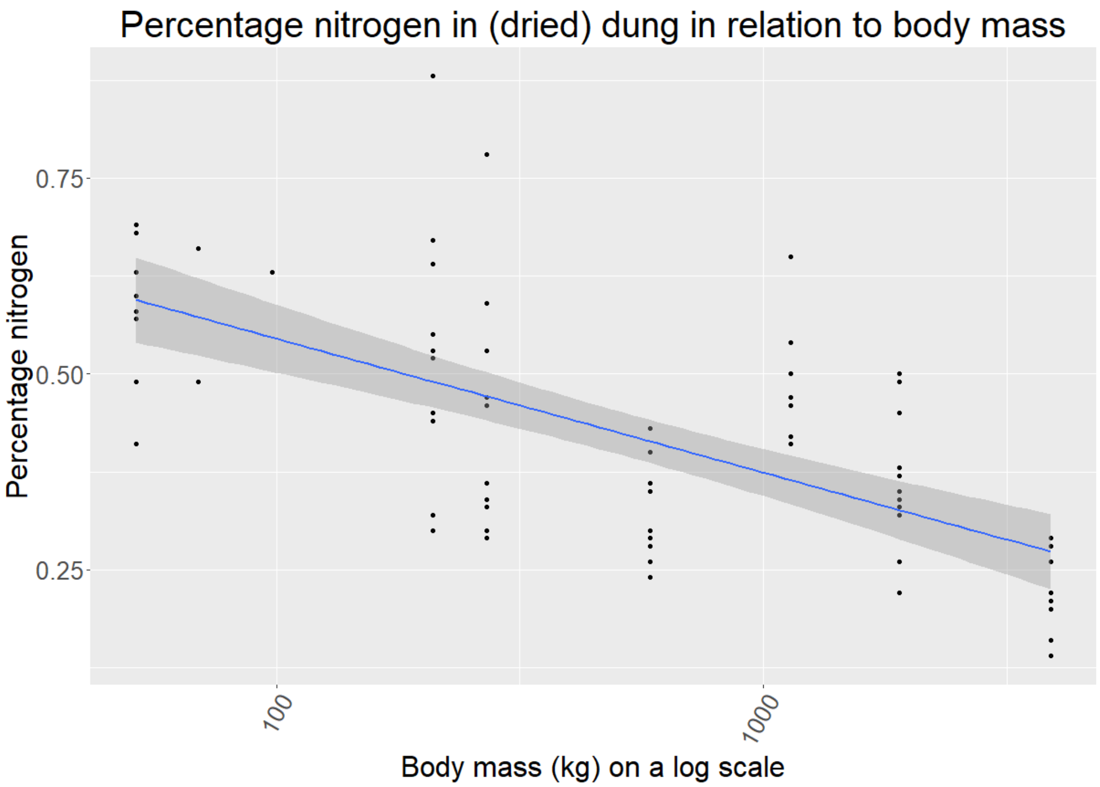


Figure 3.1.3.1: The percentage of phosphorus in (dried) herbivore dung of nine species present in HiP in relation to body mass. Body mass is plotted on a logaritmic scale

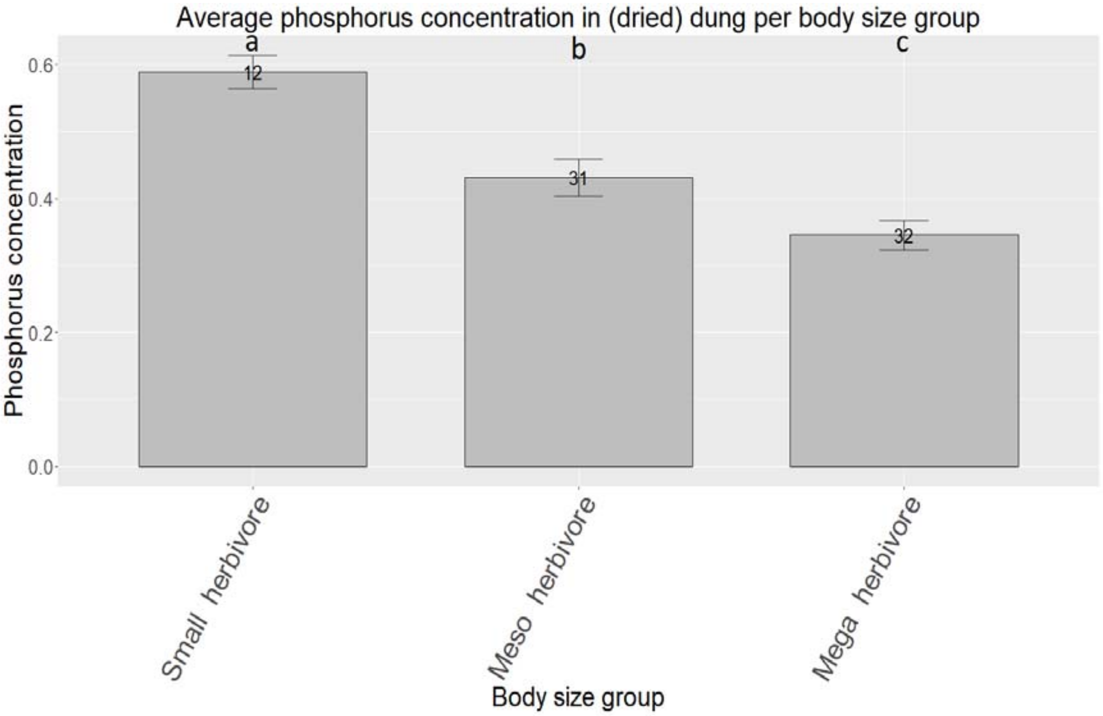


Figure 3.1.3.2: The average percentage of phosphorus plus standard error in (dried) herbivore dung (of species present in HiP) per body size category. Different letters indicate significant differences between body size categories (α=0.05). Numbers inside the barplots are representing the number of combined dung samples of each category.

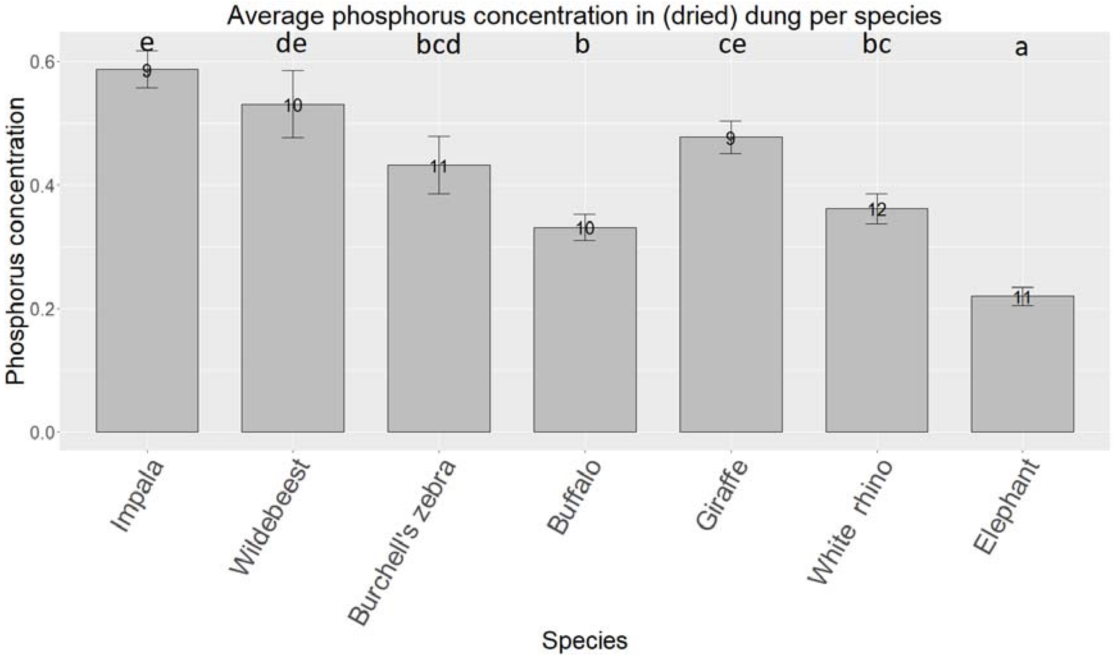


Figure 3.1.3.3: The average percentage of phosphorus plus standard error in (dried) herbivore dung of seven species present in HiP (species are ordered by body mass). Different letters indicate significant differences between species (α=0.05). Numbers inside the barplots are representing the number of combined dung samples of each species.

3.1.2 N:P ratio and the concentrations of nitrogen and phosphorus in dung in relation to feeding strategy

A significant difference was found between the feeding strategy of the herbivores and the average N:P ratio of their dung (one-way ANOVA: df= 2, F=13.146, p=<0.001). To determine where these differences lie a Tukey test was performed. The average N:P ratio in the dung of herbivore grazers differs significant from the average N:P ratio in the dung of both browsers and mixed feeders (Fig. 3.1.4.1).

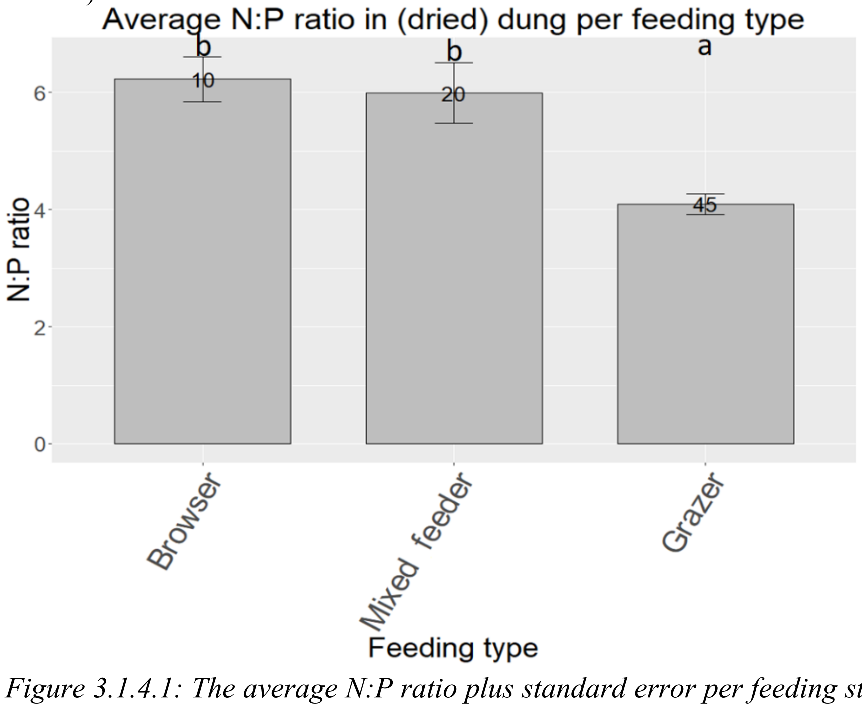


Figure 3.1.4.1: The average N:P ratio plus standard error per feeding strategy of nine species present in HiP. Different letters indicate significant differences between the different feeding types (α=0.05) Numbers inside the barplots are representing the number of combined dung samples of each category.

A significant difference was found between the feeding strategy of the herbivores and the average nitrogen concentration of their dung (one-way ANOVA: df= 2, F= 62.287, p=<0.001). The average nitrogen concentration of the dung of all feeding strategies differed significantly from each other (Fig. 3.1.4.2. left). Also, the average phosphorus concentration in dung of herbivores with different feeding strategies differed significantly (one-way ANOVA: df= 2, F= 3.2631, p= 0.044). A Tukey test was performed to show the differences. The average phosphorus concentration of the browser dung differed significantly from the average phosphorus concentration in mixed-feeder dung (Fig. 3.1.4.2. right).

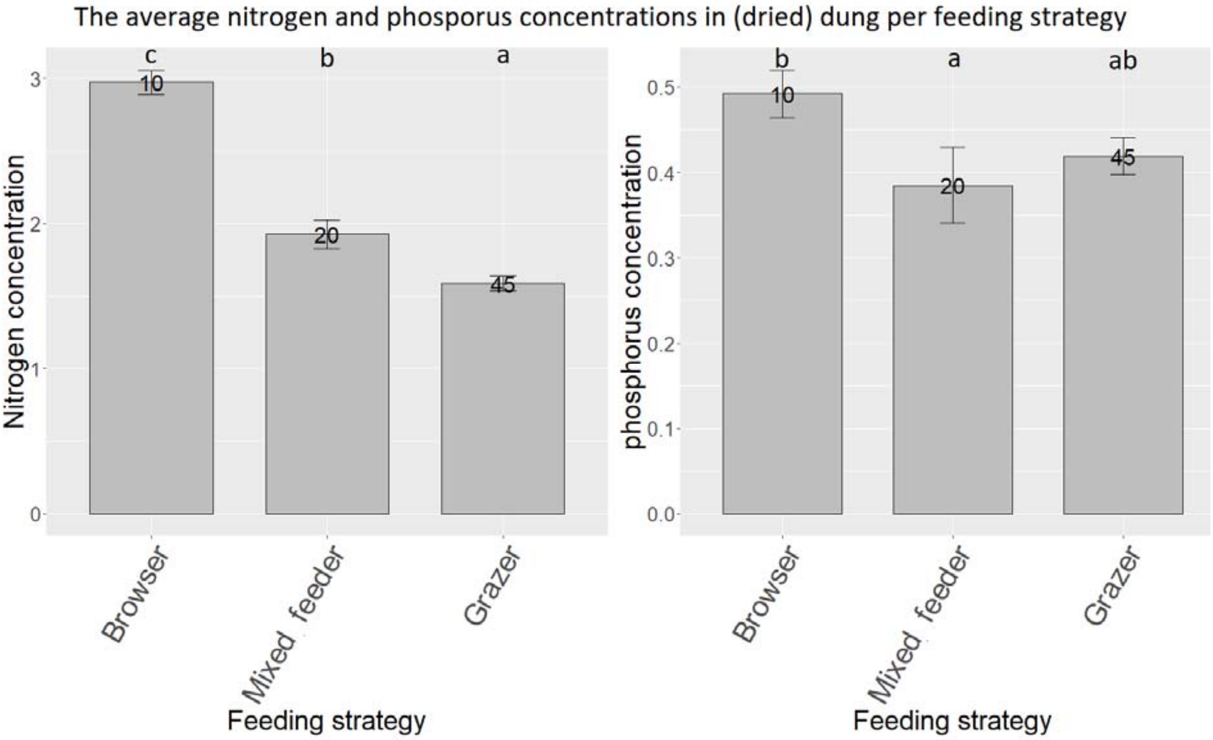


Figure 3.1.4.2: The average nitrogen (left) and phosphorus (right) concentrations plus standard errors in the dung of nine species present in HiP with different feeding strategies. Different letters indicate significant differences between the different feeding types (α=0.05). Numbers inside the barplots are representing the number of combined dung samples of each category.

3.3 N:P ratio and the concentrations of nitrogen and phosphorus in dung in relation to digestion type

No significant difference was found between ruminants and non-ruminants in the average N:P ratio's of their dung (one-way ANOVA: df=1, F= 0.0366, p= 0.8487) (Fig 3.1.5.1).

Found was that the concentration nitrogen in ruminant dung is significant higher than in non-ruminant dung (one-Way ANOVA: df=1, F= 40.862, p=<0.001) (Fig. 3.1.5.2. left). Also, the concentration phosphorus in ruminant dung is significant higher than in non-ruminant dung) (One-Way ANOVA: df=1, F= 18.136, p=<0.001) (Fig. 3.1.5.2. right).

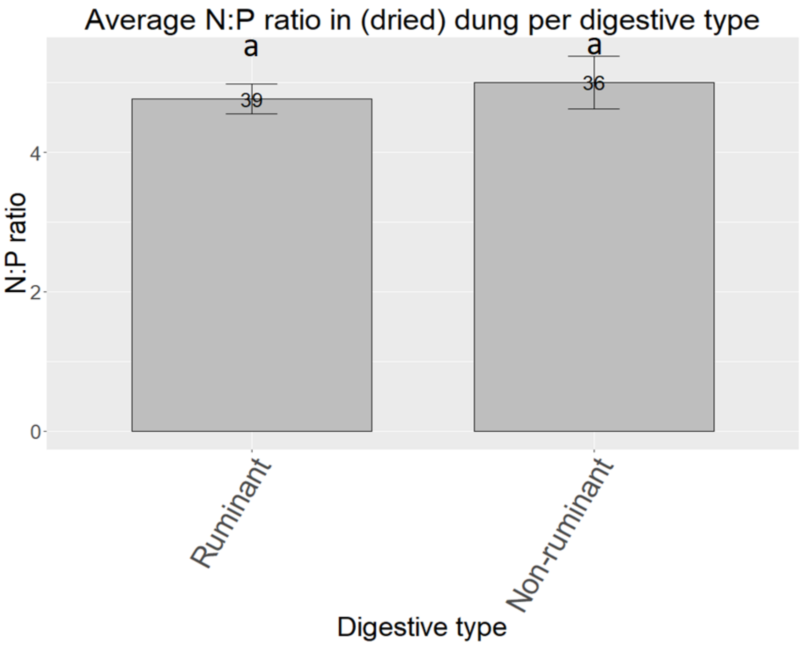


Figure 3.1.5.1: The average N:P ratio plus standard error in dung of nine species present in HiP with different digestive types. Different letters indicate significant differences between the different digestion types (α=0.05). Numbers inside the barplots are representing the sample size of each category.

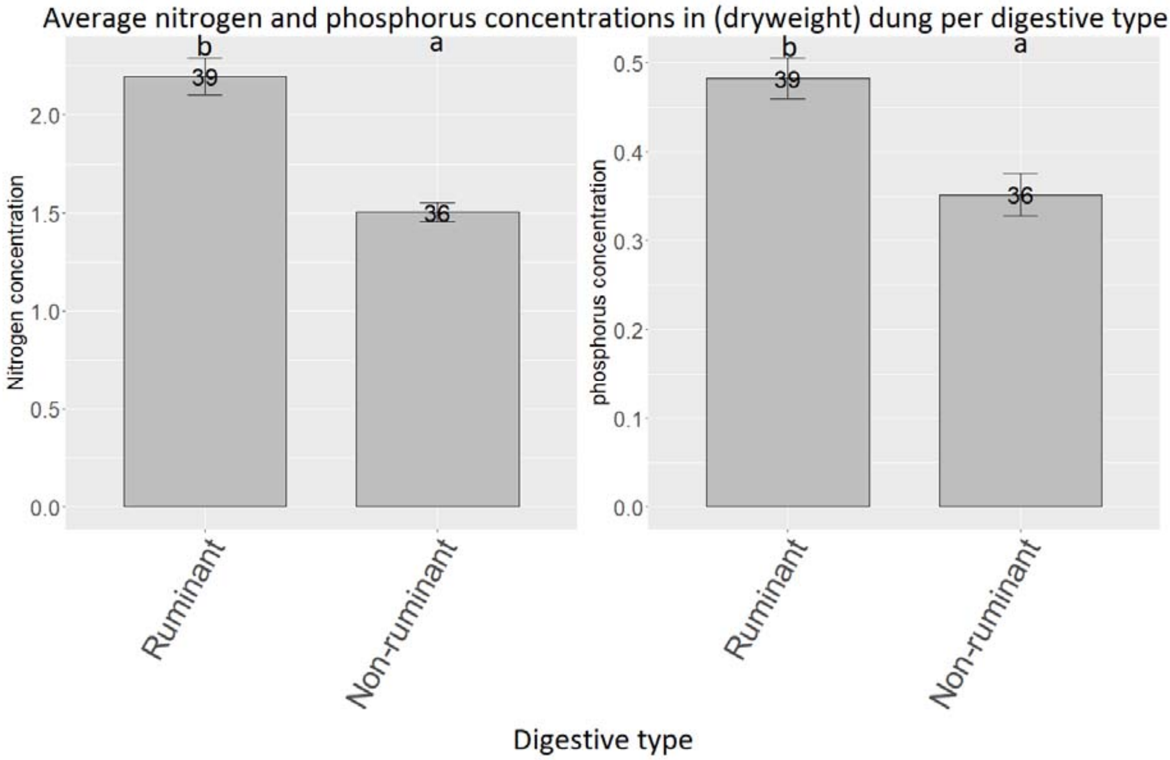


Figure 3.1.5.2: The average nitrogen (left) and phosphorus (right) concentration plus standard errors in the dung of nine species present in HiP with different digestive types. Different letters indicate significant differences between the different digestion types (α=0.05). Numbers inside the barplots are representing the number of combined dung samples per concerned category.

3.2 Results of the faecal nutrient distribution in HiP

3.2.1 The distribution of dryweight dung (kg), nitrogen (kg) and phosphorus (kg) over HiP in relation to body mass category

The map of the distribution of dung over HiP (Fig. 3.2.1.1.a) show that there are multiple hotspots with high amounts of dung, yet that these hotspots are distributed relatively evenly over the park. However, mesoherbivore dung is more concentrated in the south of the park (3.2.1.1.c) while megaherbivore dung is more concentrated in the north of the park (3.2.1.1.b). When these dung weights are converted to nitrogen content it appears that total nitrogen distribution, meso-herbivore distributed nitrogen and megaherbivore-distributed nitrogen match their respective dung distribution maps (Fig. 3.2.1.a and 3.2.1.2.a).

Figure 3.2.1.3.a show the distribution of phosphorus (kg) in dung over HiP. This map shows less hotspots and also the intensity of the hotspots is lower than in the previous maps (Fig. 3.2.1.1.a and 3.2.1.2.a). The distribution of posphorus by mesoherbivore dung shows the same patterns as the previous maps of the mesoherbivores (Fig. 3.2.1.1.b, 3.2.1.2.b and 3.2.1.3.b). However, the distribution of phosphorus by megaherbivore dung (Fig. 3.2.1.3.c) is more even and contributes less to the distribution of the total amount of phosphorus over HiP compaired to the distribution of dryweight dung and nitrogen in dung.

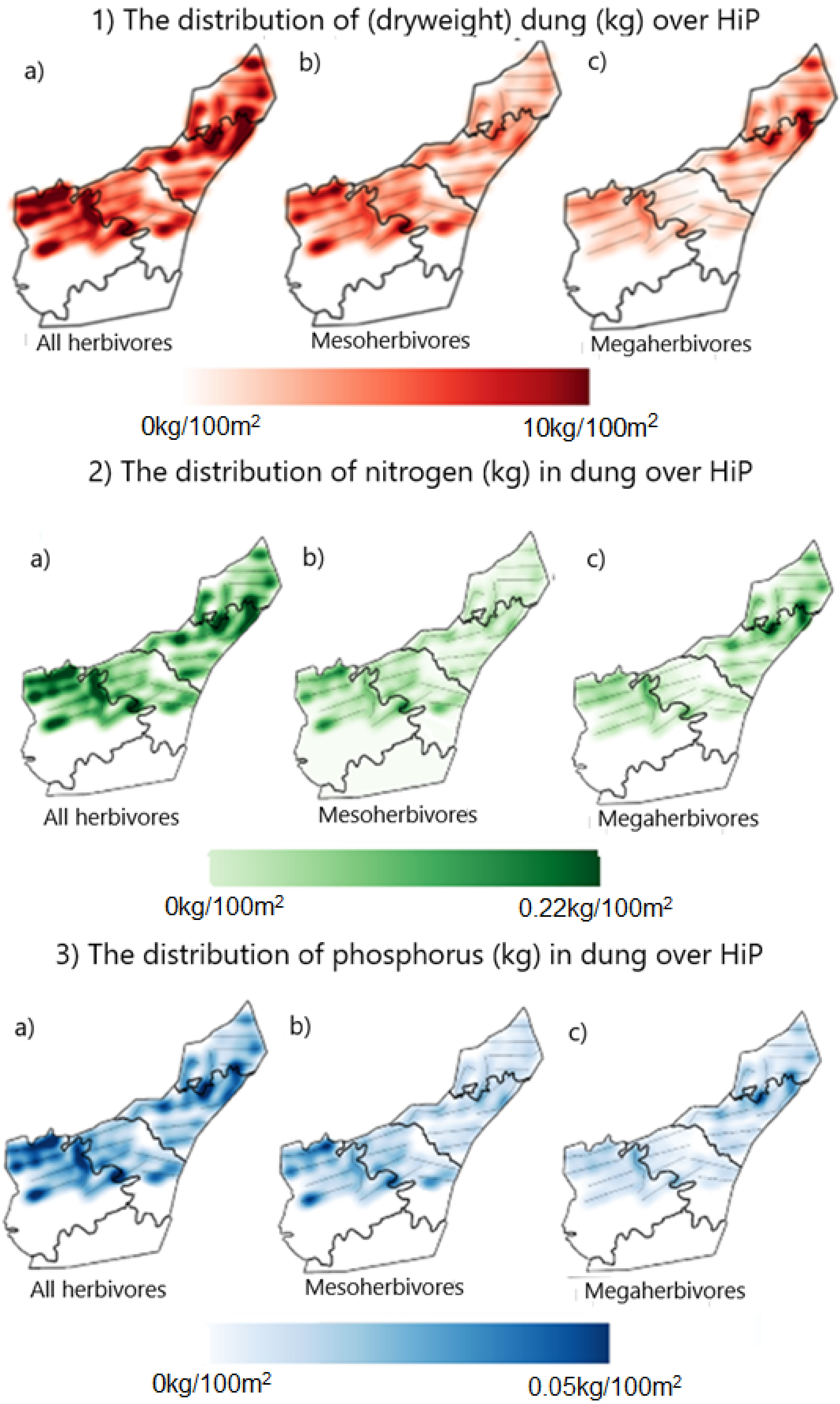


Figure 3.2.1: The distribution of dryweigt dung (1), nitrogen in dung (2) and phosphorus in dung (3) in Kg/100m^2 over HiP in relation to the body categories meso(b)- and megaherbivores(c)

3.2.2 The distribution of dryweight dung (kg), nitrogen (kg) and phosphorus (kg) over HiP in relation to feeding strategy

Figure 3.2.2 shows heatmaps of the distribution of dryweight dung, nitrogen and phosphorus over HiP in relation to feeding strategy of the various herbivores. The first column is representing the distribution of dryweight dung (Fig. 3.2.2.1.a), nitrogen (Fig. 3.2.2.2a) and phosphorus (Fig. 3.2.2.3.a) by all herbivores, and shows the same figures as the first column of Figure 3.2.1. Grazers contribute the most to the amount of dung distributed over the park (Fig. 3.2.2.1.d). Their dung is distributed relative evenly over the park, with a slightly greater concentration in the south-west and some hotspots all across the park. Mixed-feeders (Fig. 3.2.2.1.c) are contributing the second most to the distribution of dryweight dung over the park. These herbivores defecate the most in the northeast of HiP. Browsers (Fig. 3.2.2.1.b) are contributing the least to the distribution of dryweight dung over HiP. The dung of these herbivores is distributed evenly over the whole park, with the exeption of the north-east part where almost no browser dung was.

The distribution of nitrogen by herbivores with different feeding strategies (Fig. 3.2.2.2), is comparable with the distribution of dryweight dung over HiP (Fig. 3.2.2.1).

The distribution of phosphorus distributed by grazers and browsers (Fig 3.2.2.3.b and 3.2.2.3.d) is comparable with the distribution of dryweight dung and nitrogen by browsers and grazers (Fig 3.2.2.2.b and 3.2.2.2.d). The distribution of phosphorus distributed by mixed-feeders (Fig. 3.2.2.3.c) is more evenly and less concentrated in the north-east, compaired to the distribution of dryweight dung and nitrogen by mixed feeders (Fig. 3.2.2.1.c and 3.2.2.2.c).

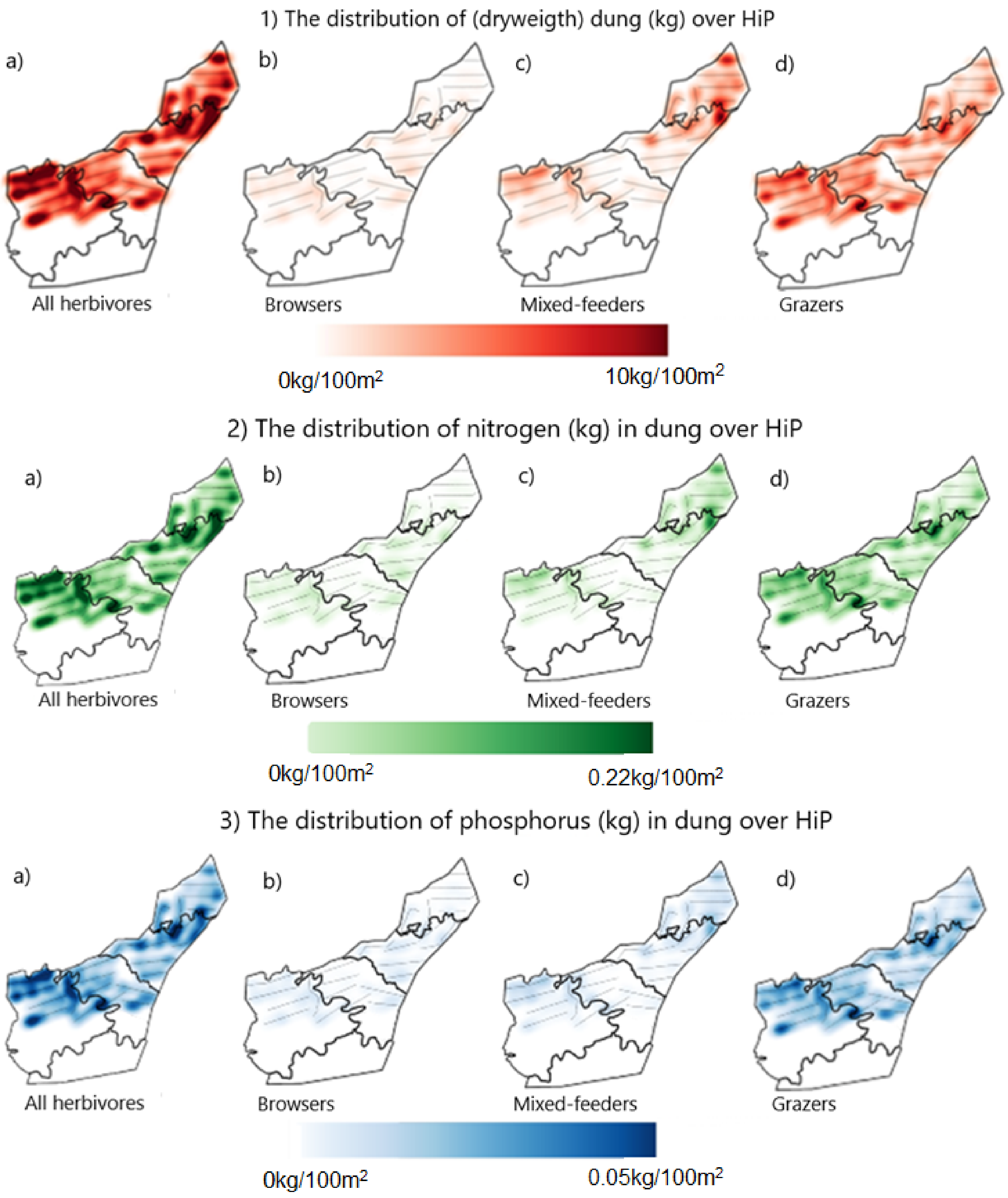


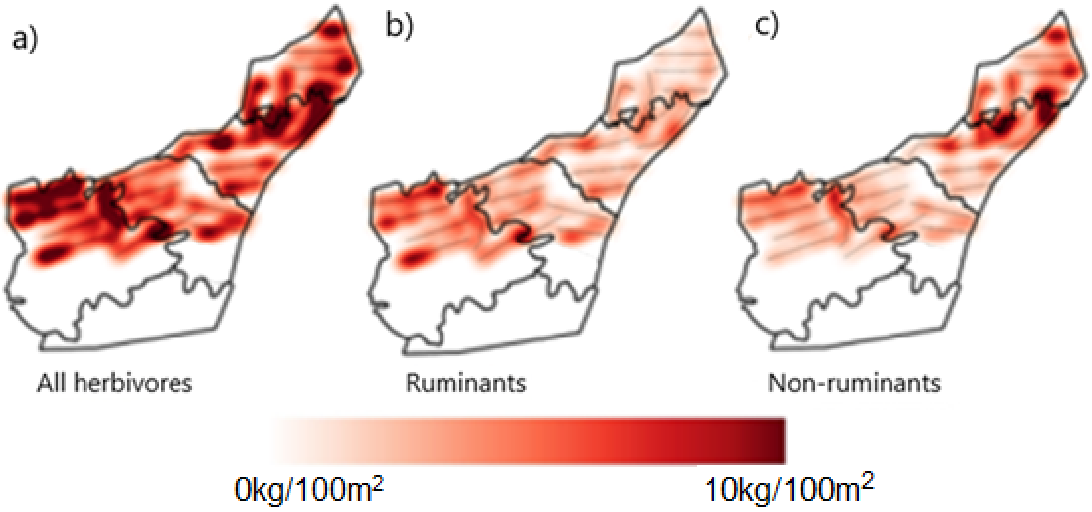
Figure 3.2.2: The distribution of dryweigt dung (1), nitrogen in dung (2) and phosphorus in dung (3) in in Kg/100m^2 over HiP in relation to the feeding strategies; browser(b), mixed-feeders(c) and grazers(d)

3.2.3 The distribution of dryweight dung (kg), nitrogen (kg) and phosphorus (kg) over HiP in relation to digestive type

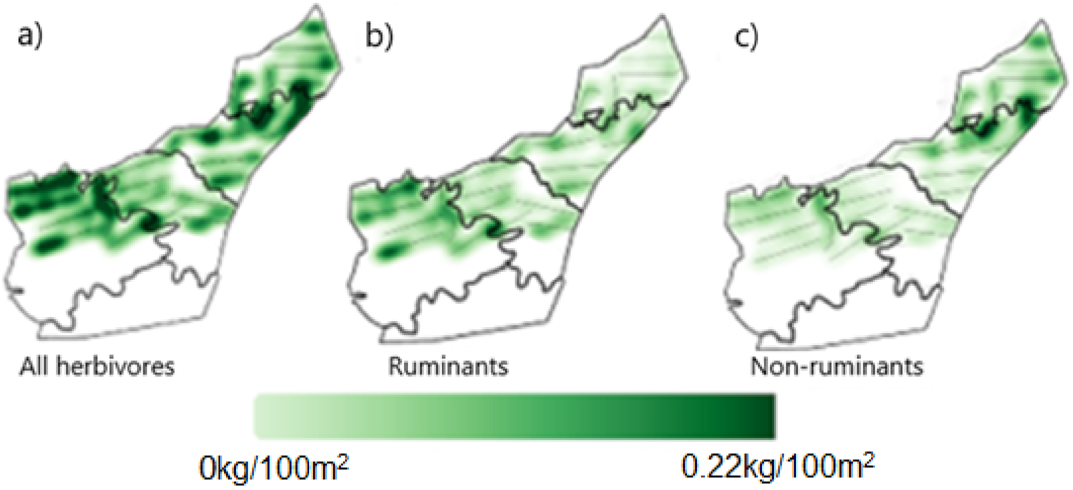
Figure 3.2.3 shows heatmaps of the distribution of dryweight dung (kg), nitrogen (kg) and phosphorus (kg) over HiP in relation to the digestive type of the various herbivores. Visible is that both ruminants and non-ruminants contributed roughly the same amount to the total amount of dung distibuted over the park (Fig. 3.2.3.1.b and Fig. 3.2.3.1.c). Ruminants deficated more in the south-western part and non-ruminants more in the north-eastern part of HiP. Nitrogen is showing the same distribution pattern as the distribution of the dryweight dung (Fig. 3.2.3.2). A small diviation is visible: the non-ruminants seem to contribute less to the distribution of nitrogen than to the distribution of dry weight dung (less rediness of the spots) (Fig. 3.2.3.2.c).

The distribution of phosphorus in ruminant dung (Fig 3.2.3.3.b) over the park is comperable to the distribution of ruminant dryweight dung and nitrogen their dung. The distribution of phosphorus in non-ruminant dung (Fig. 3.2.3.3.c) differs from the distribution of dryweight dung and nitrogen in non-ruminant dung. Visible is that there are less hotspots of phosphorus in non-ruminant dung and the hotspots are less intense (less rediness).

1) The distribution of (dryweight) dung over HiP



2)The distribution of nittogen(kg) over HiP



3)The distribution of phosphorus (kg) over HiP

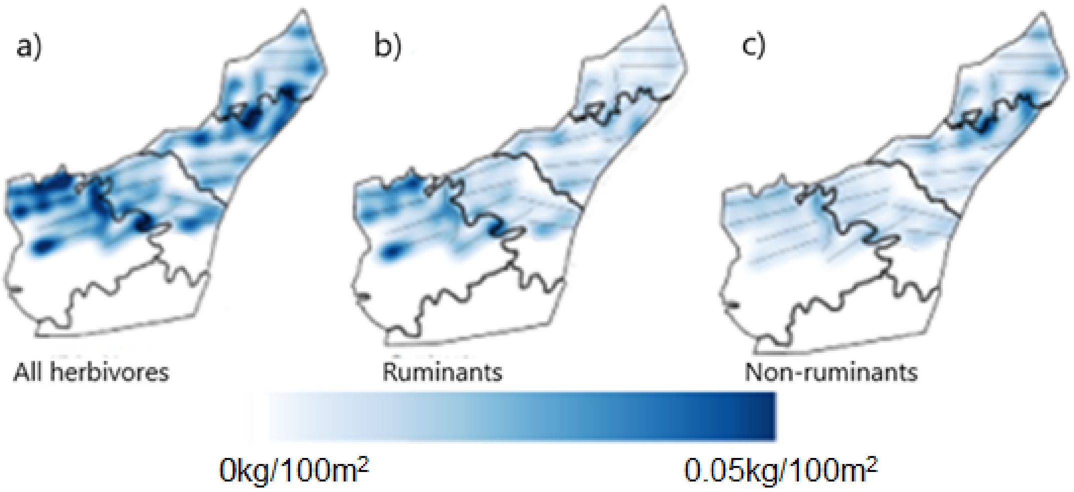


Figure 3.2.3: The distribution of dryweigt dung (1), nitrogen in dung (2) and phosphorus in dung (3) in Kg/100m^2 over HiP in relation to the digestive types; ruminant(b) and non-ruminant(c)

4. Discussion

During this study I focused on two aspects in which species differently influence nutrient dynamics: (1) the way species differ in terms of relative nutrient content in their dung and (2) the way species differ in the spatial distribution of dung and thus overall faecal nutrients over their habitat. I searched for stoichiometric differences in dung and differences in dung distribution patterns of different herbivore species who varied in body mass, feeding strategy and digestion type.

The results regarding the first aspect showed that the N:P ratio in herbivore dung increases with body mass. This is caused by a decrease in the amount of phosphorus by an increase in body mass. This is in line with the theory explained in the introduction, stating that larger herbivores need more phosphorus to produce their skeleton than smaller herbivores (Elser *et al.,* 1996; Prange *et al.,* 1979). This makes it possible that larger herbivores extract more phosphorus from their food than smaller herbivores, with the result that the larger herbivores excrete less phosphorus in their dung. No additional literature was found to support this. Also, I can confirm the hypothesis stating that browser and mixed feeder dung has a significant higher N:P ratio than grazer dung, caused by significant higher concentrations of nitrogen in the dung of browsers and mixed-feeders, as was also found by Sitters *et al.,* (2014). Lastly, the N:P ratio of ruminant and non-ruminant dung did not differ, but the nitrogen and phosphorus concentrations of ruminant dung were significant higher. This last part is not in line with the hypothesis stating that ruminant dung would contain a lower concentration of phosphorus and nitrogen compared to non-ruminant dung. An explanation for this counterintuitive result is that both body mass and feeding strategy of the animals are more important for the dung N:P ratio than digestive type. For example, two of the ruminant species were browsers (nyala and giraffe) and there were no non-ruminant browsers included in this study. Since browsers were showed to have a significant higher nitrogen concentration than non-grazers this could explain why the nitrogen concentration in ruminant dung is significant higher than in non-ruminant dung. Also, the two largest megaherbivores (white rhino and elephant) were non-ruminant. It was determined that the dung phosphorus concentration decreased with body mass, it could therefore be that the higher phosphorus concentration in ruminant dung is caused by the fact that the ruminant species had a smaller body mass range in this study. Sitters *et al.,* (2014) included the effects of ruminants versus non-ruminants in their study, they argued that dung stoichiometry could partly be explained by the different digestive types of species. However, in their study the effect of ruminants versus non-ruminants was never tested separately from differences in feeding strategy. They therefore never tested whether both feeding strategy and digestive type were influencing the results or that this was caused by the different feeding strategies. Also, the possible effects of body mass on dung stoichiometry was not included in the study of Sitters *et al.,* (2014). This means that it cannot be confirmed that digestive type had an influence on dung stoichiometry.

When the N:P ratio was shown per species it became visible that the N:P ratio of white rhino dung was significantly lower than the dung of the other megaherbivores (elephant and giraffe). White rhino dung therefore did not conform to the hypothesis stating that the N:P ratio in dung increases with body mass. However, the changes in dung phosphorus concentration from giraffe to white-rhino to elephant follows the prediction stating that the dung phosphorus concentration decreases with body mass. White rhino is the only grazer megaherbivore included in this study. It was found that grazer dung has a significant lower N:P ratio than browser and mixed-feeder dung. The lower N:P ratio in white-rhino dung can possibly be explained by the fact that they are grazers. The differences in the dung nutrient content of the three megaherbivore species imply that the consequences of the extinction of one megaherbivore species can deviate from the consequences of one of the other species going extinct. The possible differences between in consequences of the extinctions of the three megaherbivores species will be discussed later.

Regarding the second aspect (the way species differ in the spatial distribution of dung and thus overall faecal nutrients over their habitat) my study showed that megaherbivores are more concentrated in the north-east versus the south-west part of the park. This is not in line with my hypothesis stating that megaherbivores would be evenly distributed over HiP. In comparison, mesoherbivores are more concentrated in the south-west of the park, which is in line with the hypothesis. This last result was also obtained by Cromsigt *et al.,* (2009) which showed that some of the smaller herbivores (impala, wildebeest and warthog) are significantly clustered in the south and south-west of HiP. The same patterns are visible for the distribution of nitrogen in dung of mega and mesoherbivores. A possible reason for not getting the same results on megaherbivores as Cromsigt *et al.,* (2009) is that they only included white rhino as a megaherbivore in their study. Elephant and giraffe were excluded. It is likely that the white rhino is more evenly distributed over the park than the other mega herbivores as can be derived from the results showing the distribution of dung and nitrogen in dung by herbivores with different feeding strategies. These results show that dung and nitrogen in dung are more evenly distributed by grazers (like white rhino's) than by mixed feeders (like elephants). The same pattern is visible for the distribution of nitrogen in dung of mega and mesoherbivores. Also, found was that megaherbivores contribute less to the distribution of phosphorus than mesoherbivores. This is in line with the conclusion, that an increase in body mass leads to an increase in the N:P ratio of dung (caused by a decrease in the concentration of phosphorus). So even though megaherbivores contribute quite a lotto the distribution of both dung and nitrogen they are less contributing to the distribution of phosphorus.

Furthermore, I found that grazers contribute far more to the distribution of phosphorus than mixed-feeders and browsers. The most logical explanation for this is that most species included in this study are grazers (5/9). Even tough grazers also contribute more to the input of dung and nitrogen, especially compared to browsers, the difference in the input of phosphorus between mixed-feeders and grazers is larger, looking at the amount of phosphorus which is distributed. These differences can be explained by the significantly different N:P ratio's in herbivores with different feeding strategies, caused by a higher concentration of nitrogen in browser and mixed-feeder dung. It is therefore logical that the hotspots caused by nitrogen in browsers and mixed-feeders are more intense than the same hotspots showing the amount of phosphorus distributed by animals of these feeding strategies. Since the N:P ratio of grazers is relative low it is also logical that the distribution of nitrogen and phosphorus over the park by grazers are comparable. However, it is important to realize that mixed-feeders only consist of two species in this study, elephant and impala. This are two species from opposite ends of the body gradient. Elephants have the highest density of all species in HiP (Table 2.1.1). It could therefore be that they are too strongly influencing the data of mixed-feeders, and other patterns would be visible if more mixed-feeder species were included. Also, the browser feeding strategy only consists of two species, nyala and giraffe, by including more species in the analysis different patterns could emerge. I therefore recommend to repeat this study in different savanna systems with different species compositions.

Grazer and browser dung was more evenly distributed over the park compared to mixed-feeder dung which was more concentrated in the north-eastern part of HiP. This is in line with the findings of Cromsigt *et al.,* (2009) stating that grazers are more evenly distributed than non-grazers. However, studies showed that the home ranges of elephants are large (ranging from 40 km^2 in the Kruger National Park, to 1800 km^2 in Tsavo East National Park, Kenya (Shannon *et al.,* 2006) compared to the home range of white-rhino's (ranging from 0.7 km^2 to 15 km^2 in HiP (Owen-Smith & Smith, 1973)). This means that the dung counts of elephants are less reliable than the dung counts of the white-rhino, since the first has a tendency to migrate. This makes it possible that the elephants migrate to the northern part of the park in the dry season, but move south in the wet season. Such a migration pattern is not visible in this study, since dung was counted in the months August to November (dry season). To not miss migration patterns in the future, I recommend to not only count the dung at the end of the dry season but also at the end of the wet season.

The distribution of dung of ruminants versus non-ruminants showed that ruminants are more concentrated in the south and non-ruminants more in the north, which is comparable with the distribution of dung by, respectably, grazers and mixed-feeders. This is likely caused by the fact that the most abundant grazers are ruminant (with the exception of white rhino) namely: buffalo, wildebeest and zebra, and the most abundant non-ruminant is a mixed-feeder (elephant). When looking at the distribution of nitrogen and phosphorus in ruminant dung, it can be stated that the phosphorus and nitrogen distribution are directly linked. All spots with a high input of nitrogen also show a high input of phosphorus. This is not the case for the distribution of nitrogen and phosphorus by non-ruminants. The spots showing high nitrogen in the north-east part of HiP are less well reflected looking at the distribution of phosphorus in the north-east part of HiP. This is not in line with the conclusion that ruminant and non-ruminant dung do not differ in N:P ratios. This is likely caused by the wider body mass gradient in non-ruminants (ranging from warthog to elephant) compared to ruminants (ranging from impala to giraffe).

It is important to mention that the average weight of a dung pile for this study is based on a small sample size (3-5 measurements per species) (Unpublished data). It was estimated that on average white rhino middens contain 100 dung piles. This is a rough estimation which is based on personal experience of multiple experienced scientists (pers.com: Cromsigt, Druce, le Roux., 2018). No literature was found describing the average amount of dung piles per white rhino midden. Nevertheless, I do believe that the results obtained in this study are valid. This because an inaccurate estimate of the amount of dung, nitrogen and phosphorus do not influence the relative spatial differences showed.

My study showed that the distribution of nitrogen and phosphorus are depending on which species make up the herbivore community. The herbivore communities of African savannas will change in the future caused by, among others, climate change and poaching (Ripple *et al.,* 2015; Valeix *et al.,* 2008). These changes in climate and therefor herbivore communities can have multiple consequences for the savanna systems and the nutrient distribution, as will be explained in the next paragraphs. Both the impact on the extinction of megaherbivores on the nutrient distribution in HiP and the impact on other savanna systems will be discussed. Note that losing megaherbivores will not only have effect on the distribution of dung and redistribution of nitrogen and phosphorus via dung, other effects of losing the worlds megaherbivores are described in detail in the article of Ripple *et al.,* (2015).

The impact of the disappearance of megaherbivores on the distribution of nutrients in dung would be the highest in the north-east part of HiP where the megaherbivore dung was most abundant. However, it is incorrect to assume that losing the megaherbivores in HiP would not have consequences on the density of smaller herbivores. It is likely that the disappearance of megaherbivores would cause an increase in the numbers of smaller herbivores, since more food and habitat will become available for these smaller species. A study of Fritz et al., (2002) showed that the abundance of meso mixed feeders and browsers declined when mega herbivores were abundant. The researchers suggest that megaherbivores may compete with the meso mixed-feeder species for food or they may alter the vegetation communities unfavourably. Meaning that when the mega herbivores disappear from a savanna system an increase will likely be visible in the numbers of browsers and mixed-feeders.

When it is assumed that the total amount of dung input will be the same in HiP after losing the megaherbivores, because of an increase in the amount of dung produced by small herbivores, then the total input of phosphorus through herbivore dung will be higher, caused by the higher percentage of phosphorus in small herbivore dung. The amount of nitrogen distributed by herbivores will be comparable to the current situation. The effects will be mostly visible in the north-west part of HiP with the highest concentration of megaherbivores. However, the herbivore community has changed before in the past. A massive decline of large mammalian species emerged at the end of the Pleistocene in North and South America, northern Eurasia and Australia (Owen-Smith, 1989; Ripple *et al.,* 2015; Rule *et al.,* 2012). The heavily reduced number of megaherbivores caused the impact of these species on the vegetation to be removed. This most likely caused a reduction in habitat diversity which lead to less availability of food for smaller herbivores which participated in the extinction of a major number of the smaller herbivore species (Owen-Smith, 1989; Ripple *et al.,* 2015). This implies that the current loss of megaherbivores can also cause a decrease of smaller herbivores. However, Owen-Smith (1989) argues that African savanna systems could prove to be more resistant to smaller herbivore losses as a result of megaherbivore loss. This because the geomorphic factors and low and unregular rainfall enhances spatial heterogeneity and vegetation quality independently of large herbivore impact. This confirms hypothesis, stating that a decrease in the number of megaherbivores will lead to an increase in smaller herbivores.

I showed that the dung N:P ratio of browsers differs significant from that of grazers in HiP. Sitters *et al.,* (2017) came to the same conclusions in a nature reserve in Kenya. Meaning that there are similarities in dung stoichiometry between different parks. However, more research is necessary to determine in which way different climates, vegetation and water availability are influencing dung stoichiometry and the spatial distribution of dung. It would be interesting to study whether the same conclusions on the impact of body mass, feeding strategy and digestive type are also applicable to systems other than savanna's, like tropical rainforests or tundra's. Neither this or the study of Sitters *et al.,* (2017) address seasonal changes in dung nutrient content distribution. This can result in missing out on migration patterns of herbivores. Also, it is known that some species show dietary changes from season to season. For example: impala's are known to switch their feeding strategy from mainly grazing during the wet seasons to browsing during the wet season (du Toit., 2003). To strengthen the conclusions made regarding dung nutrient content and distribution I recommend to repeat the data collection in all seasons.

Researchers state that dung with a low N:P ratio is lower quality dung, since low N:P ratio's will create N-limited conditions, giving N_2 fixing tree seedlings an advantage over grasses (Lambers *et al.,* 2008; Sage *et kal.,* 1987; Sitters *et al.,* 2017; Vitousek *et al.,* 2002). Considering my data, which shows that the N:P ratio in dung increases with body mass and is significantly higher in browser dung, this would mean that megaherbivores and browsers (with a high N:P ratio) stimulate the growth of non-N_2 fixing grasses while smaller herbivores and grazers stimulate the growth of N_2 fixing trees. However, the absolute amounts of nitrogen and phosphorus increase on a spot with every dung pile regardless of the dung quality. These increases in both nutrients in the soil creates an advantageous situation for non-N_2 fixing grasses, since they usually use nitrogen and phosphorus more efficient than N_2 fixing seedlings, making it most likely that those become dominant over trees in areas with high dung input (Sitters *et al.,* 2017; Vitousek *et al.,* 2002). It can therefore be stated that an increase in the amount of dung increases the likelihood of an open vegetation structure with as dominant group C_4 grasses. Important to note is that the vegetation structure is not only depending on the nutrient dung content but also on the direct feeding patterns of the herbivores and on non-herbivore related influences as, for example: climate, weather, fire and soil (Govender *et al.,* 2006; Sankaran *et al.,* 2003; Sankaran *et al.,* 2005). HiP is currently plagued by woody encroachment all over the park (Wigley *et al.,* 2010). This increase is not only visible in HiP but emerges in parks, commercial ranching areas and communal farming area all over the African continent (Roques *et al.,* 2001; Sankaran *et al.,* 2008; Wigley *et al.,* 2010). This shift in vegetation is driven by chances in (human) alterations of fire-frequencies, grazing intensity, nitrogen deposition, and stated by multiple researches as main the factor: rising atmospheric CO_2 concentrations (Archer *et al.,* 1995; Buitenwerf *et al.,* 2012; Grover & Music, 1990; Wigley *et al.,* 2009; Wigley *et al.,* 2010). A possible way to deal with the increase of woody encroachment could be to increase the number of non-ruminants, browsers and mega herbivores to stimulate the redistribution of nitrogen as much as possible, favouring the conditions for C_4 grasses to grow. More research is necessary to test whether this would be a proper approach.

A different direct consequence of climate change is the change of rainfall patterns (Hulme *et al.,* 2001). Different rainfall patterns could favour different herbivore species. It is known that the total biomass of large savanna herbivores is positively related to mean annual rainfall (Coe *et al.,* 1976; East., 1984). Coe *et al.,* (1976) considered that this relationship is due to the effect of water availability on the herbivores food supply. A study Trenbeth (2011) has shown that Southern Africa has experience a decrease in precipitation in the period 1979-2008. Expected is that this trend will continue this century with the current rates of climate change (Trenbeth, 2011). With the previous knowledge this would mean that there will be a decrease in biomass of large savanna herbivores, making it even more likely that large and megaherbivores will be driven to extinction. Another study of Valeix *et al.,* (2008) argued that grazers should be more affected by changes in rainfall patterns than browsers and mixed-feeders, because the herbaceous layer responds more strongly to precipitation than those the woody cover of a savanna system. White rhino is a grazer which will be effected by a decrease in rainfall making it even more likely that this species will be driven to extinction. Browsers and mixed-feeders will be less effected (Valeix *et al.,* (2008) by a decrease in rainfall making it more likely that the herbivore community will be favoured towards browsers, mixed-feeders and ruminant grazers. This will cause a shift in the nutrient distribution by herbivores. The overall distribution of phosphorus by dung will probably be decreased and the distribution of nitrogen by dung will be increased.

Another way in which the species community of Africa are effected is by the replacements of wildlife by cattle. Before humans started to establish nature reserves, wildlife was not restricted by the areas they now live in (Burkey, 1995). These nature reserves create “islands” of isolated mammalian populations. The animals living in the reserves can only distribute nutrients within these reserves, which makes the current nutrient distribution by herbivores living in these reserves unnatural. Different patterns in nutrient distributions could become visible if the species were not restricted within the nature reserves. To study the effects of restricted areas on the nutrient distribution there should be looked for different nutrient patterns of nature reserves with variations in surface area. It is important to include big nature reserves like Kruger National Park to create a complete as possible overview. Also, it is important to study the effects of cattle on the distribution of nutrients and to compare this to the nutrient distribution by wildlife to get a better insight in the change in dung nutrient fluxes caused by the transition from wildlife to cattle.

Furthermore, it would be interesting to study how the interaction between the quality of an habitat and predation risk influence the distribution of different sized herbivore dung and herbivores dung belonging to species with feeding strategies. Large herbivores are less vulnerable to predation than small herbivores (Sinclair *et al.,* 2003), which makes it possible for them to use a wider range of habitats, because they can use habitats that are too risky for smaller species. It is interesting to test whether this is indeed visible when looking at the distribution of dung by different species.

5. Conclusion

Two aspects in which species differently influence nutrient dynamics were studied in this thesis: (1) the way species differ in terms of nitrogen and phosphorus concentrations in their dung and (2) the way species differ in distributing dung and thus overall nutrients. The concentration of nitrogen and phosphorus in herbivore dung depends on: body mass, feeding type and digestive strategy of the different herbivore species. Phosphorus concentrations in dung decrease with body mass, and is lower in browsers and non-ruminants. Nitrogen concentration in herbivore dung mainly depends on the feeding strategy and digestive type of the animal, being higher in non-ruminants, browsers and mixed feeders compared to grazers and ruminants.

The impact of herbivores on the distribution of nitrogen and phosphorus is found to be highly complex. Differences between species in body mass, feeding strategy and digestive type all contribute the concentrations of nitrogen and phosphorus in dung and therefore the distribution of these nutrients over HiP. The expected result of megaherbivore extinction in HiP, when looking at the nutrient distribution, will have the strongest effect on the total distribution of phosphorus through herbivore dung. It is likely that the density of small herbivores will increase in absence of megaherbivores, which will increase the input of phosphorus, caused by the higher concentration of phosphorus in small herbivore dung. This favours the growth of N_2 fixing trees, increasing the likelihood of (further) woody encroachment in HiP. This effect will be most visible in the north-west part of HiP were megaherbivores are most concentrated.

The consequences of megaherbivore extinctions in other nature reserves will depend on the current species composition and the identities of these species living in these areas. However, for a complete understanding of what will happen when megaherbivores are driven to extinction, studies which will combine the effects of herbivory with the nutrient distribution by herbivores are strongly recommended.

Overall, it can be stated that the dung nutrient distribution by mammalians with different characteristics is highly complex. The composition of the herbivore community is changing and to give a complete prediction of the effects of changes in the dung nutrient distribution it is important to conduct additional research.

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Popular science summary

African savanna megaherbivores (herbivores with a body mass of over 1000kg) are treated by extinction caused by, among others, climate change and poaching for body parts (ivory and horns). African herbivores are known to have large impacts on savanna systems and since there is a high change of losing this group of animals it is important to predict to consequences of their extinction on the habitats they live in.

Herbivore dung contains nutrients like nitrogen and phosphorus, which are relatively rare in savanna systems. Different plant species need different concentrations of nitrogen and phosphorus in the soil to grow. By defecating in a certain spot herbivores can influence soil nitrogen and phosphorus concentrations and can therefore change the availability of these nutrients for different plant species. This can change the structure and/or the composition of the plant species in an area.

The main objective of this thesis was to determine how body mass, feeding and digestive type (ruminant, non-ruminant) of various savanna herbivores influences the distribution of dung, nitrogen and phosphorus. I did this by searching for differences in the concentrations and ratios of nitrogen versus phosphorus in the dung of various herbivore species. Also, I searched in which way different species differ in the way they distribute dung (and therefor nitrogen and phosphorus) over an area.

During January to April 2018, I collected dung from all abundant herbivore species in Hluhluwe-Imfolozi Park (HiP). The nitrogen and phosphorus concentration in the dung samples were determined. I found that the nitrogen to phosphorus (N:P) ratio in dung increases with body mass, this is caused by lower dung phosphorus concentrations in larger herbivores. The N:P ratio in browser and mixed-feeder dung is higher than the N:P ratio in grazer dung, this is caused by higher concentrations of nitrogen in browser dung. Furthermore, I showed that ruminant dung contains a higher dung nitrogen and phosphorus concentration than non-ruminant dung.

To determine how dung (and therefore nitrogen and phosphorus) are distributed over HiP, I combined my data (dung phosphorus and nitrogen concentrations) with data from a long term study, in which herbivore dung was counted along 24 line transects. After combining these two datasets I can conclude that the impact of different herbivore species on the distribution of dung (and thus nitrogen and phosphorus) is highly complex. Differences in body mass, feeding strategy and digestive type all contribute to the way in which dung, phosphorus and nitrogen in dung are distributed over HiP.

The expected result of the extinction of megaherbivores in HiP, will be a decrease in the amount of phosphorus distributed through herbivore dung. The nitrogen distribution through herbivore dung is expected to show minimal change. The overall effect of megaherbivore extinction will differ depending on the characteristics (feeding strategy and digestive type) of the megaherbivores living in a certain area.

Possible consequences of megaherbivore extinctions for nature reserves are changes in the number of smaller herbivores and vegetation structures.

Appendix 1

Table A.1.1: Number of samples per combined sample per species. The date of when the first and the last sample were collected per combined sample are also visualized.

Species	Combined sample	Location	Number of samples	Date first sample	Date last sample
Buffalo	1BH	Hluhluwe	4	1/30/2018	2/2/2018
	2BH	Hluhluwe	3	3/15/2018	3/15/2018
	3BH	Hluhluwe	3	2/3/2018	2/3/2018
	4BH	Hluhluwe	5	1/30/2018	2/1/2018
	5BH	Hluhluwe	3	2/1/2018	2/1/2018
	6BH	Hluhluwe	2	3/13/2018	3/13/2018
	7BH	Hluhluwe	2	2/2/2018	2/2/2018
	1BI	Imfolozi	2	3/19/2018	3/21/2018
	2BI	Imfolozi	2	3/19/2018	3/21/2018
	3BI	Imfolozi	1	3/21/2018	3/21/2018
Elephant	1EH	Hluhluwe	6	2/2/2018	2/2/2018
	2EH	Hluhluwe	6	3/2/2018	3/2/2018
	3EH	Hluhluwe	3	2/2/2018	2/9/2018
	4EH	Hluhluwe	4	2/9/2018	2/9/2018
	5EH	Hluhluwe	1	3/1/2018	3/1/2018
	6EH	Hluhluwe	3	3/6/2018	3/6/2018
	7EH	Hluhluwe	1	2/10/2018	2/10/2018
	1EI	Imfolozi	1	2/1/2018	2/1/2018
	2EI	Imfolozi	2	3/19/2018	3/19/2018
	3EI	Imfolozi	3	3/19/2018	3/21/2018
	4EI	Imfolozi	1	3/21/2018	3/21/2018
Giraffe	1GH	Hluhluwe	2	1/29/2018	1/29/2018
	2GH	Hluhluwe	2	2/16/2018	2/16/2018
	3GH	Hluhluwe	5	2/16/2018	2/16/2018
	4GH	Hluhluwe	2	2/23/2018	2/23/2018
	5GH	Hluhluwe	2	3/15/2018	3/15/2018
	6GH	Hluhluwe	2	4/4/2018	4/4/2018
	7GH	Hluhluwe	1	2/26/2018	2/26/2018
	1GI	Imfolozi	1	3/21/2018	3/21/2018
	2GI	Imfolozi	1	3/28/2018	3/28/2018
Impala	1IH	Hluhluwe	3	1/29/2018	1/29/2018
	2IH	Hluhluwe	1	2/2/2018	2/2/2018
	3IH	Hluhluwe	6	2/16/2018	2/16/2018
	4IH	Hluhluwe	4	3/2/2018	3/2/2018
	5IH	Hluhluwe	4	4/5/2018	4/5/2018
	6IH	Hluhluwe	5	4/5/2018	4/5/2018
	1II	Imfolozi	8	2/28/2018	2/28/2018
	2II	Imfolozi	7	2/28/2018	2/28/2018
	3II	Imfolozi	2	3/21/2018	3/21/2018
Nyala	1NH	Hluhluwe	5	3/6/2018	3/6/2018

Warthog	1WAH	Hluhluwe	3	3/2/2018	3/2/2018
	1WAI	Imfolozi	3	2/28/2018	2/28/2018
White rhino	1WRH	Hluhluwe	2	1/29/2018	1/29/2018
	2WRH	Hluhluwe	5	1/31/2018	1/31/2018
	3WRH	Hluhluwe	4	2/2/2018	2/2/2018
	4WRH	Hluhluwe	2	3/1/2018	3/1/2018
	5WRH	Hluhluwe	3	3/2/2018	3/2/2018
	6WRH	Hluhluwe	5	3/13/2018	3/13/2018
	7WRH	Hluhluwe	3	4/4/2018	4/4/2018
	1WRI	Imfolozi	2	3/28/2018	3/28/2018
	2WRI	Imfolozi	5	2/24/2018	2/24/2018
	3WRI	Imfolozi	3	3/19/2018	3/19/2018
	4WRI	Imfolozi	2	3/21/2018	3/21/2018
	5WRI	Imfolozi	2	3/28/2018	3/28/2018
Wildebeest	1WIH	Hluhluwe	5	1/29/2018	1/29/2018
	2WIH	Hluhluwe	4	1/29/2018	2/1/2018
	3WIH	Hluhluwe	8	2/16/2018	2/16/2018
	4WIH	Hluhluwe	4	3/2/2018	3/2/2018
	5WIH	Hluhluwe	3	4/4/2018	4/4/2018
	6WIH	Hluhluwe	3	4/4/2018	4/4/2018
	1WII	Imfolozi	3	2/28/2018	2/28/2018
	2WII	Imfolozi	7	2/28/2018	2/28/2018
	3WII	Imfolozi	4	3/19/2018	3/21/2018
	4WII	Imfolozi	3	3/28/2018	3/28/2018
Zebra	1ZH	Hluhluwe	1	2/14/2018	2/14/2018
	2ZH	Hluhluwe	1	2/14/2018	2/14/2018
	3ZH	Hluhluwe	4	2/16/2018	2/16/2018
	4ZH	Hluhluwe	1	4/4/2018	4/4/2018
	5ZH	Hluhluwe	3	2/23/2018	2/23/2018
	6ZH	Hluhluwe	7	3/2/2018	3/2/2018
	1ZI	Imfolozi	3	3/19/2018	3/19/2018
	2ZI	Imfolozi	2	3/21/2018	3/21/2018
	3ZI	Imfolozi	3	3/28/2018	3/28/2018
	4ZI	Imfolozi	1	3/28/2018	3/28/2018

Appendix 2

Table A.2.1: The average wet weight (g), average water content (unit), average dry weight (g), average percentage of nitrogen, average percentage of phosphorus and the average N:P ratio of a dung pile per species

Species	**Average wet weight of a dung pile**	**Average water content**	**Average dry weight of a dung pile**	**Average percentage of nitrogen**	**Average percentage of phosphorus**	**Average N:P ratio**
Buffalo	593.66	79.41	122.21	0.016	0.0033	5.07
Elephant	931.82	74.41	238.42	0.016	0.0022	7.58
Giraffe	293.77	59.02	120.38	0.030	0.0048	6.45
Impala	45.70	63.81	16.54	0.023	0.0059	4.05
Nyala	45.70	66.56	15.28	0.027	0.0063	4.21
Warthog	147.44	69.95	44.31	0.018	0.0058	3.24
White-rhino	853.97	80.40	167.39	0.016	0.0036	4.70
Wildebeest	356.65	73.09	95.98	0.018	0.0053	3.67
Zebra	704.74	77.83	164.33	0.012	0.0043	3.09

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