(Wisenten, 2010)

Herbivore effects on nutrient spatial distribution in a coastal dune ecosystem in The Netherlands

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EXECUTIVE SUMMARY

Herbivores can alter ecosystems in many ways. One way is through the redistribution of nutrients. Nutrient redistribution is caused by herbivores grazing in one area and defecating in another or frequenting some sites more than others. This research looks at how European bison (*Bison bonasus*), Konik (*Equus caballus*), Roe deer (*Capreolus capreolus*), Fallow deer (*Dama dama*) and European rabbit (*Oryctolagus cuniculus*) affect nutrient distribution in the Kraansvlak. It was hypothesised that all of the herbivores faeces will be distributed non-randomly and that the European bison and the Konik will have larger amounts of nitrogen and carbon in their faeces but not higher concentrations.

The location of European bison, Roe deer and Fallow deer, Konik and European rabbit faeces in 18 1-hectare quadrats was mapped and the total amount of faeces in each quadrat weighed. A subsample of the faeces from each species was taken from each dung patch so that the nitrogen, carbon and phosphorus contents could be compared.

A one-way ANOVA was the used to show if there was any variation between the nutrient contents of the four herbivores' dung. It was found that there was a variation between the nitrogen contents in the faeces of the four species and that there was no variation in the amount of carbon between the four species' dung. A Bonferroni correction showed that the percentage of nitrogen was different between bison & deer fresh dung, and Konik & deer fresh dung.

Maps displaying the location and nutrient contents in each of the herbivores' faeces were produced using the software tool ArcMap in ArcGIS. They showed that the faeces of bison, Konik and deer was densely distributed around the lake whereas rabbit faeces was distributed sparsely in the northern and southern ends of the park. Overall, bison and Konik contributed the highest amounts of nitrogen and carbon to the Kraansvlak even though their faeces had a lower concentration of nitrogen and carbon compared to deer and rabbit faeces. The significance of these results is that the herbivores influence the spatial distribution of nutrients by defecating in certain areas more than others which may alter the nutrient balance if they graze in different areas.

Contents

Introduction

The dunes of the Zuid-Kennemerland National Park in the Netherlands were once species-rich due to the long history of grazing by herbivores (Grootjans et al., 2013; Plassmann, Edwards-Jones et al., 2009). Overtime there has been a decline of herbivores and in their absence the area's biodiversity has become threatened by the encroachment of tall grass, shrubs and trees (Cromsigt et al., 2007; Kooijman & van der Meulen, 1996; Kooijman, A. M., & Smit, A, 2001). The European rabbit (*Oryctolagus cuniculus*) was once abundant in the area but the population reduced by nearly 90% in the twentieth century due to the diseases myxomatosis and viral hemorrhagic disease (Cromsigt et al., 2007; Grootjans et al., 2013). It is also thought that the European bison (*Bison bonasus*) once roamed the dunes but became extinct due to hunting and habitat loss (Cromsigt et al., 2007).

In 2007, the European bison were introduced into the Kraansvlak area within in the Kennermerland National Park to help return the ecosystem to its previous state. As well as helping to rehabilitate the coastal dunes in the Kraansvlak their introduction to the area also helped increase their population size. The European bison have been declared as a vulnerable species by the International Union for Conservation of Nature (IUCN, 2008). There are only around 2800 bison left in the wild (Cromsigt et al , 2007). This is why it is important to conserve the European bison as a wild species and to establish populations in protected areas such as the Kraansvlak (Deinet et al., 2013; Kuemmerle, 2010).

When species are introduced to an area they need to be closely monitored.
It is still not known what effects they will have on the biodiversity of the area. Fauna can increase plant diversity through grazing, help to disperse seeds or contribute to the heterogeneous distribution of nutrients in soil through their excreta (Willott et al., 2000). Grazing animals have been known to significantly influence the long-term nutrient balance through irregular fecal and urine deposition patterns vs nutrient consumption (Augustine et al., 2003). This can then lead to changes in plant composition. Introducing species to an enclosed area or an area they have not occupied for a long period of time can cause their population to grow too high and they can start to adversely affect the ecosystem. In grass heaths and coastal sand dunes, rabbits have been shown to change the soil profile (Willot et al., 2000). This can result in an initial increase in diversity (Moss & Hassall, 2006). Although,

prolonged disturbance to the soil profile can lead to a reduction in diversity (Moss & Hassall, 2006). In dune grasslands in Belgium the impacts of grazing by large herbivores depends on the size of the population, area and on soil acidity. Although grazing can be an appropriate management tool to maintain or even increase plant biodiversity, it may negatively affect plant species' richness, where soil resources limit plant biomass production (Tahmasebi et al., 2008).

Problem definition and aim

One of the ways plants receive the nutrients essential for their growth is through the nutrients returned to the soil through faeces (Whitehead, 2000). Nutrients from faeces are also released more quickly than nutrients from plant litter (Sitters et al., 2014). Herbivores can consequently contribute to plant species richness by accelerating nutrient turnover (Knapp et al., 1999). In the grasslands of Yellowstone National Park (USA), ungulate dung and urine comprise a major input of nitrogen to the ecosystem, representing an amount equivalent to 27% of the nitrogen mineralised annually (Augustine & Frank, 2001).

Nutrient cycling may also be decreased depending on how herbivores use an area (Bakker et al., 2004). Cattle can decrease nutrient cycling due to nitrogen being distributed unevenly via their faeces (Ford et al., 2012). In a study done on the effects of the European rabbit on soil fertility, concentrations of nutrients in soils from rabbit latrines were significantly greater relative to controls in each community (Willott et al., 2000). Horses and rabbits can change the spatial patterns of nutrients because they feed over a wide area but defecate in a small area (Schultz et al., 2006). The differences in feeding and defecation behaviour may cause a reduction in nutrients in the wider grazing range but a greater enrichment of small areas within it (Schultz et al., 2006).

The purpose of this research is to show what the spatial pattern of European bison, Konik horse (*Equus caballus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and European rabbit faeces is in the Kraansvlak and to compare the nutrient contents of their faeces.

Research questions:

- How do the nutrient concentrations in the faeces of European bison, roe & fallow deer, European rabbit and Konik compare?
- What is the distribution pattern of the faeces of the most important herbivores (European bison, roe & fallow deer, European rabbit and Konik)?
- What are the nutrient contents of faeces per hectare and what is the distribution of these nutrients over the area?

It could be expected that the herbivore that has the highest percentage of nutrients in its faeces will have the most influence on the ecosystem by increasing the productivity of certain plants. An increase in the input of nutrients from dung may be more favourable for certain species of vegetation and increase their primary production (Heil & Diemont, 1983). If one species of vegetation requires greater amounts of nutrients than another, then it will be more prevalent in areas with higher nutrients. For example, fertiliser experiments done on the growth of calluna vulgaris in the Netherlands found that an increase in nitrogen caused Calluna vulgaris (a heathland species) to be replaced by Festuca ovina (a grassland species) as the dominant species (Heil & Diemont, 1983). The herbivore that has the greatest influence on nutrient cycling and species composition will also depend on the amount of dung deposited into the area by each herbivore and the spatial distribution of the dung. It is hypothesised that deer and rabbit will have higher concentrations of nutrients but European bison and Koniks will contribute larger amounts of nitrogen per hectare.

The spatial distribution of faeces in the Kraansvlak will also have an influence on the ecosystem. If there is greater density of faeces in one location then there will be more nutrients deposited into that area even if the dung individually has on average low nutrient concentrations. Large herbivores can redistribute substantial amounts of nutrients (Van der Waal et al., 2011). For example, if the bison or Konik have not been defecating in the same areas that they were grazing in, the nutrients will not be returned to the area that they were removed from which will result in a depletion of nutrients in that area (Van der Waal et al., 2011). A depletion of nutrients will have an effect on the composition of the ecosystem by altering which species grow there (Sitters et al., 2014). If the changes to the vegetation structure is large it could affect the functioning of the ecosystem (Ihse, 2007; Isbell & Wilsey, 2011).

The density of the herbivores and the size of Kraansvlak will both affect the spatial distribution of faeces (Lamoot et al., 2004). Deer, cattle, rabbits, and horses have all been shown to use latrines (Edwards & Hollis,1982; Willot, 2000; Lamoot et al., 2004). In a Dutch heathland the excreta of cattle was found to be deposited over only 2.5% of their grazing range and that 75% of the heathland was excreta free after it had been grazed for 10 years (Schultz et al., 2006). It is expected then that each of the herbivores will defecate in a non-random spatial distribution.

Methods

Study area

The study site was an area closed off to the public called the Kraansvlak. The Kraansvlak is located in the National Park Zuid-Kennemerland in the Netherlands. The site was originally around 230 hectares then in 2012 it was expanded to 280 hectares (Kemp, 2011). Recently another area was added making it approximately 300 hectares (Figure 1). The Kraansvlak is comprised of a variety of habitats including coniferous and deciduous forests, areas of large open sandy dunes, scrub and grassland (Cromsigt et al., 2007). The area is separated from the rest of the national park by an electric fence (Kemp, 2011). A water company called PWN and an environmental agency called ARK Nature manage the National Park.

Koniks were introduced to the area in 2009. In 2012 there was a herd of 14. There is currently a herd of 18 bison. Other herbivores that can be found in another fenced off part of the national park include highland cattle, galloway cattle, sheep, shetland ponies and goats (Cromsigt et al , 2007).

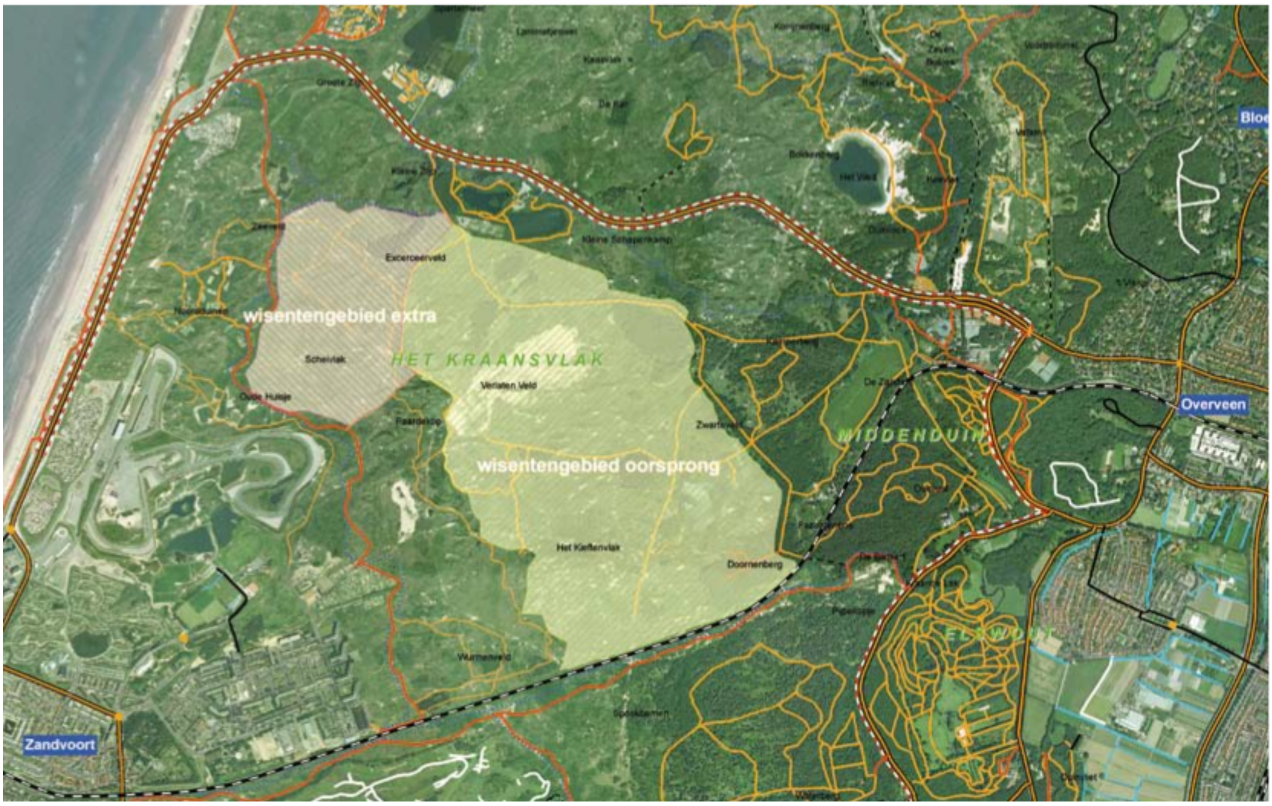


Figure 1. Map of the Kraansvlak (Cromsigt, Kemp, Spier & Rijn, 2007).

Data collection in the field

The research was conducted in 2014 in April and May which is spring in The Netherlands. The weather was mostly sunny with a few days of light showers. The mean temperature for April was 10.3 Celsius and the mean precipitation was 52 millimetres. The mean temperature for May was 14.8 Celsius and the mean precipitation was 59 milimetres. Information was collected in the field using 18, 1 hectare quadrats. To ensure that sampling adequately represented the area, quadrats were evenly distributed over the area. To do this, a grid with cells of 1 hectare in size was placed over a digital map of the area and numbers were added to every second grid cell (Figure 2). The GPS coordinates of the centre of each of the quadrats (grid cells) to be sampled were recorded so that they could be located in the field. To reduce bias, the order the quadrats were sampled in was random. The order was based on which quadrat's number appeared first in a list of numbers generated by a random number generator in the software tool Microsoft Excel.

For sampling efficiency, the area was divided into four equally sized areas which were called A, B, C and D (Figure 2). Instead of walking randomly, which may be from one side of the park to another, quadrats in area A were sampled first then quadrats in area B, then C and D. For nutrient analysis a subsample of the faeces of each of the species (deer, bison, Konik horse and rabbits) was collected from each of the full bags of dung that had been collected for weighing. Initially 100 quadrats were going to be sampled with samples of faeces taken from every third quadrat. Although, after the first few days in the field it was realised that it would take longer than estimated to sample each quadrate so it was decided to aim for 20 quadrats and to take samples of faeces from every quadrate. In the end it was possible to sample 18 quadrats with samples of dung taken in 15 of the quadrats (Figure 2). Quadrats that samples of faeces were not collected in were quadrats 4, 8 and 69 since they were visited on the first few days in the field and were apart of the original sampling design.

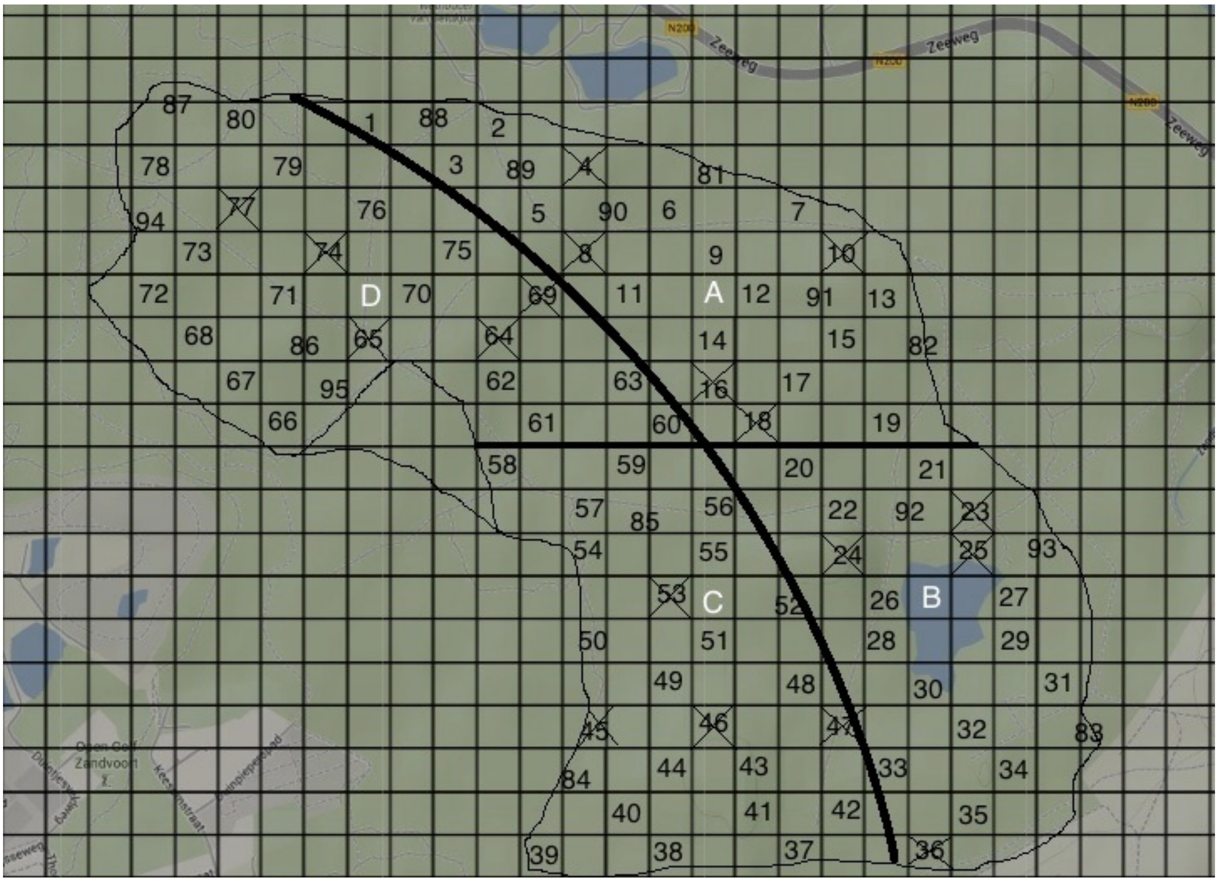


Figure 2. Map of the Kraansvlak used to locate quadrats for field work with the location of the 18 sampled quadrats. The map has been divided into four areas called A, B, C and D and has a grid with cells of 1 hectare placed over the top.

Identifying dung

Bison are the largest herbivores in the area so their dung is the largest. Rabbit pellets are around 6 millimetres long and consist of finely chewed fragments of grasses since rabbits do not ruminate (Britannica, 2014; Rueda et al., 2008). The pellets of deer are black and shiny with no obvious contents since they ruminate (Howie, 2001). The pellets are cylindrically shaped and are usually separated but in summer can be a single amorphous lump (Howie, 2001). Konik horses are the second largest herbivore in the park. Their dung is larger than deer dung but smaller than bison dung and clumped together with visible plant material.

The rate faeces breaks down at is dependent on the weather, the number of invertebrates present, and its location in the landscape (Williams & Warren, 2004). The time it takes cattle dung pat to decompose can range from a few weeks to several years and deer faeces degrade within three to eight weeks (Gillet et al., 2010; Williams & Haynes, 1995). As faeces is broken down, nutrients are lost. Rain can decrease the phosphorous concentration of faeces from leaching (Stapelberg et al., 2008).

To determine if there were any changes in the amount of nutrients in the faeces over time, the age of the sampled faeces was recorded. A scheme was used to help determine the age of bison dung (Figure 3). The age classes for Konik, deer and rabbit faeces was fresh and old and was found by looking at its colour and appearance. Bison dung had three age classes: fresh (less than 1 week old), intermediate (1 to 3 weeks old) and old (older than 3 weeks). These age classes were determined with the help of a ranger from PWN. If the colour was dark and the dung was very soft and moist it was classified as fresh. If the dung pat was not fresh, it was opened to see if there was a clear gradient between two colours (the bottom of the dung pat is a dark brown and the top is a light brown). If there was, then it meant that the dung had started to lose moisture and was older than if it was all dark brown so it was classified as intermediate. If there were plants growing out of the dung, many insects through it, it was all light brown in colour and it was very hard, it was classified as old.

In area without shadow:

1.	2.	3.
- Thin or no dry layer	- Clear dry layer <1/3 of thickness dung pat - Sharp transition between moist and dry - Sometimes macrofauna	- Dry layer >1/3 of thickness dung pat - Gradient between moist and dry - Vegetation growing through dung pat - Sometimes macrofauna
Fresh	***Intermediate***	***Old***

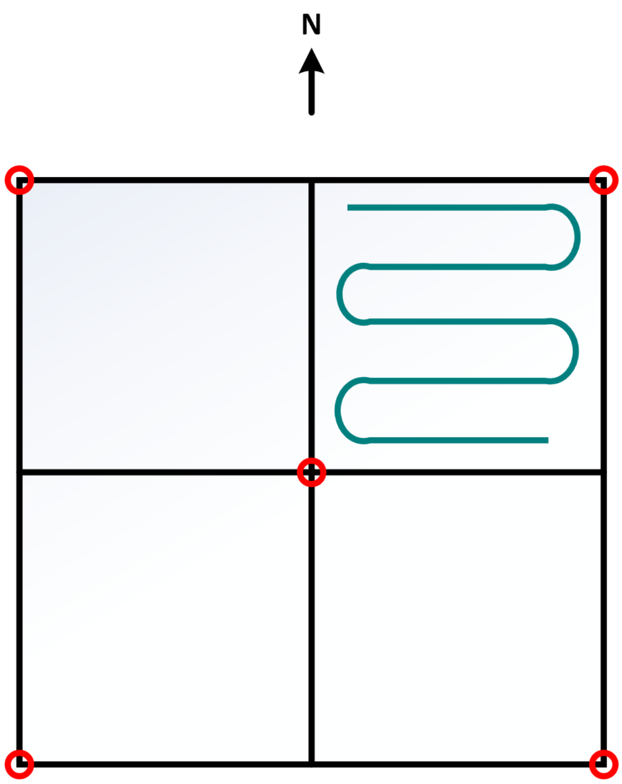
In shadowy area:

1.	2.	3.
- No dry layer	- Clear dry layer <1/4 of thickness dung pat - Sharp transition between moist and dry - Sometimes macrofauna	- Gradient between moist and dry - May be vegetation growing through dung pat - Sometimes macrofauna
Fresh	***Intermediate***	***Old***

Figure 3. Procedure for determining the age of bison dung.

Sampling procedure

So that the border of each 1 hectare quadrat could be seen when there were hills or dense vegetation, each quadrat was divide into four subplots (Figure 4). A map of the vegetation and landscape features was then drawn. The location of each of the species' faeces was also recorded to see if the distribution was random or non-random. Random was defined as if the herbivore had no preferred location to defecate in and non-random was defined as if the there was a preferred location, for example, in open areas. Parallel transects were then walked in each of the four plots until the whole quadrat was covered (Figure 4). Grid cells located on permanent bodies of water were excluded.



- Flag placed on opposing corners to mark out each plot in the 1 hectare quadrat
- Direction walked to locate dung
- N The orientation of each quadrat was placed facing North
- A 1 hectare quadrat divided into four parts

Figure 4. Diagram of sampling procedure in the field

The sampling method that was used to locate faeces is similar to distance sampling. A time threshold was established for each quadrat based on what has been used for the same species in previous studies. When no dung was found within the time period the next quadrat was started although this did not occur since dung was found in every quadrat sampled. For rabbits, the time taken to search a quadrat was 15 minutes (Feral scan, 2011). For deer, initially it was thought a total of 4.8 minutes was needed per quadrat (Alves, 2013). However, since deer like to defecate in dense vegetation it actually took around 30 minutes. Bison and Konik horse dung is relatively large so it took less than 5 minutes to sight. The optimal time threshold to search for each of the species dung in 1 quadrat was 1 hour. Since sighting the dung is not the only activity that was conducted, more time per quadrat was needed. The time taken to weigh and sample all of the dung took another hour. The time needed for sampling also varied slightly depending on the type of vegetation or landscape the quadrat was in. For instance, bison mostly avoided densely vegetated, hilly areas so there was less dung to weigh and therefore less time was needed for quadrats with hills and dense shrubs.

All of the dung of bison, Konik, deer and rabbits found in each quadrat was weighed in the field using electronic scales. A scale with a hook was used to weigh the dung of bison and Konik so that a large amount could be placed in a bag and attached to it. For deer and rabbit dung a flat kitchen scale was used. The scales with a hook weighed up to 20 kilograms and the kitchen scales weighed up to 5 kilograms. Both scales were in metric units. For sampling efficiency the weight of rabbit dung was estimated through observation since there were vast amounts of rabbit dung spread out over large areas. To do this, a sample of rabbit dung was collected and weighed once. From this sample it could be seen what size 10 grams looked like and then the total amount of dung could be estimated through observation without scales.

After weighing and emptying the bags of dung, a subsample was taken from each of the dung piles. This ensured that the dung taken for nutrient analyses adequately represented the entire quadrat. The sample of bison dung was taken from the middle of the dung pat. Samples of each of the species' dung was going to be collected for nutrient analysis in every fifth quadrat and then with the results, the nutrient distribution for the rest of the area was going to be calculated. However, since the number of quadrats sampled was reduced from 100 to 18, the sampling procedure was changed and samples were taken from every quadrat. In the first 2 days of field work the original sampling procedure was followed and there were 3 quadrats where there was no dung taken for nutrient analysis.

Nutrient analyses

The dung collected at the end of each day in the field was stored in a freezer. Once the field work was complete the dung was taken from the freezer and weighed in containers. The containers were also weighed separately. The samples were then placed in an oven at 72 °C for 48 hours. Other studies have dried faeces for the same amount of time but at temperatures ranging from 50 °C to 80 °C (Vaieretti et al., 2013). The temperature of 72 °C was chosen for this research because a large amount of faeces was placed in the oven and a higher temperature would result in a considerable loss of nitrogen (Sharkey, 1970). After the dung was completely dried it was weighed again. Any stones or plant material was removed then the samples were ground so that they were completely homogenous using a mortar and pestle and an electronic grinder.

The dung samples were weighed to 10 milligrams in tin containers and then sealed. After every 10 samples a tin without a sample (blank), a tin with either atropine or acetanilide and a tin with nicotinamide was also added to the analyses. The nicotinamide acted as a reagent and the atropine and acetanilide was used to calibrate the measurements. The blank went through all steps of the procedure. The blank was used to account for any contamination that may occur from the chemicals used in the analysis (Combs et al., 2003).

Each sample was measured for nitrogen and carbon contents on a fisons NA 1500 NCS. There is a Dumas flash combustion setup with CrO_3 and silvered cobaltic oxide (to catch the SO_2). This method of carbon and nitrogen analysis was chosen as it has been used in other studies on biological processes (Fukuda et al., 1998; Mayor & Solan, 2011; Royer et al., 2001).

Calculations were used to convert analyses results from percent dry weight to what it would be in “as-is” results (fresh sample). With the weight (grams) of the dung and its total moisture content, the total percentage of nutrients in the fresh samples was calculated using the following equations:

$$\%moisture = \frac{fresh\ sample\ and\ container - dry\ sample\ and\ container}{fresh\ sample\ and\ container - empty\ container} \cdot 100$$

- **Fresh sample** is the weight of the faeces sample before being oven dried
- **Dry sample** is the weight of the faeces sample before being oven dried
- **Fresh sample and container** is the combined weight of the fresh sample and the container.
- **Dry sample and container** is the weight of the dry sample and the container.
- **Empty container** is the weight of the container without any sample in it.
- All weight measurements in grams (g)

To convert the total nitrogen and carbon value to a fresh basis:

$$fresh\ weight\ value = dry\ weight\ value \cdot \left(1 - \frac{\%moisture}{100}\right)$$

The total amount of nitrogen and carbon could then be calculated using the following equation:

$$weight\ of\ faeces \cdot \frac{\%nitrogen\ in\ fresh\ faeces}{100}$$

The total amount of nitrogen per quadrat (gN / ha) was calculated by adding the total amount of nitrogen from each of the species' dung in each of the quadrats. The same was done to find the total amount of carbon per hectare (gN / ha).

GIS integration

The location of dung was recorded using a Global Positioning System (GPS) unit. The coordinates of rabbit, Konik, bison and deer dung were only recorded every third time a cluster of dung was found since it would have been too time consuming to record the location of all of the dung. The dung of roe and fallow deer were treated as one since roe deer are rare and it would have been be difficult to tell the dung apart. Often the dung of one of the herbivores was very close to the dung of another herbivore so the same GPS coordinate was recorded for both of the herbivores dung. So that location and nutrient contents of each of the species dung did not overlap, a map was created for each species rather than combining the location of each of their dung into one map.

The location of dung, the total amount of dung found in each quadrat and the percentage of nutrients found in the dung of all of the herbivores in each quadrat was then placed over a vegetation map of the area using ArcMaps (Esri, 2012). A table with geographical coordinates of bison, deer, rabbit and Konik dung was uploaded into ArcMap and projected to the WGS 1984 coordinate system (Esri, 2014). Maps were created for each of the four species to show how the percentage of nutrients in their dung is spatially distributed over the Kraansvlak. Graduated colours were used for the different percentages of nitrogen and carbon. To show how the weight of the dung from each species varied, graduated symbols were used. Graduated symbols were also used to show what the distribution of the weight of nitrogen and carbon is per hectare from the dung of the four species.

Statistical analysis

The number of samples collected for the three different ages of bison dung are not equal so the chance of incorrectly reporting a significant difference in the means is greater. The group with the larger number of samples may have larger variances.

The three assumptions of a one-way analysis of variance were not violated when the results were checked with a Q-Q plot and a scatter plot. A one-way analysis of variance (ANOVA) was then used to test for variation between nutrient (C, N and P) contents in bison, Konik, deer and rabbit dung of different ages. A one-way ANOVA was also done to see if there was any variation in the nitrogen and carbon contents of the dung of the four species. It is expected that there will be variation between the percentage of nutrients in dung of different ages and different species. The null hypothesis for the ANOVAs was that the percentage of nutrients in fresh, intermediate and old dung will not vary and that nutrient contents will be the same in bison, Konik, deer and rabbit dung. If ANOVA showed that there was a variation between groups, a post hoc t-test and a Bonferroni correction was used to show which groups varied (Townend, 2012).

Results

The results are ordered so that they correspond to the order of the research questions stated in the introduction. In the map figures, there is an area inside the border of the Kraansvlak that does not have vegetation or landscape features. This is due to the map of the vegetation and landscape features dating from before the Kraansvalk was extended. The fecal nitrogen and carbon concentrations are reported as a percentage of the dry matter by mass. The weight of nitrogen and carbon is reported in grams which was obtained using the two equations mentioned in the methods. The full results of each ANOVA and the mean and total weight of the nutrients in the dung of the four herbivores from the total area sampled can be found in appendix A.

The variation of nutrient contents

The results of the one-way ANOVA on the percentage of nitrogen in bison dung of different ages show that there is a significant variation between the three groups. There is variation between the percentage of nitrogen found in fresh, intermediate and old bison dung so the null hypothesis that there is no variation is rejected (Table 1). Fresh bison dung has an average nitrogen percentage of 2.07 and old dung has an average nitrogen percentage of 1.41 (figure 5).

A post hoc t-test and a Bonferroni correction on bison dung showed that the percentage of nitrogen was significantly different between fresh and old dung ($p = 0.003$) and intermediate and old dung ($p = 0.001$). There was shown to be no statistically significant differences between the fresh and intermediate aged groups ($p = 0.97$).

There was a statistically significant difference in the percentage of nitrogen found in fresh Konik dung compared to old Konik dung as determined by the one-way ANOVA ($F = 16.641$ and $p = 0.0008$) (Table 1).

Table 1. Results of a one-way ANOVA on the percentage of nitrogen in fresh, intermediate and old bison dung, fresh and old Konik dung, fresh and old deer dung and fresh and old rabbit dung

Species	F	P-value	F critical value
Bison	8.04	0.003	3.59
Konik	16.641	0.0008	4.493
Deer	0.009	0.923	4.667
Rabbit	0.025	0.876	4.493

The ANOVA on percentage of carbon in differently aged bison dung showed that there is no significant difference between the means and there is no variation between the percentage of carbon in bison dung with three different ages (Table 2).

There is no significant variation between the percentage of carbon found in fresh and old Konik dung. The one-way ANOVA has an f critical value which is larger than the F statistic and p is greater then 0.05 (Table 2).

Time did not have a significant effect on the amount of nitrogen or carbon found in rabbit and deer dung ($p > 0.05$) (Table 1 & 2). The amount sampled could have influenced the results of the ANOVA. There are only 5 samples of fresh rabbit dung and 13 samples of old rabbit dung for which the nutrient contents were analysed.

Table 2. Results of a one-way ANOVA on the percentage of carbon in fresh, intermediate and old bison dung, fresh and old Konik dung, fresh and old deer dung and fresh and old rabbit dung

Species	F	P-value	F critical value
Bison	0.180	0.836	3.59
Konik	1.046	0.321	4.493
Deer	1.570	0.232	4.667
Rabbit	0.021	0.884	4.493

There was a statistically significant difference between the percentage of nitrogen found in fresh bison, Konik, deer, and rabbit dung as determined by the one-way ANOVA ($F = 10.51$ and $p = 0.0003$) (Table 3).

A post hoc t-test and a Bonferroni correction was used to show how the percentage of nitrogen varied between the four species' dung. It showed that the percentage of nitrogen in bison & Konik, and bison & rabbit fresh dung did not differ but it was different between the fresh dung of bison and deer. Konik and deer also had significantly different percentages of nitrogen in their fresh dung but Konik and rabbit did not. There was also no difference between the percentage of nitrogen in deer and rabbit fresh dung.

Table 3. Results of a one-way ANOVA comparing the percentage of nitrogen in fresh bison, Konik, deer and rabbit dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	8.436	3	2.812	10.513	0.0003	3.196
Within groups	4.547	17	0.267			
Total	12.984	20				

A one-way ANOVA showed that there is no statistically significant difference between the percentage of carbon in fresh bison, Konik, deer and rabbit dung (Table 4).

Table 4. Results of a one-way ANOVA comparing the percentage of carbon in fresh bison, Konik, deer and rabbit dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	25.346	3	8.448	0.673	0.580	3.196
Within groups	213.346	17	12.549			
Total	238.692	20				

The percentage of nitrogen was highest in deer faeces with the mean percentage being 1.26 more than the concentrations found in bison faeces and 1.54 percent more than the concentrations found in Konik faeces. There was almost no difference in the amount of nitrogen found in fresh deer faeces compared to old deer faeces. The concentration of nitrogen in rabbit faeces also did not vary much with age. Old Konik faeces has the smallest concentration of nitrogen (Figure 5).

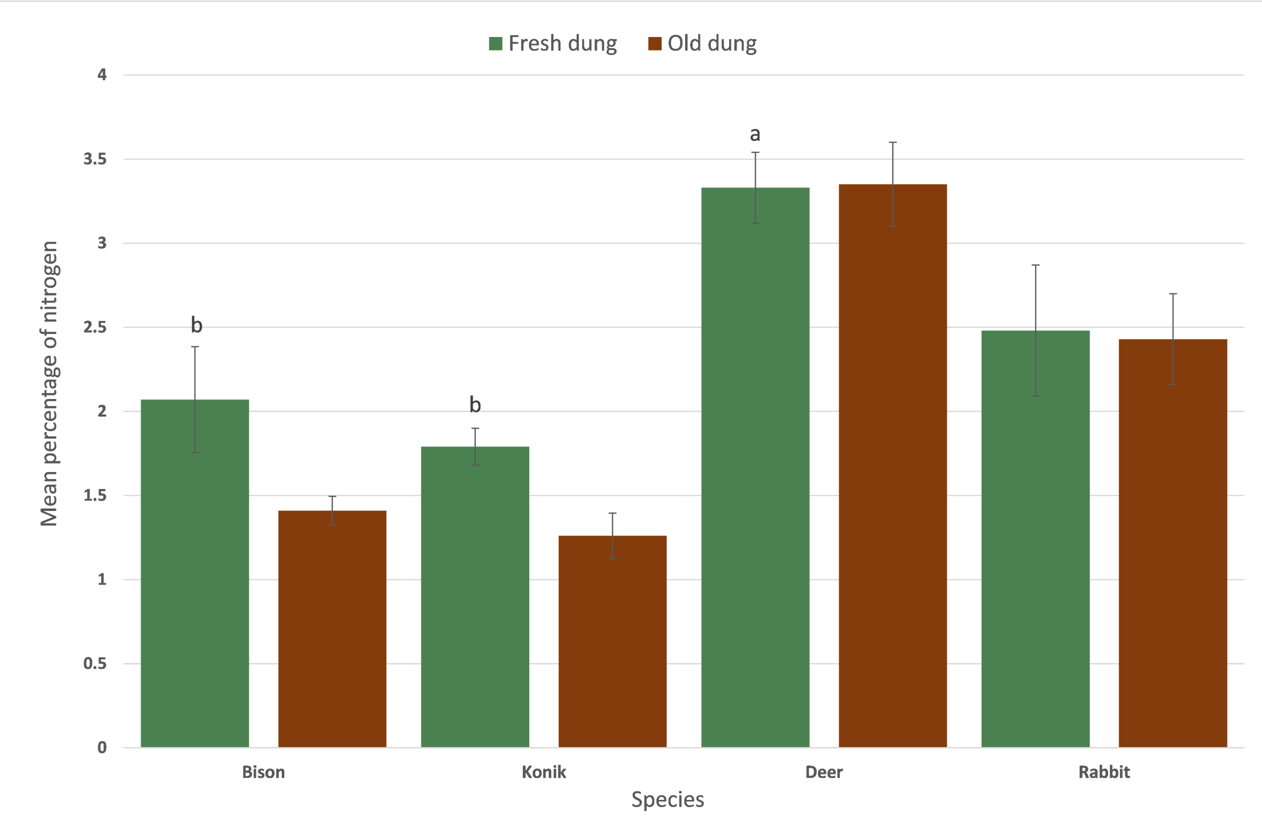


Figure 5. Percentage of nitrogen (mean ± SD) in fresh and old faeces of European bison (n = 3), Konik (n = 6), roe & fallow deer (n = 7) and European rabbit (n = 5) found in the kraansvlak. The letters a and b above the bars indicate significant differences ($P < 0.05$) in nitrogen concentrations between fresh deer and bison faeces and fresh deer and Konik faeces.

Deer dung also had the highest mean percentage of carbon and the greatest difference between the percentage of carbon in fresh and old dung. The mean percentage of carbon was greater in older dung Konik horse dung than fresh. The percentage of carbon in Konik dung was the most similar to the amount found in bison dung (Figure 6).

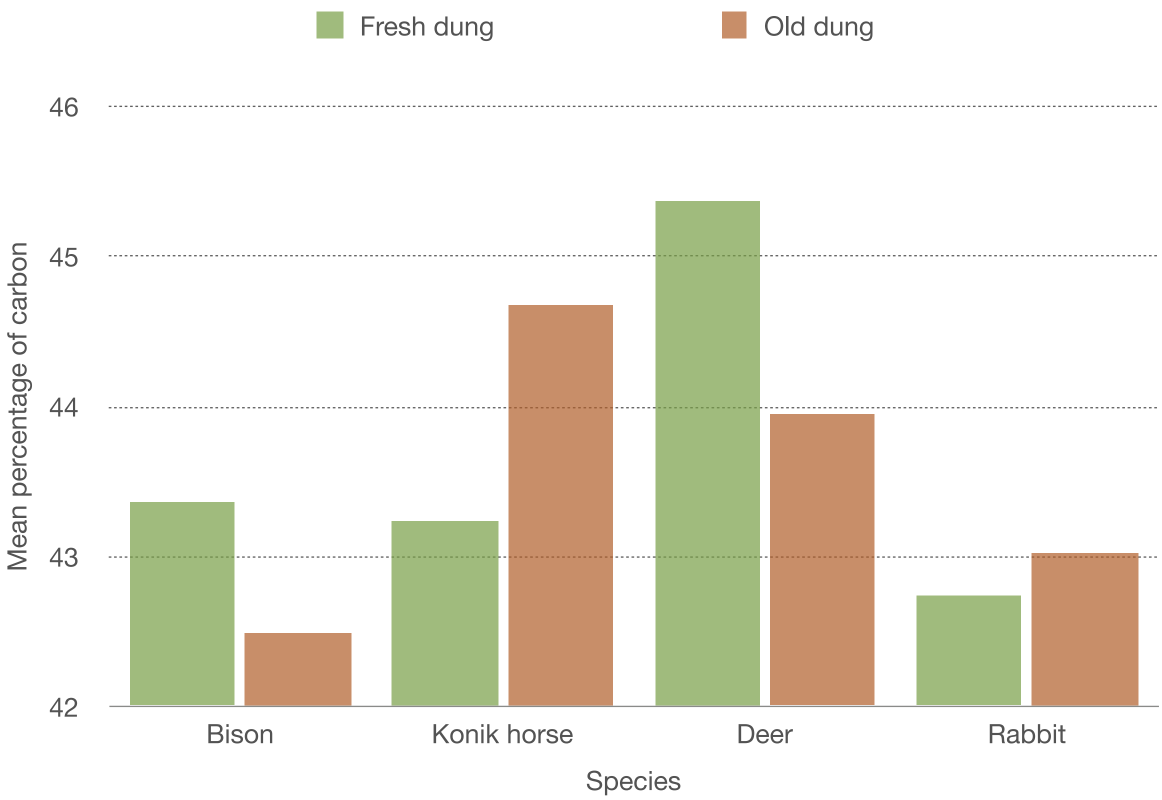


Figure 6. Percentage of carbon (mean ± SD) in fresh and old faeces of European bison (n = 3), Konik (n = 6), roe and fallow deer (n =7) and European rabbit (n = 5) found in the kraansvlak.

Nutrient contents and the spatial distribution of faeces

Deer, bison, rabbit, and Konik dung all preferred to defecate in a different location in the landscape. Bison almost always avoided defecating in areas with dense shrubs. Koniks visited areas with dense shrubs more than bison did but it was still not common to find Konik dung amongst dense shrubs. Deer dung was mainly found in densely vegetated areas and rabbits preferred open areas. Rabbits and deer were found to use latrine areas. In contrast Koniks defecated anywhere they visited (Table 5).

Table 5. Location of bison, Konik, deer and rabbit dung and the mean percentage of nitrogen and carbon in fresh dung

Species	Spatial pattern in the landscape	Mean nitrogen content in fresh dung and standard deviation	Mean carbon content in fresh dung and standard deviation
Bison	Non-random distribution in areas of open grassland or small shrubs and near water	2.07, 0.63	43.37, 2.75
Konik	Non-random distribution in areas of open grassland and small to medium shrubs	1.79, 0.22	43.23, 3.85
Deer	Non-random distribution in densely vegetated areas	3.33, 0.42	45.37, 1.60
Rabbit	Non-random in open areas near burrows	2.48, 0.78	42.74, 5.22

Nitrogen contents and spatial distribution

Nitrogen concentrations of the four herbivores faeces is evenly spread out over the area. Bison dung with the highest percentage of nitrogen (represented by red dots) was found in the west with dung with lower concentrations of nitrogen near the lake. The dung of Konik, fallow and roe deer had a higher percentage of nitrogen near the lake. Rabbit dung was found more in the west near the bison dung with high nitrogen contents (Figures 7, 8, 9 & 10).

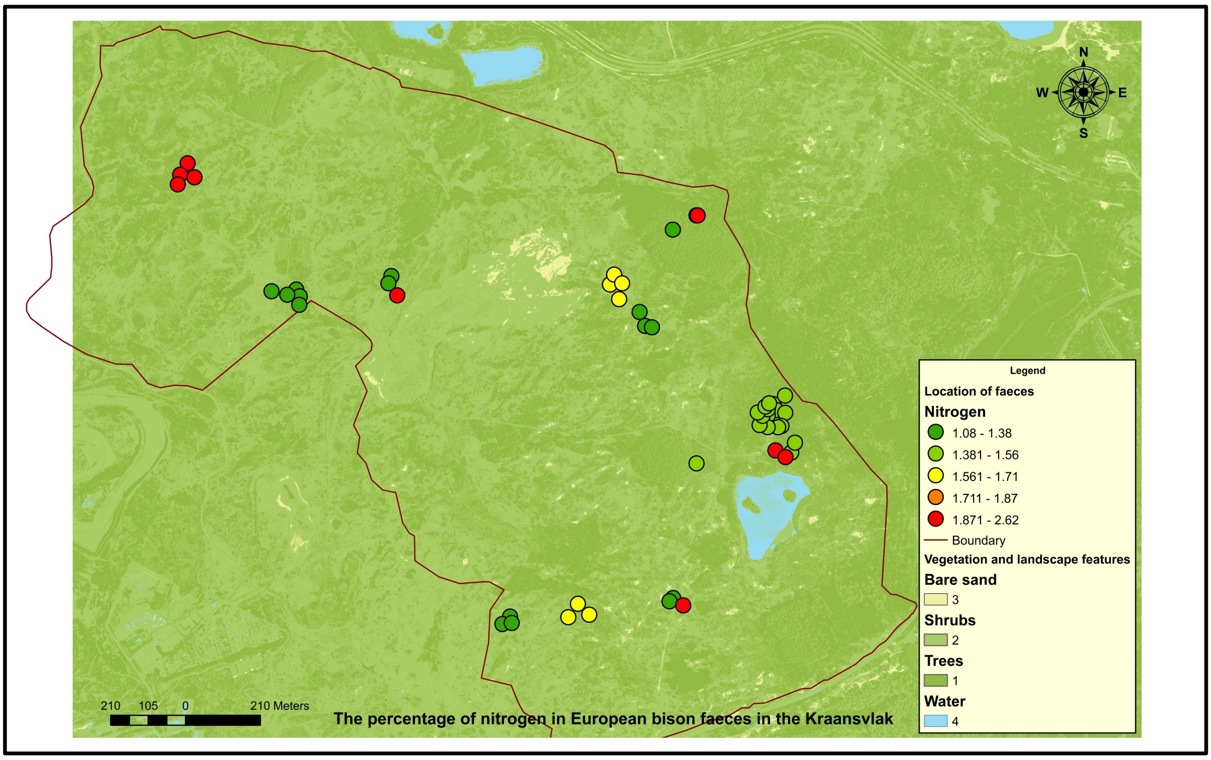


Figure 7. The percentage of nitrogen in European bison dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

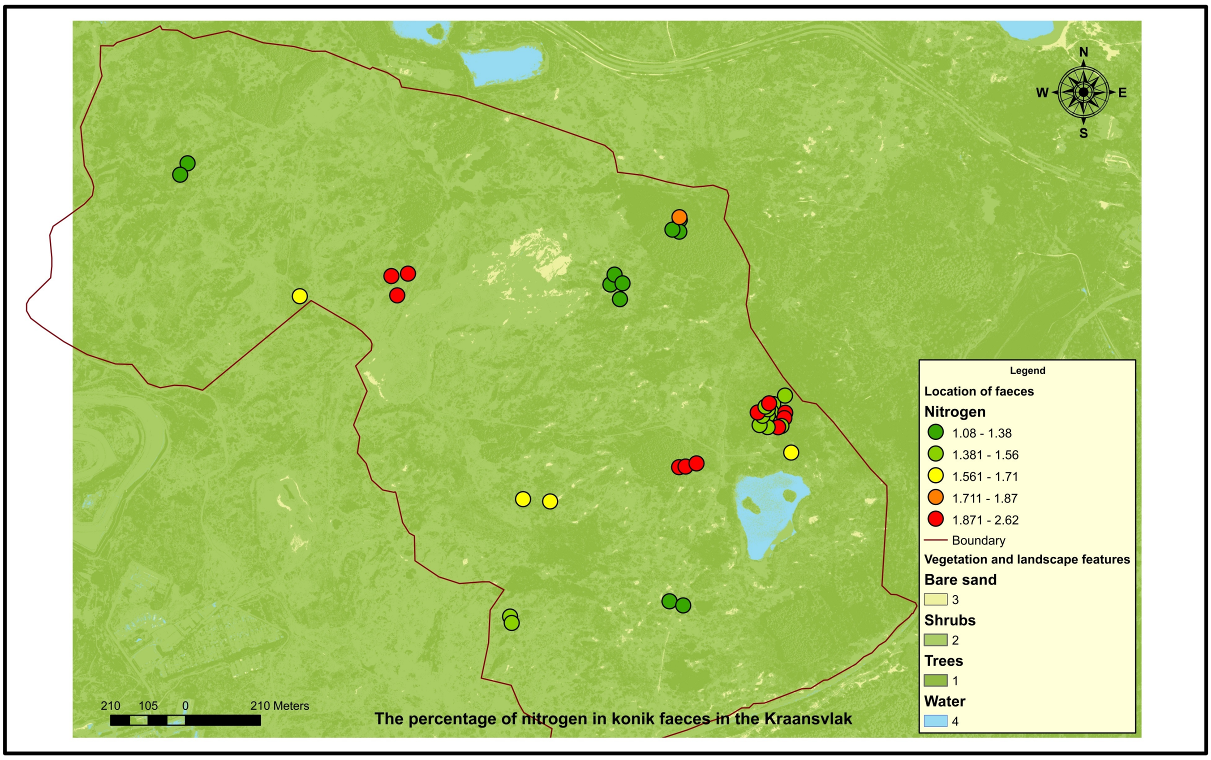


Figure 8. The percentage of nitrogen in Konik dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

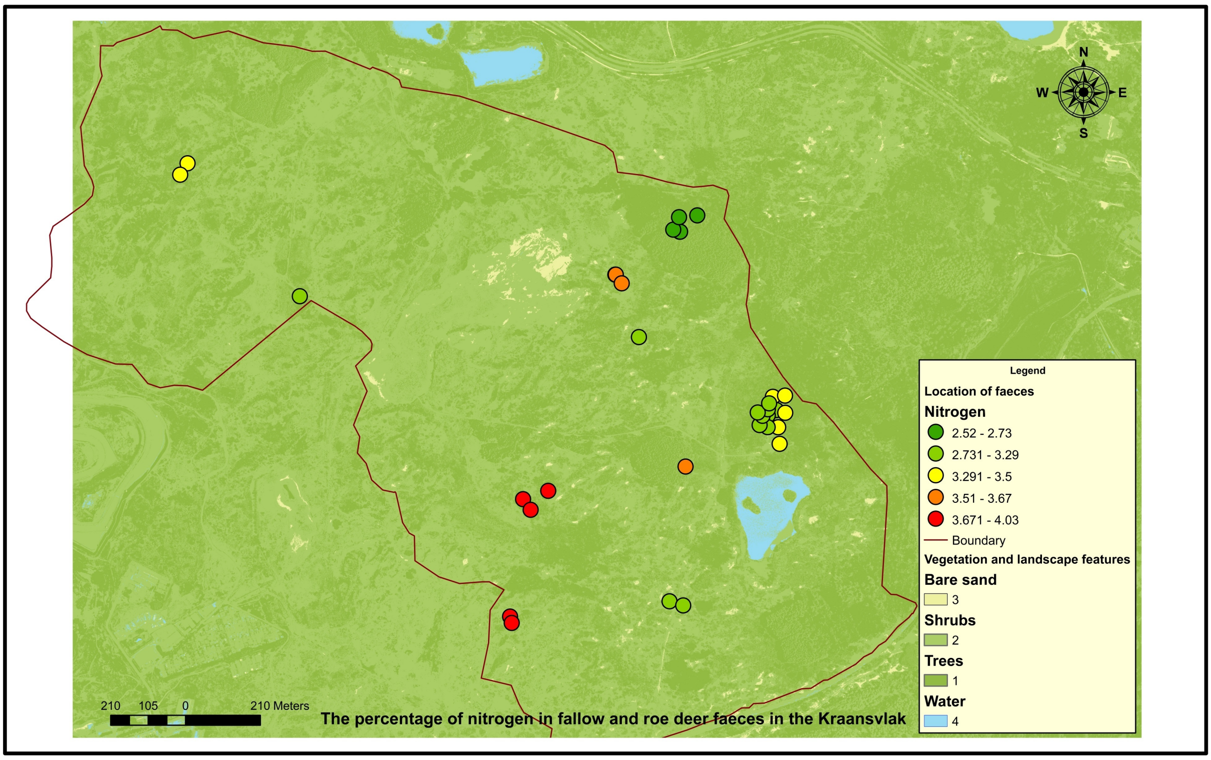


Figure 9. The percentage of nitrogen in fallow and roe deer dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

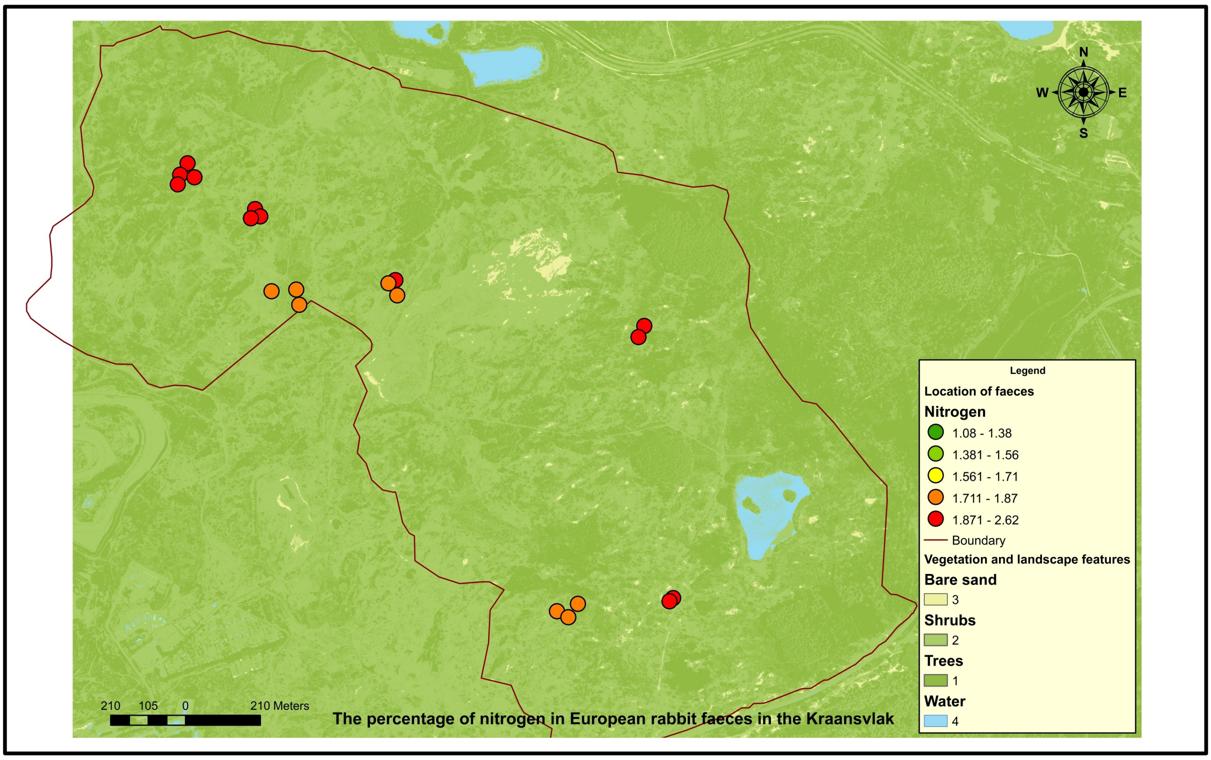


Figure 10. The percentage of nitrogen in European rabbit dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

The weight of nitrogen in the dung of all of the herbivores but the rabbit was greatest around the lake. Bison and Konik dung contributed the most nitrogen to the area. The distribution of the nitrogen was also clumped around the lake. The amount of nitrogen in bison faeces was distributed the most evenly over the area. The Konik faeces around the lake had greater amounts of nitrogen. The weight of nitrogen in the dung of rabbits was greatest in the far west end and at the opposite end below the lake. Overall, with the combination of bison and Konik faeces, the east side of the Kraansvlak had greater amounts of nitrogen (areas A and B) (Figure 11, 12, 13 & 14).

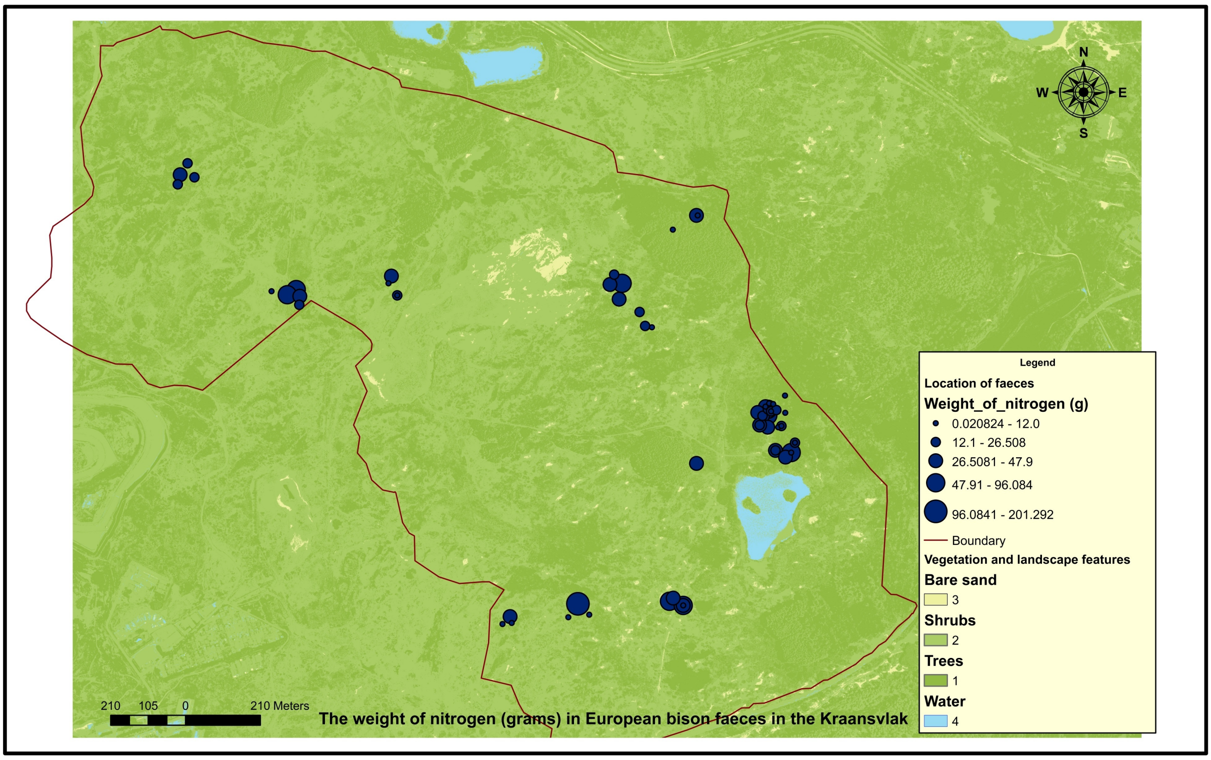


Figure 11. The weight of nitrogen (grams) in European bison dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

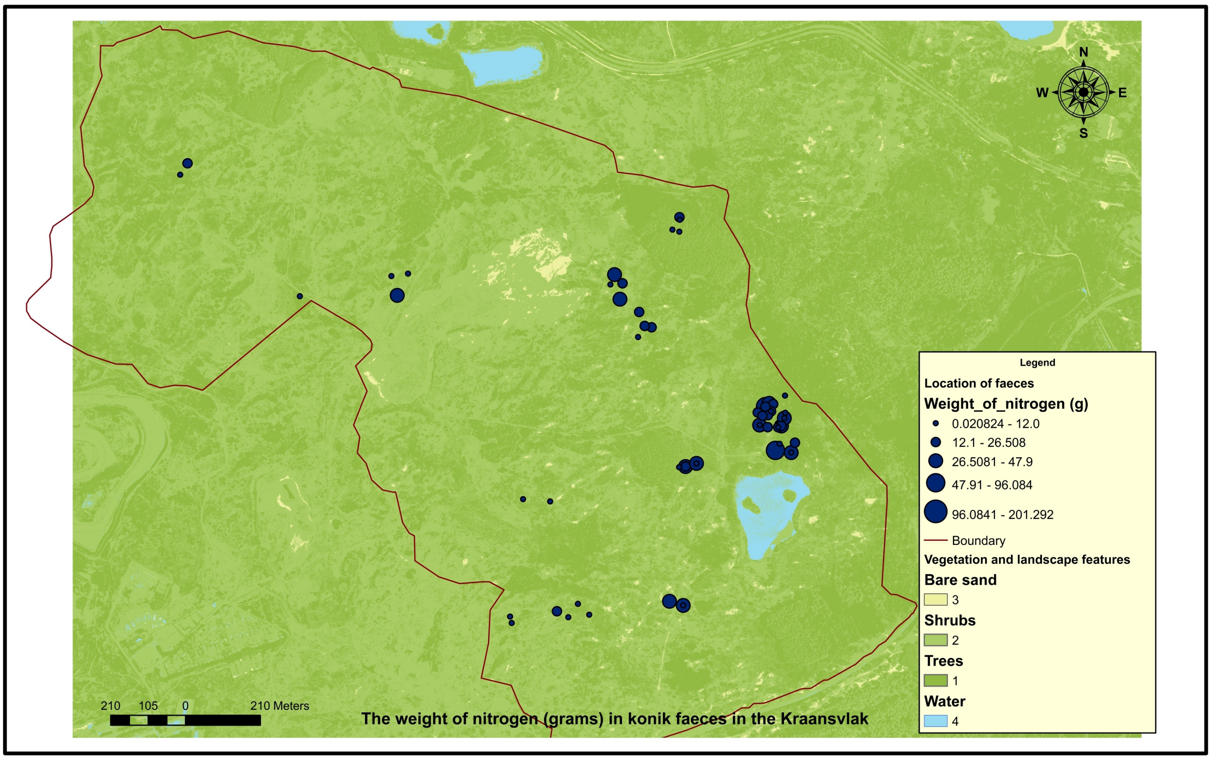


Figure 12. The weight of nitrogen (grams) in Konik dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

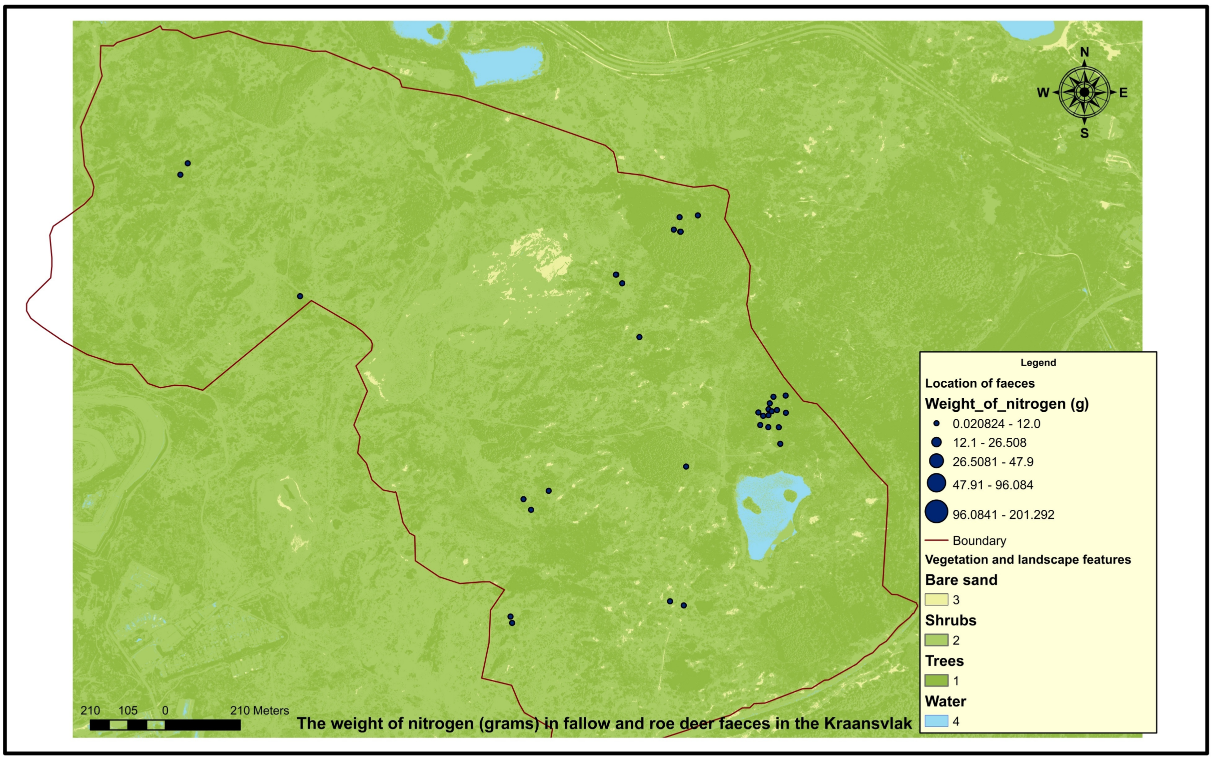


Figure 13. The weight of nitrogen (grams) in fallow and roe deer dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

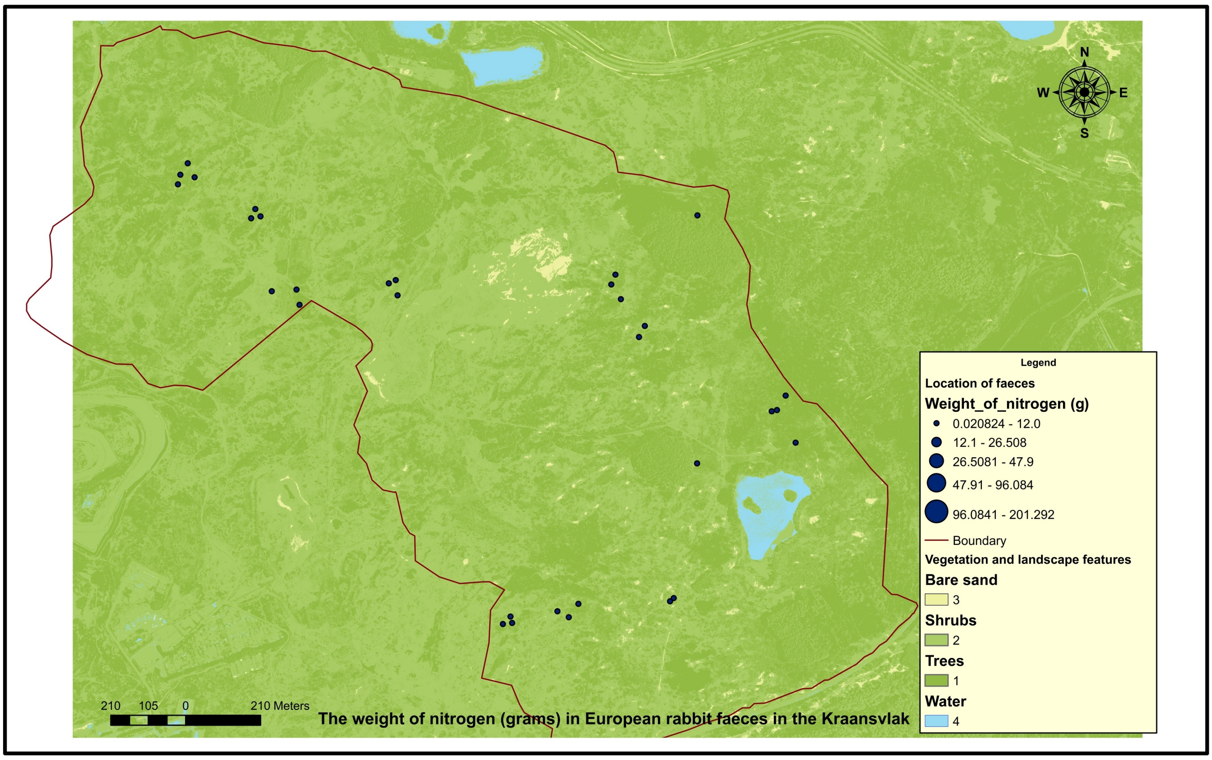


Figure 14. The weight of nitrogen in European rabbit dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

Carbon contents and spatial distribution

Bison and Konik faeces concentrations of carbon were both distributed differently over the area. The faeces of bison closest to the lake had the lowest concentrations of carbon whereas the Konik faeces closest to the lake had the highest concentrations of carbon. The deer faeces with highest concentrations were in the centre of the park and the rabbit faeces with the highest concentrations of carbon were north of the lake. Based on the faeces of the four herbivores each having high concentrations of carbon in different locations, the distribution of carbon over the area is fairly even (Figures 15, 16, 17 & 18).

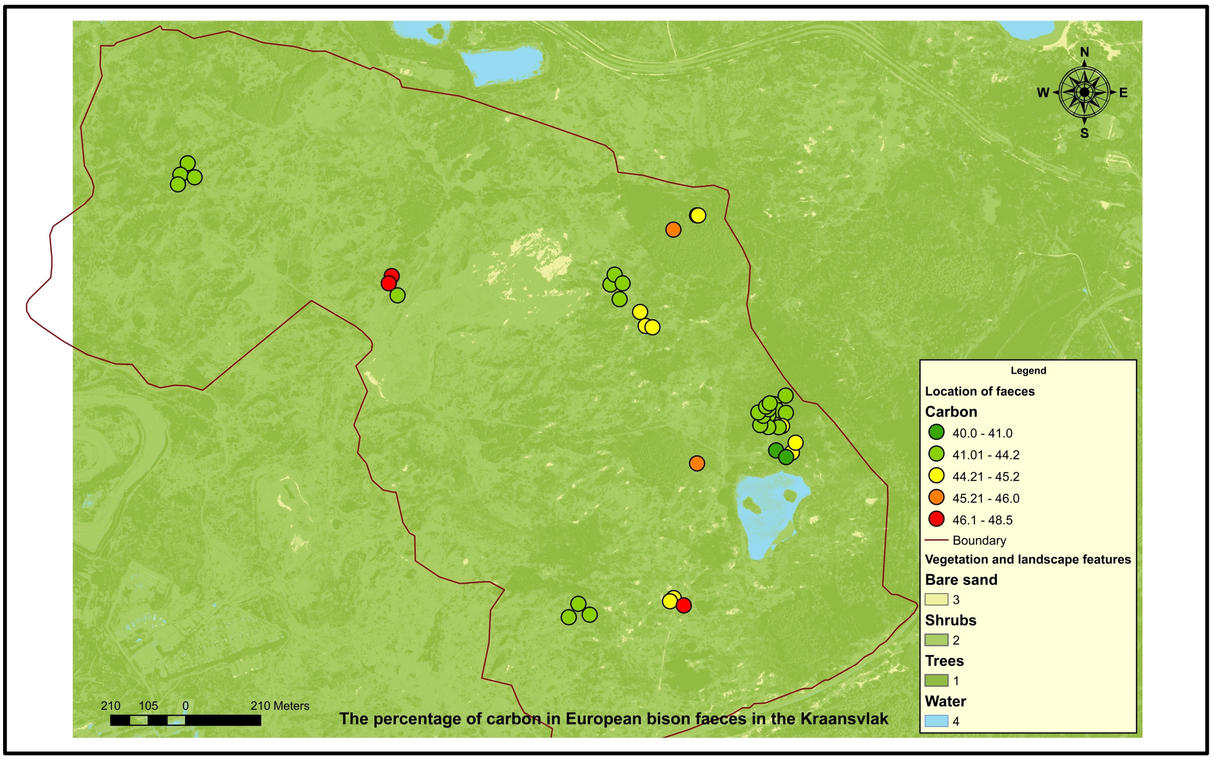


Figure 15. The percentage of carbon in European bison dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

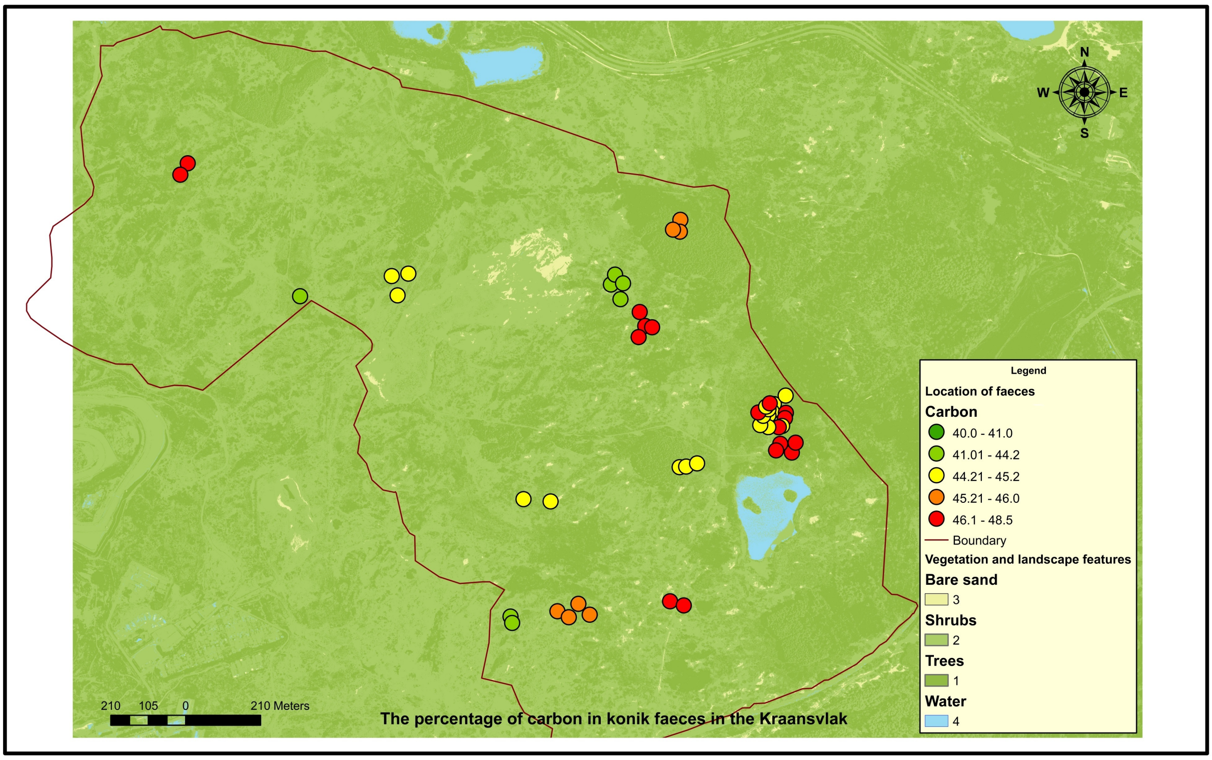


Figure 16. The percentage of carbon in Konik dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

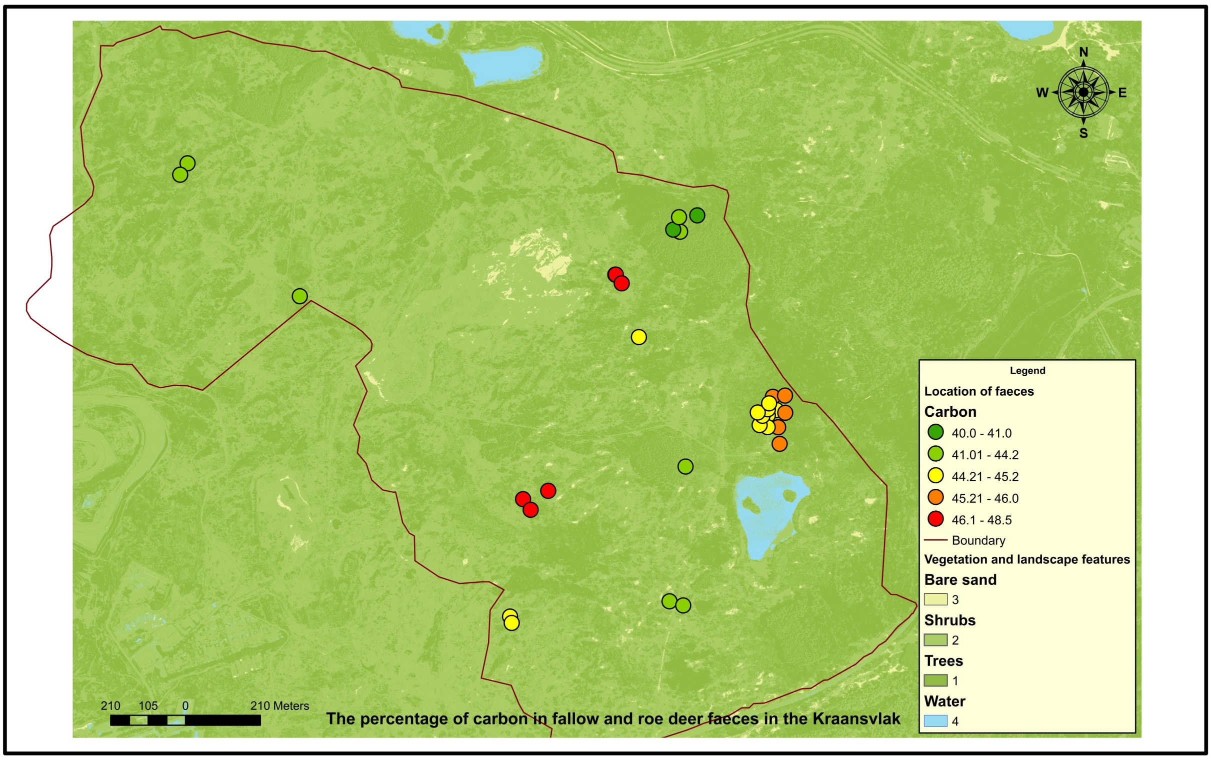


Figure 17. The percentage of carbon in fallow and roe deer dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

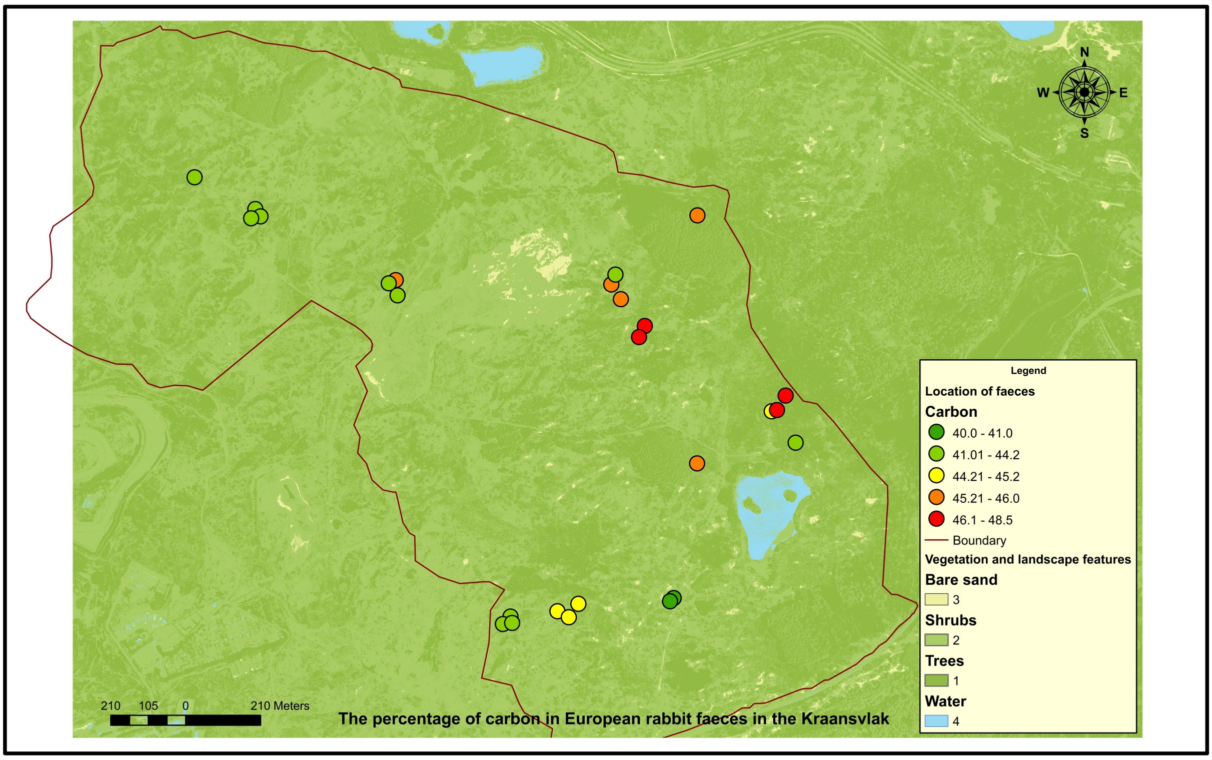


Figure 18. The percentage of carbon in European rabbit dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

Deer and rabbit dung contributed very little amounts of carbon to the 18 hectares sampled. In any one location the amount of carbon in their faeces did not exceed 350 grams. Bison faeces had the highest amount of carbon and was the most evenly distributed over the area. The amount of carbon in bison dung went up to 5000 grams in one location. Carbon from Konik dung was concentrated mainly around the lake. Since deer and rabbit contribute very little amounts of carbon, the carbon from Konik and bison faeces makes the distribution of carbon over the entire area less uniform. The area with the highest amount of carbon is the east side of the kraansvlak (areas A and B) (Figures 19, 20, 21 & 22).

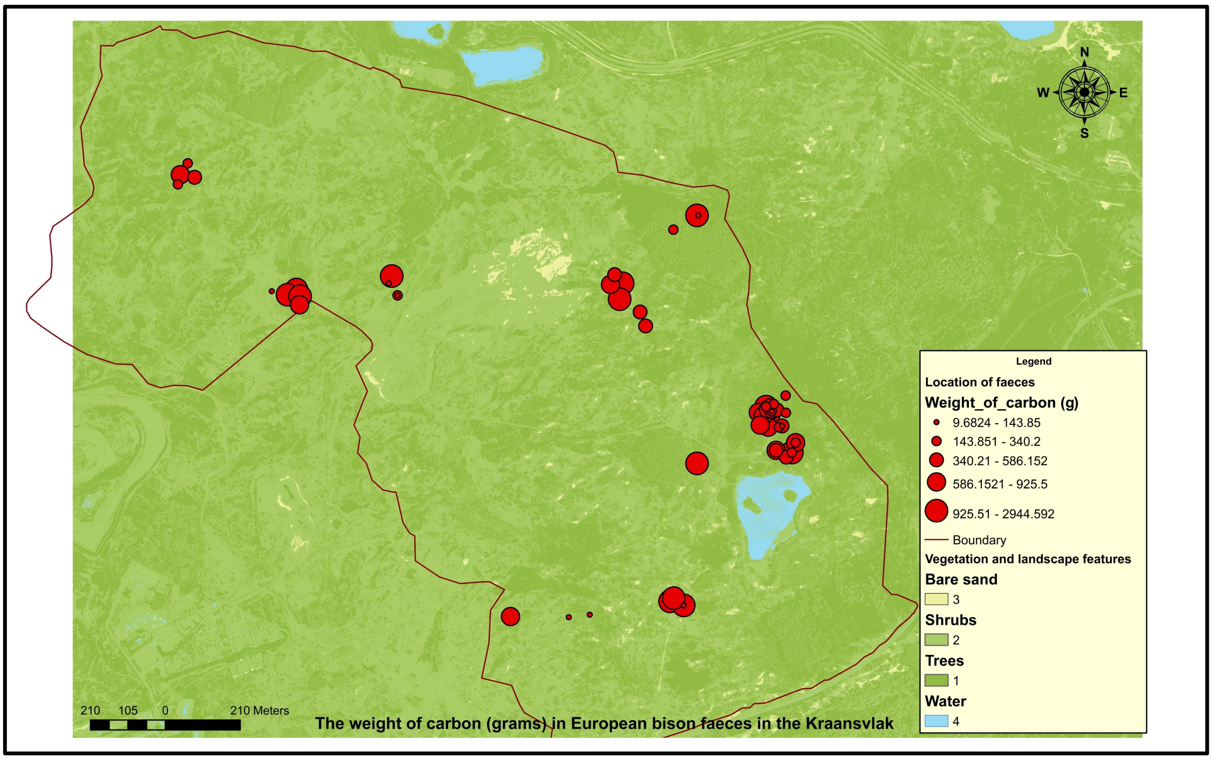


Figure 19. The weight of carbon (grams) in European bison dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

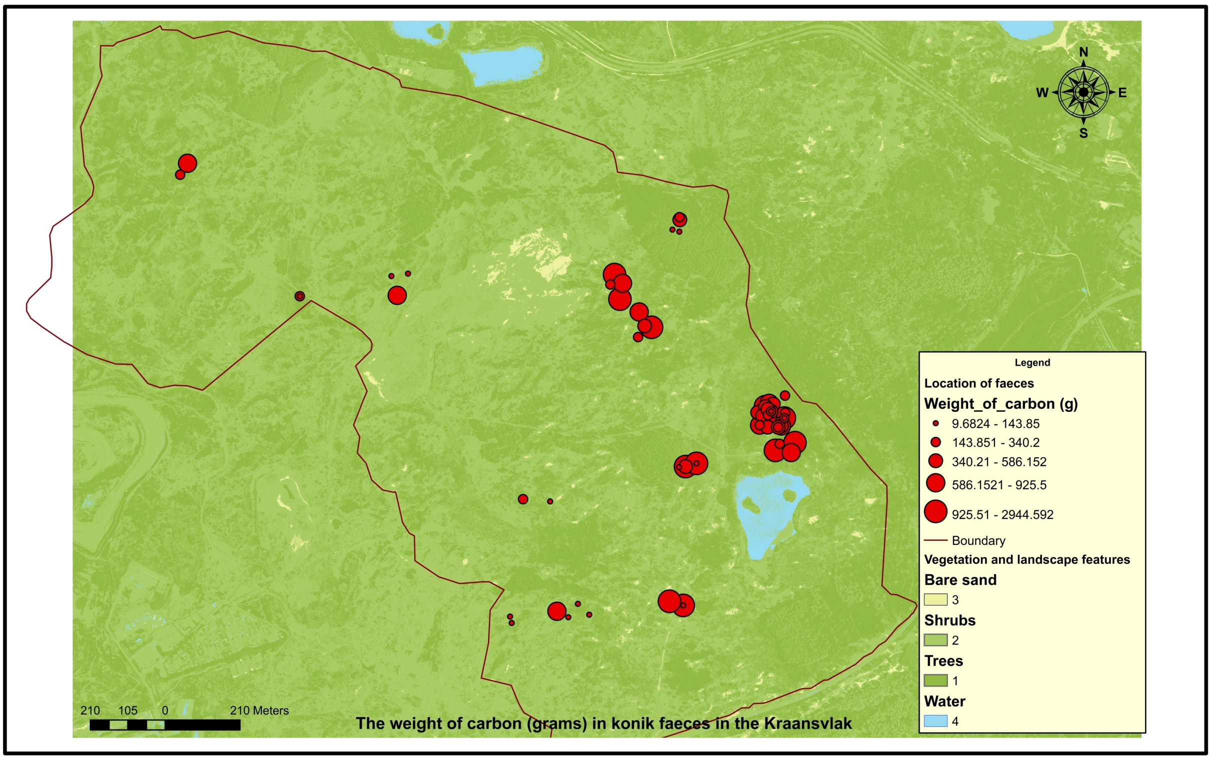


Figure 20. The weight of carbon (grams) in Konik dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

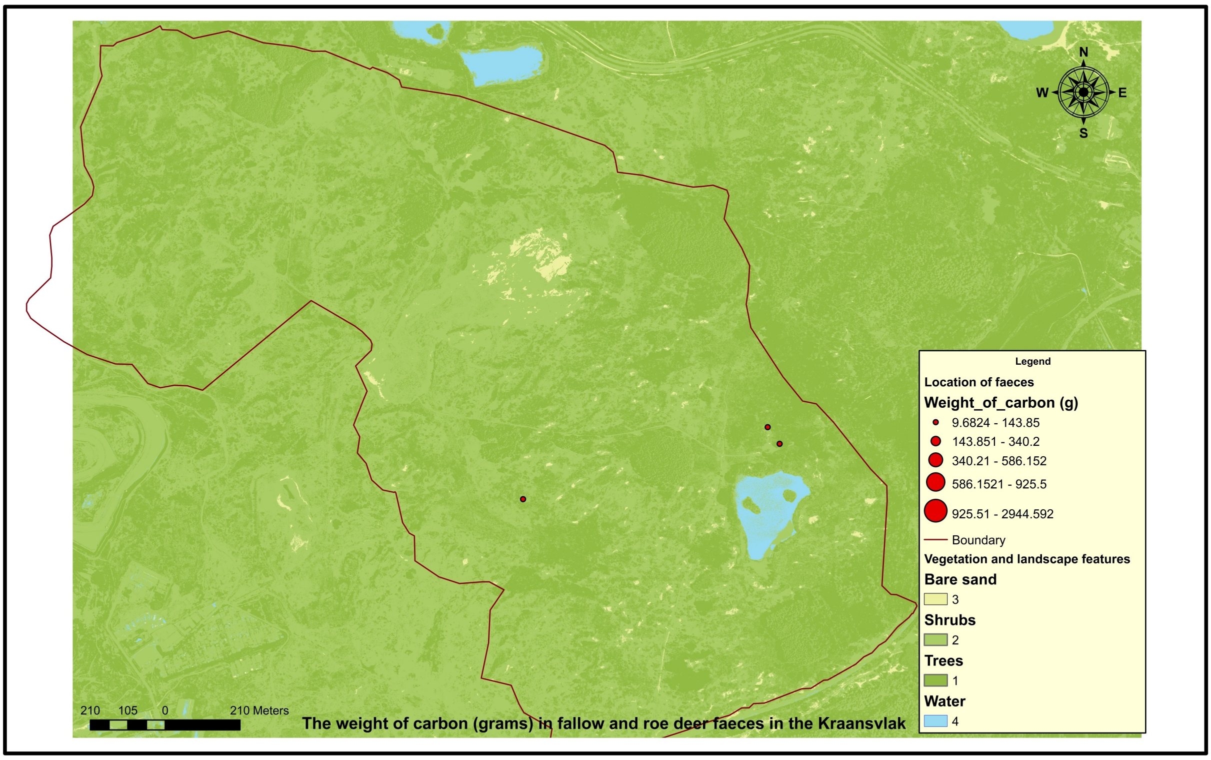


Figure 21. The weight of carbon (grams) in fallow and roe deer dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

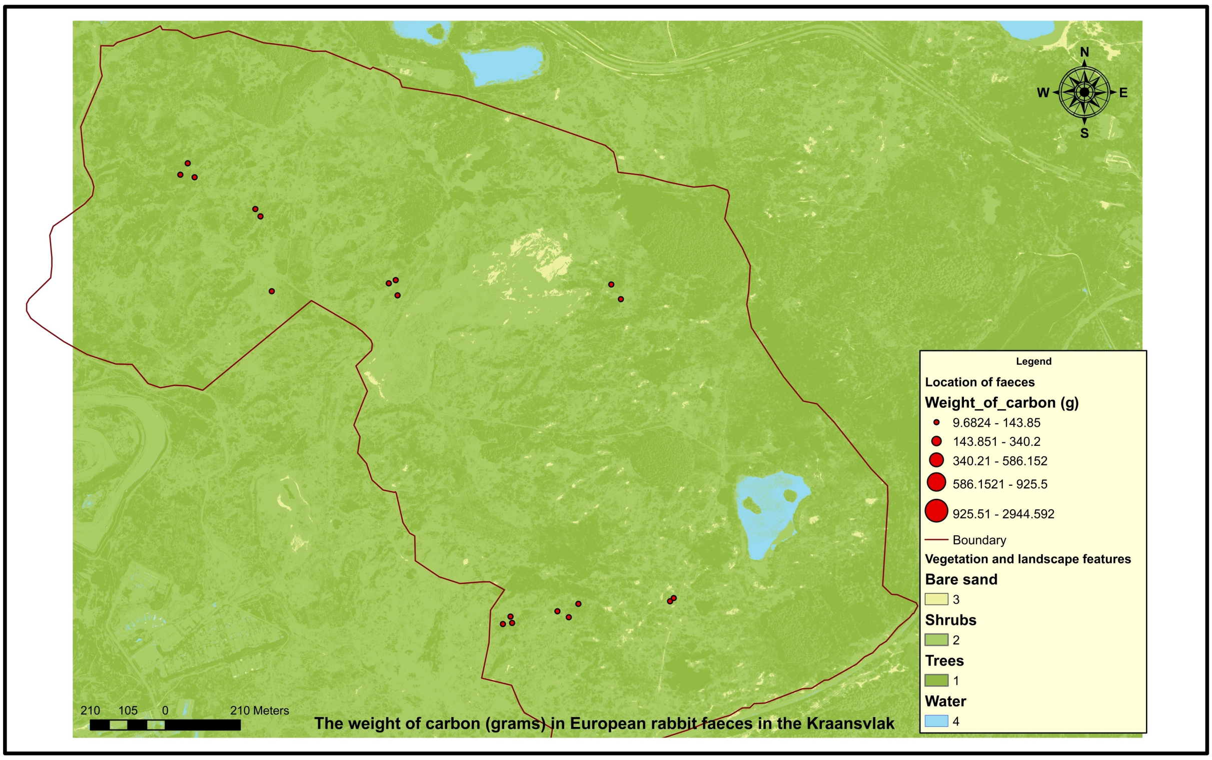


Figure 22. The weight of carbon (grams) in European rabbit dung in 14 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

Total weight of faeces, the total nutrients in faeces and its spatial distribution

The quadrat with the most amount of bison and Konik dung was quadrat 23 which was located close to the lake. The quadrat with the least amount of bison and Konik dung was quadrat 74 which was near the border that is furthest away from the lake. This area only contained rabbit dung and the surrounding area had higher amounts of rabbit dung than in other areas. The quadrat with the least amount of rabbit dung was quadrat 4 and deer dung was quadrat 4, 36 and 46. Bison contributed the most amount of dung per hectare, followed by Konik, rabbit and deer. Area A had 75.55 grams of nitrogen, area B had 202.77 grams of nitrogen, area C had 69.27 grams of nitrogen and area D had 77.67 grams of nitrogen (Table 12). The results for nitrogen and carbon in quadrat 36 were absent from the laboratory results due to human error.

Table 12. Total weight (grams) of bison, Konik, deer and rabbit dung and the total weight of nitrogen and carbon in 18 1 hectares quadrats in the kraansvlak.

Quadrat	Nitrogen (gm)	Carbon (gm)	Bison	Konik	Deer	Rabbit
4	-	-	3700	10750	0	0
8	-	-	15800	10294	29	160
10	27.3	564.1	11840	9380	75	2
16	31	659.7	39530	33100	72	128
18	17.3	502	13028.2	11970	35	30
23	160.2	3395.7	154900	84950	181	12
24	16.6	360.5	9250	12730	8	10
25	25.9	664.4	41800	25270	174	10
36	-	-	10900	7030	0	103
45	23.5	407.8	4378.7	76	15	530
46	14.6	441.4	20639	2170	0	230
47	31.2	757.9	30800	10510	39	1000
53	13.8	344.2	31700	11705.7	133	500
64	19.8	493.9	9414	3575	40	324
65	17.2	399.8	29571	1680	22	170
69	-	-	54350	14040	29	510
74	11.1	217.3	0	0	0	270
77	29.5	542.9	6970	5040	18	575
Total	439	9751.6	488570.9	254270.7	870	4564

The weight of bison and Konik dung was greater than deer and rabbit dung and was very densely distributed around the lake. Rabbit dung was evenly distributed through the top and bottom areas. Compared to the other three herbivores there was very little deer dung (Figure 23, 24, 25 & 26).

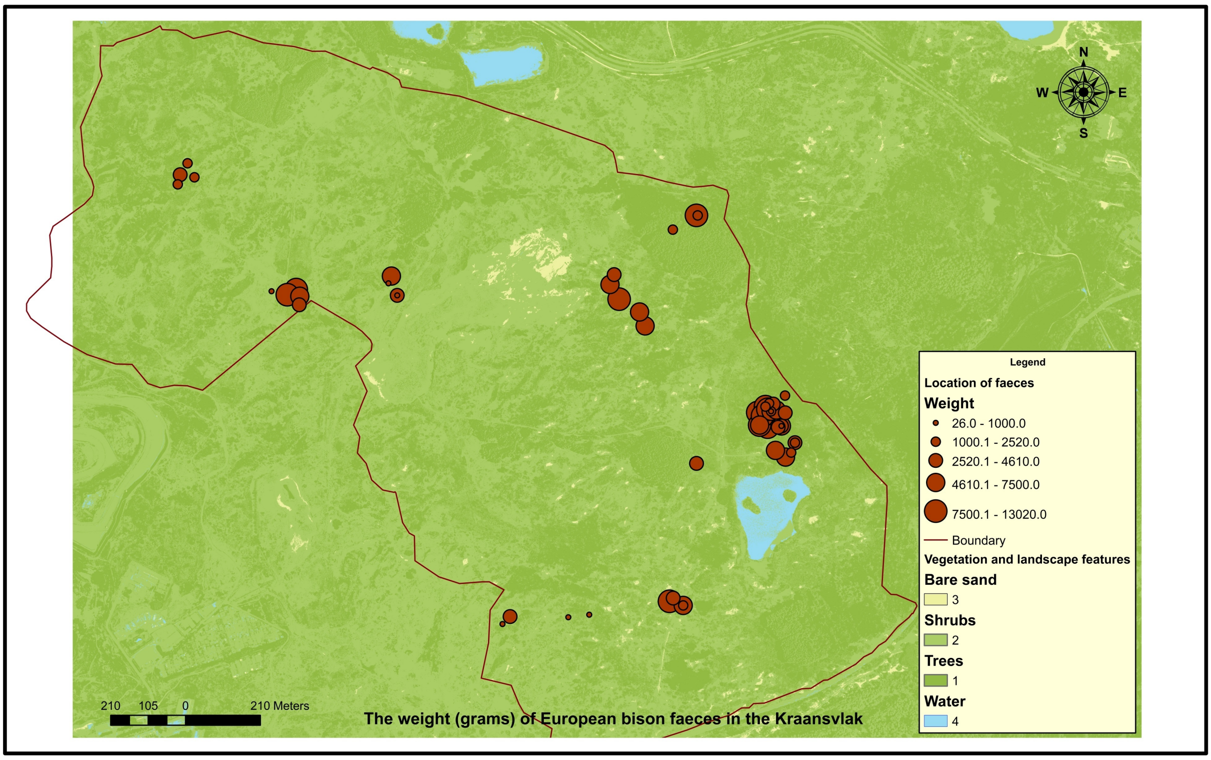


Figure 23. The weight (grams) of European bison dung in 18 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

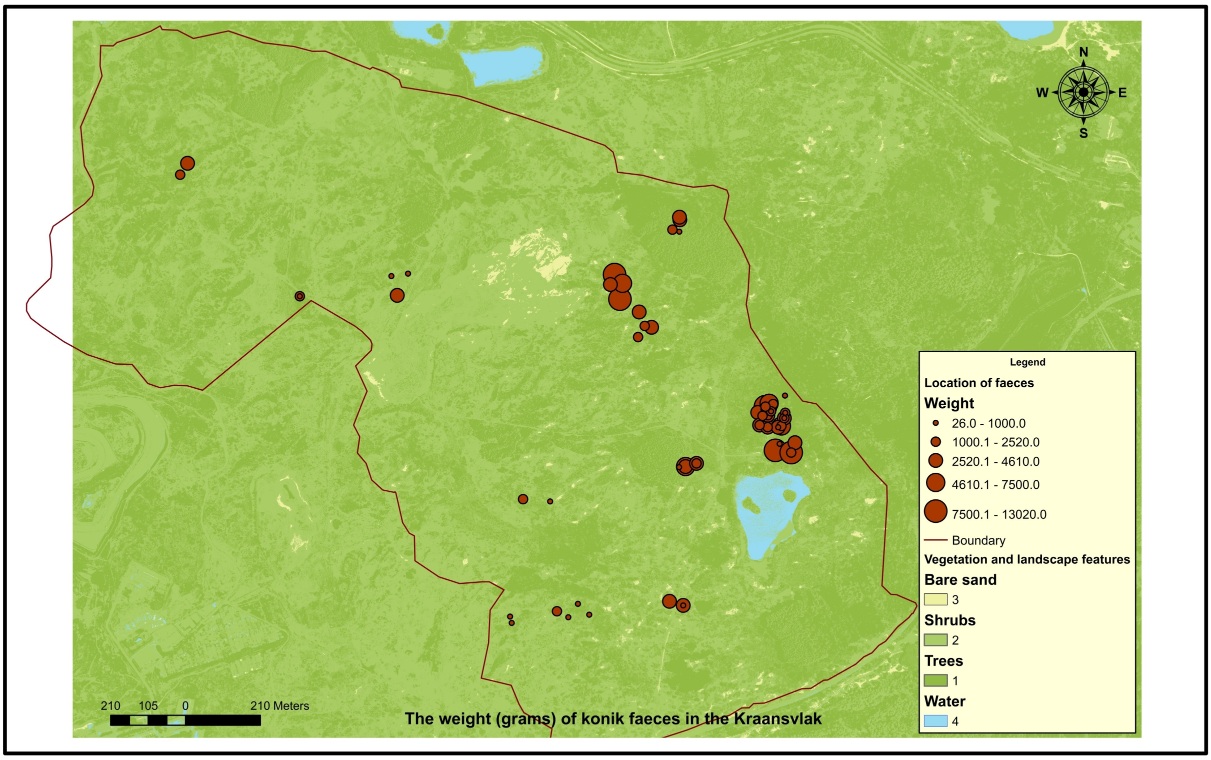


Figure 24. The weight (grams) of Konik dung in 18 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

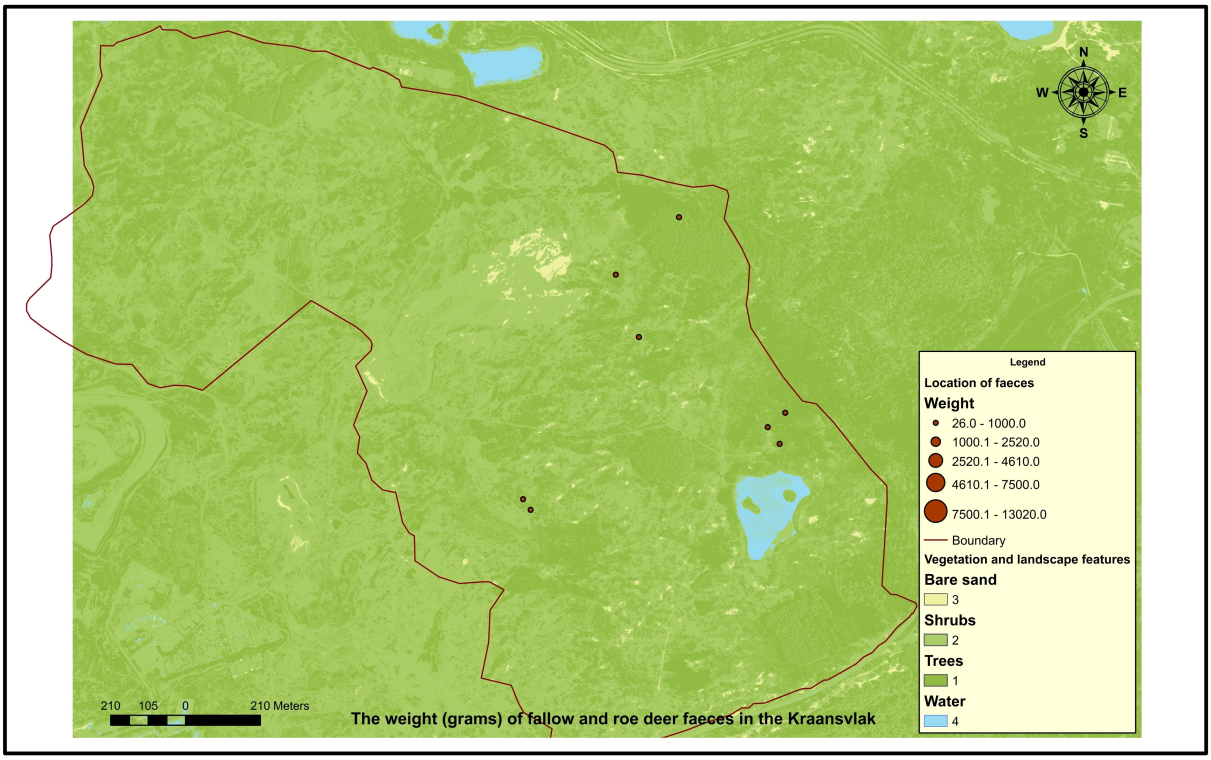


Figure 25. The weight (grams) of fallow and roe deer dung in 18 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

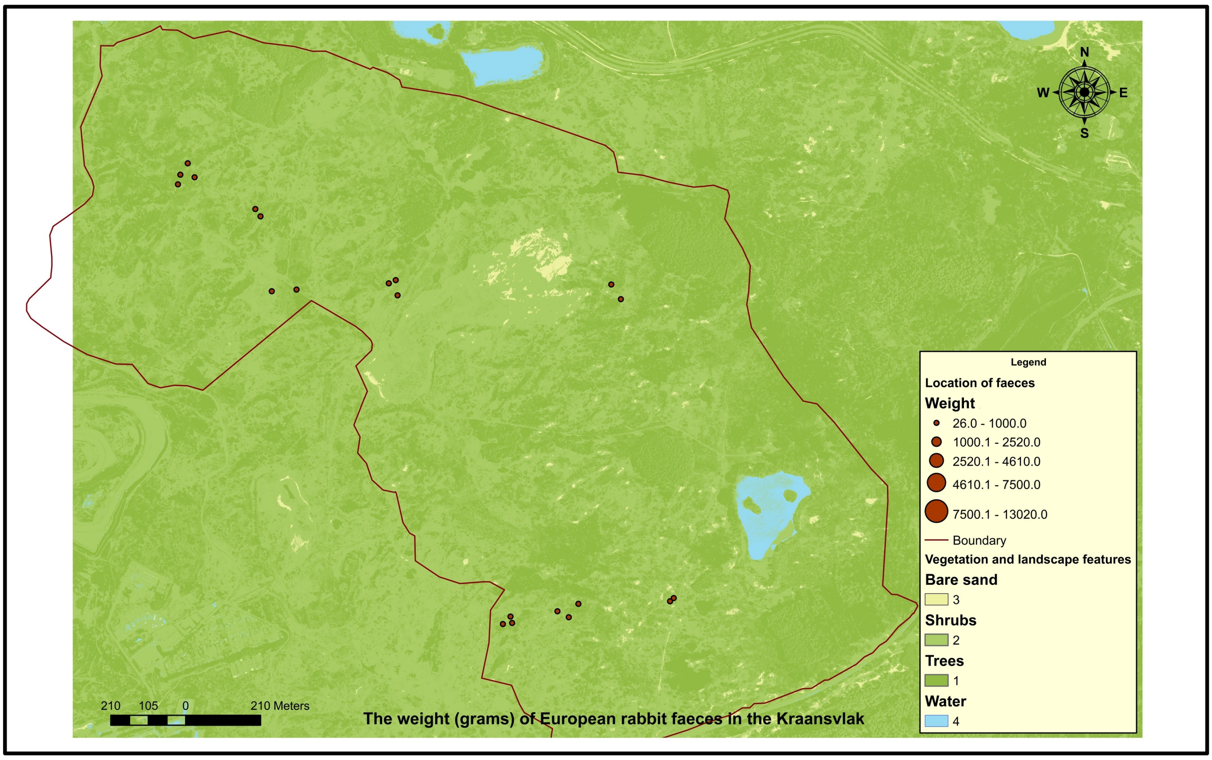


Figure 26. The weight (grams) of European rabbit dung in 18 hectares of the Kraansvlak area in the Zuid-kennemerland National Park.

Discussion

The nitrogen contents were found to significantly vary between bison and Konik dung of different ages but did not significantly vary between rabbit and deer dung of different ages. Since the amounts of nitrogen in bison and Konik dung were significantly less overtime compared to deer and rabbit dung, it could indicate that in bison and Konik dung nitrogen is returned to the soil at a faster rate. This could be due to the herbivores both being large and their dung pats also being large, meaning that more water is lost and therefore more nutrients are leached into the soil (Baker et al., 2004). The large return of nutrients from the introduced herbivores' faeces into the soil will have an effect on the rate of the nutrient cycle (Bakker et al., 2004). If nutrients are more readily lost from bison and Konik faeces it could accelerate nutrient turnover in the Kraansvlak (Knapp et al., 1999).

Fresh deer faeces had the highest percentage of nitrogen and carbon followed by fresh rabbit faeces. These results are to be expected as roe deer and rabbits are both browsers. The faeces of browsers have higher nitrogen concentrations than the faeces of grazers (Sitter et al., 2014). When comparing deer faeces in the Kraansvlak to what was found in Axis deer pellets which had 1.7% nitrogen, deer faeces had a much higher concentration of nitrogen (Moe and Wegge, 2008). Depending on where they graze, deer may have a greater effect than the other herbivores on the nutrient cycle and species composition in the areas they defecate in.

Deer faeces may have higher nitrogen concentrations due to the season the sampling was conducted in. There will be a variation in nitrogen concentrations in all of the herbivores' faeces throughout the year due to change in season and vegetation (Burns et al., 2009; Grant, 2000; Stapelberg et al., 2008). For example, in winter when there is less grass available bison eat bark (Smitskamp, 2011). The nitrogen concentration of rabbit faeces was higher than those of bison faeces. The nitrogen concentrations of rabbit faeces have also been found to be higher then cow faeces (Bakker et al., 2004).

Rabbit and deer had faeces with higher percentages of nutrients however they contributed much less to the area in terms of total weight of nutrients. The amount of nutrients deposited to each area may then have more of an effect than the higher concentrations of nutrients. Bison and Konik both have larger amounts of nutrients in their feaces due to their

size. Bakker, et al (2004). found that different sized herbivores have different effects on nitrogen cycling within the same habitat. Although bison and Konik contribute larger amounts of nutrients they would also take away larger amounts through grazing.
The maps of nitrogen concentrations showed that each of the herbivores faeces with high nitrogen concentrations were all in a different location to each other. Where there were bison faeces of high nitrogen concentrations Konik faeces found in the same location had much lower nitrogen concentrations. The spatial distribution of nitrogen concentrations was fairly even across the landscape.

Konik faeces with the highest concentrations of carbon were located close to lake; Bison faeces with higher concentration of carbon were located in only one place where the concentrations of carbon in Konik faeces were high. Deer and rabbit faeces had low concentrations of carbon in the west of the area and higher concentrations closer to the lake. The distribution of carbon over the area was also fairly uniform. The amount of carbon in bison, deer and rabbit dung was also evenly spread out over the area. In contrast, the Konik dung found near to the lake has higher amounts of carbon compared to dung found in other areas.

As hypothesised, the distribution of bison, Konik, deer and rabbit faeces was non-random. This corresponds to a study done on the distribution of excreta on free-ranging cattle, ponies and fallow deer which showed that the location of their excreta was non-random (Edwards & Hollis,1982) and a study done on the redistribution of nutrients due to herbivores showed that available phosphorous can be concentrated near shade and watering areas (Franzluebbers, et al 2000).

Bison and Koniks, the two largest herbivores in the Kraansvlak, were the greatest contributors of nitrogen and carbon. Large herbivores have been found to increase nitrogen availability in grassland ecosystems from the nitrogen found in dung and urine (Frank, 2008). Although deer faeces had the highest percentage of nitrogen, the total weight of deer faeces in the whole area was less than the weight of nitrogen from bison, Konik and rabbit faeces. Bison and Konik dung contributed the greatest amount of nitrogen in terms of weight to the area. Since bison and Konik put in more nutrients per hectare than deer and rabbit they have a greater influence on the nutrient cycle.

Depending on the species of herbivore there can be different amounts of nutrients that are eventually returned to the same area that they are taken from (Mohamed, 1998). In enclosed areas like the Kraansvlak, bison and horses can drive vegetation dynamics through dung deposition and grazing. When the spatial distribution of faeces is different for each animal it can create a moving mosaic of nutrient availability (Gillet et al., 2010). Large herbivores have been known to cause nutrient enrichment of some locations while depleting other areas (Auerswald et al., 2010).

A study done to understand how free ranging Konik horses defecate found that Koniks continue to graze where they defecate (Maurice, 2004). Although Konik horses preferred to defecate in certain areas, this could be because there was better quality foliage in those areas or they could be drinking and resting locations. The distribution may also be non-random for the bison and Koniks because the size of the populations have become too large for the size of the area (Lamoot et al., 2004). Gillet et al., (2010) showed dung density is patterned in a heterogenous way if the paddock is large and there is a small number of cattle.

The distribution of bison faeces was non-random due to bison avoiding dense shrubs and frequently visiting the lake. Large herbivores are known to cause concentrations of nutrients by excreting in patches (Auerswald et al., 2010). The quadrat just north of the lake had the highest amount of bison dung. This may be because the bison frequently visited the lake to drink. Bison are like cattle in that they have resting areas, this could explain why the bisons' dung was more dense around the lake and had a non-random distribution (Auerswald et al., 2010; Guo et al., 2009). Truett et al., (2001) found that American bison also prefer sites near water and gentle slopes. White et al. (2001) found that the density of faeces around a water tank were greater when cattle were under heat stress and Grant et al., (2000) and Silva et al., (2013) found it is not uncommon for faeces to be concentrated around water points or where animals rest (Grant et al., 2000).

Deer dung was more dense near the lake and to the north end of the Kraansvlak. There are also greater amounts of Konik faeces on the east side of the Kraansvkal. This means that nitrogen and carbon inputs will be greater near the lake. Rabbit faeces was distributed away from vegetation in obvious latrines. The total amounts of nutrients deer and rabbit contributed were very small compared to bison and Konik.

The quality of vegetation for foraging, temperature, intensity of slope, density of vegetation and distance to fences and water can all influence the spatial distribution of the faeces of cows (Silva et al., 2013). The electronic fence could be a reason why some areas are less attractive to the herbivores. Auswald et al., (2010) found that the only reason for cattle to go near an electronic fence was to use the shade near by or to visit water troughs (Auerswald et al., 2010). Excreta of cattle was found to increase in density with distance to a fence (Auerswald et al., 2010).

The period of activity may also have an effect on how faeces have been distributed. Bison have been found to be more active during the growing season which is from April to June (Smitskamp, 2011). In the breeding season, American bison stay as one herd and prefer sandy flat areas. For the rest of the year they are more likely to visit hilly and wooded habitats (Steuter et al., 2011).

The habitual latrine sites of rabbits will be associated with localised soil nutrient enrichment and greater plant growth (Feeley, 2005). Grazing lawns require high phosphorous concentrations. The removal of nutrients due to deer grazing and defecating in different locations could lead to low soil phosphorous levels (Moe & Wegge, 2008).

As large herbivores tend to graze in preferential areas in their habitat and often move to other localities for resting, there can be a redistribution of nutrients over an area and areas often become partly nutrient-poorer and partly nutrient-richer (Kooijman and smit, 2001; Gillet et al., 2010). This can induce a directional drift in plant succession. In one season the patchiness of dung deposition has a direct impact on local vegetation dynamics by altering biotic interactions and nutrient availability (Gillet et al., 2010).

How the distribution of nutrients may change the species composition

A study done on the impact of cattle dung on plant species in Sweden found that cattle dung can impact vegetation in three ways: (1) by changing the relative abundance of species in the soil seed bank under dung, and/or (2) by influencing the deposition of seeds in the dung, and/or (3) by intensifying the growth of some species through nutrient release (Dai, 2000). Consequently, in areas with high dung pat density, plant species which react positively to high nutrient soil content will be more abundant.

One of the factors that would affect the distribution of nutrients and requires more research is if the herbivores in the Kransvlaak eat herbage near dung patches. Cattle have been known to reject herbage near dung patches for some time even if there is good quality food nearby so it is possible that bison do the same (Auerswald et al., 2010). Bison and the other grazers are also known to prefer regrowth with higher nitrogen and will return to heavily grazed sites. This then causes a patchwork overtime of heavily grazed and lightly grazed areas. In the heavily grazed sites plant richness increases (Truett et al., 2001). In the first paragraph it was mentioned that bison and Konik could increase the amount of nitrogen input into the soil and accelerate nutrient turnover. This would only happen in patches due to the spatial location of their faeces. This would be similar to the outcome of a study by Baker et al. (2004), which found that under cattle grazing only a few patches receive all nitrogen and most areas had net nutrient removal.

In a study done by Smitskamp, (2011) GPS fixes were used to find what habitat bison and Konik were most commonly found in. The habitat most preferred by bison and Koniks was rough grassland. Grass was also the main component of their diet. Both species avoided open water although Konik horses were shown to be frequently found south of the lake. If most of the nutrients are coming from grasses then the herbivores will be contributing more nutrients to the other types of vegetation since they take the nutrients from the grassland through foraging and input the nutrients to other areas containing shrubs and other types of vegetation through excretion (Smitskamp, 2011). Moe and Wegge (2008) found that deer feed almost exclusively on the grasslands, but they spend only 24% of their time in this type of habitat. Accordingly, an estimated 10.1 tons of dung (DM) were deposited outside the grasslands each month from February to May. This amount converts to 2.02 tons in each of the other five types habitat, if randomly distributed and of equal size (Moe & Wegge, 2008).

Herbivores have been shown to increase plant species' richness and diversity in grassland vegetation (Burns et al., 2009). On the Great Plains (USA), bison have reduced the height of grasses both by selectively removing mid-grasses, to the advantage of shortgrass species, and by selecting for genetically dwarfed forms of some species (Truett et al., 2001).
Even though the studies by truett et al. (2001) and by Smitskamp (2011) show that bison prefer to eat grasses and can reduce unwanted grass encroachment, management authorities should still monitor population sizes since all of the herbivores in the Kraansvlak have preferred areas to defecate in which with large population sizes could lead to

undesirable tall grass and shrub encroachment. As found in a study done by Poinsatte (2009), the addition of American bison faeces to plots meant nitrogen increased in the soil along with an increase in vegetation biomass. A study on reindeer by Van der Wal et al. (2004), also found that an increase in the density of reindeer caused an increase in faeces which meant that grass abundance also increased. Management authorities also need to consider how the redistribution of nutrients relates to the effects of atmospheric deposition. An increase in nitrogen from excrement and nitrogen deposition in one area will cause nitrogen enrichment of that area. This will mean that certain species of vegetation will favour the area over others (Fottner et al., 2007).

Conclusion

This research contributes to the knowledge of how introduced large herbivores could affect the distribution of nutrients in coastal sand dunes in the Netherlands. The results showed that the four different species of herbivore could each alter the ecosystem in a different way due to the varying concentrations of nitrogen they have in their dung, the varying amounts of nutrients they contribute to the area and the different spatial distribution of their dung. Through defecating in preferred locations, the European bison and Konik have contributed large amounts of nutrients to areas they most likely use for resting or drinking. Rabbits and deer faeces were sometimes found in areas where there were little amounts of bison and Konik faeces and there were also significantly higher nitrogen concentrations between the faeces of deer and the faeces of Konik and bison. Although deer faeces had higher nitrogen concentrations it contributed the lowest amount of nitrogen to the area. By defecating more in a particular area and having large amounts nutrients in their faeces, bison and Konik could have a greater influence on the nutrient cycle in the Kraansvlak. To help managers protect the plant diversity in the Zuid-Kennemerland National Park the information in this thesis could be used in combination with information about where the herbivores graze to see if nutrients are redistributed.

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Appendix A

Table 1. Results of a one-way ANOVA on the percentage of nitrogen in fresh, intermediate and old bison dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	2.056	2	1.028	8.04	0.003	3.59
Within groups	2.173	17	0.127			
Total	4.230	19				

Table 2. Results of a one-way ANOVA on the percentage of carbon in fresh, intermediate and old bison dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	4.965	2	2.482	0.180	0.836	3.59
Within groups	234.283	17	13.781			
Total	239.249	19				

Table 3. Results of a one-way ANOVA on the percentage of nitrogen in fresh and old Konik dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	1.099	1	1.099	16.641	0.0008	4.493
Within groups	1.056	16	0.066			
Total	2.155	17				

Table 4. Results of a one-way ANOVA on the percentage of carbon in fresh and old Konik dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	8.217	1	8.217	1.046	0.321	4.493
Within groups	125.64	16	7.852			
Total	133.857	17				

Table 5. Results of a one-way ANOVA on the percentage of nitrogen in fresh and old deer dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	0.002	1	0.002	0.009	0.923	4.667
Within groups	2.822	13	0.217			
Total	2.824	14				

Table 6. Results of a one-way ANOVA on the percentage of carbon in fresh and old deer dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	7.676	1	7.676	1.570	0.232	4.667
Within groups	63.553	13	4.888			
Total	71.229	14				

Table 7. Results of a one-way ANOVA on the percentage of nitrogen in fresh and old rabbit dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	0.009	1	0.009	0.025	0.876	4.493
Within groups	5.927	16	0.370			
Total	239.249	19				

Table 8. Results of a one-way ANOVA on the percentage of carbon in fresh and old rabbit dung

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P-value	F critical value
Between groups	0.273	1	0.273	0.021	0.884	4.493
Within groups	201.948	16	12.621			
Total	202.222	17				

Table 9. Mean weight and total weight of nitrogen, carbon and phosphorous per hectare from bison, Konik, deer and rabbit dung.

	Carbon	Nitrogen	Phosphorous
Bison		28.22, 1947.23	
Konik	522.48, 37618.72	15.73, 1148.44	
Deer		0.32, 13.17	
Rabbit	29.35, 1085.90	1.63, 58.82	

Appendix B

Table 1. Data collected in 18 hectares of the Kraansvlak

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
4	Bison	52.395333	4.565783	1400	1400	Fresh
4	Konik	52.395333	4.565783	3000	3000	old
4	Bison	52.395333	4.565783	500	500	old
4	Konik	52.395150	4.565917	750	750	old
4	Konik	52.395150	4.565917	5750	5750	old
4	Konik	52.395483	4.565783	1500	1500	old
4	Konik	52.395517	4.566117	500	500	old
4	bison	52.395850	4.566417	1800	1800	old
8	bison	52.393583	4.566217	8740	8740	old
8	Konik	52.393583	4.566217	1990	1990	old
8	rabbit	52.393583	4.566217	30	30	old
8	Konik	52.393400	4.566033	1390	1390	old
8	deer	52.393400	4.566050	20	20	old
8	Konik	52.393750	4.566150	1140	1140	old
8	bison	52.393867	4.566283	4370	4370	old
8	Konik	52.393867	4.566300	4850	4850	old
8	rabbit	52.393867	4.566317	110	110	old
8	bison	52.393950	4.552683	2690	2690	old
8	Konik	52.393950	4.552700	924	924	old
8	rabbit	52.393950	4.552717	20	20	old
8	deer	52.393950	4.552733	9	9	old
10	Konik	52.393667	4.574833	3840	3840	old
10	bison	52.393783	4.575517	8160	8160	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
10	rabbit	52.393783	4.575533	2	2	old
10	deer	52.393783	4.575550	5	5	old
10	bison	52.393783	4.575567	1750	1750	intermediat e
10	Konik	52.393367	4.574817	790	790	old
10	deer	52.393367	4.574833	25	25	old
10	deer	52.393367	4.574850	10	10	fresh
10	Konik	52.393417	4.574533	1500	1500	old
10	bison	52.393417	4.574550	1930	1930	old
10	deer	52.393417	4.574567	9	9	old
10	deer	52.393733	4.574800	26	26	fresh
10	Konik	52.393733	4.574817	3250	3250	fresh
16	bison	52.392017	4.571983	6390	6390	old
16	Konik	52.392017	4.572000	3000	3000	old
16	rabbit	52.392017	4.572017	40	40	old
16	bison	52.392267	4.572150	2580	2580	old
16	Konik	52.392267	4.572167	10330	10330	old
16	rabbit	52.392267	4.572183	8	8	old
16	deer	52.392267	4.572200	16	16	old
16	deer	52.392267	4.572217	36	36	fresh
16	deer	52.392050	4.572467	20	20	fresh
16	bison	52.392050	4.572483	18840	18840	old
16	Konik	52.392050	4.572500	6750	6750	old
16	bison	52.391650	4.572367	8140	8140	old
16	bison	52.391650	4.572383	2370	2370	intermediat e
16	Konik	52.391650	4.572400	13020	13020	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
16	rabbit	52.391650	4.572417	80	80	old
16	bison	52.391883	9.116667	1210	1210	old
18	Konik	52.391333	4.573200	3500	3500	old
18	bison	52.391333	4.573217	4790	4790	old
18	bison	52.388867	4.578683	2480	2480	intermediate
18	rabbit	52.390983	4.573417	15	15	old
18	Konik	52.390983	4.573433	2520	2520	old
18	bison	52.390983	4.573450	5750	5750	old
18	Konik	52.390950	4.573717	4610	4610	old
18	bison	52.390950	4.573733	8.17	8.17	old
18	Konik	52.390700	4.573167	1340	1340	old
18	rabbit	52.390700	4.573183	15	15	old
18	deer	52.390700	4.573200	35	35	fresh
23	deer	52.389233	4.578750	5	5	fresh
23	bison	52.389050	4.578767	2800	2800	intermediate
23	Konik	52.389050	4.578767	1900	1900	old
23	rabbit	52.389267	4.579250	8	8	fresh
23	Konik	52.389267	4.579250	750	750	old
23	bison	52.389267	4.579250	1400	1400	old
23	deer	52.389267	4.579250	2	2	fresh
23	Konik	52.388867	4.578683	750	750	fresh
23	Konik	52.388867	4.578683	400	400	old
23	bison	52.388867	4.578683	500	500	old
23	bison	52.388867	4.578683	6500	6500	intermediate
23	Konik	52.388867	4.578683	2200	2200	fresh

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
23	deer	52.388867	4.578683	1	1	old
23	rabbit	52.388867	4.578683	2	2	old
23	Konik	52.388867	4.578683	1900	1900	old
23	rabbit	52.388900	4.578900	2	2	fresh
23	bison	52.388900	4.578900	5000	5000	intermediate
23	deer	52.388900	4.578900	15	15	fresh
23	deer	52.388900	4.578900	2	2	old
23	bison	52.388833	4.579267	3750	3750	intermediate
23	deer	52.388833	4.579267	31	31	fresh
23	Konik	52.388833	4.579267	1000	1000	old
23	Konik	52.388833	4.579267	1400	1400	fresh
23	Konik	52.388700	4.579233	750	750	fresh
23	Konik	52.388700	4.579233	4100	4100	old
23	Konik	52.388700	4.579233	1400	1400	fresh
23	bison	52.388500	4.579117	1000	1000	old
23	bison	52.388500	4.579117	5900	5900	intermediate
23	Konik	52.388500	4.579117	7500	7500	fresh
23	Konik	52.388500	4.579117	1500	1500	old
23	bison	52.388500	4.579117	3500	3500	old
23	deer	52.388467	4.578983	22	22	fresh
23	Konik	52.388467	4.578983	1000	1000	old
23	deer	52.388467	4.578983	2	2	old
23	Konik	52.388467	4.578983	3000	3000	fresh
23	bison	52.388467	4.578983	3250	3250	intermediate

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
23	deer	52.388467	4.578983	12	12	fresh
23	Konik	32.388700	4.578883	3250	3250	fresh
23	bison	32.388700	4.578883	9800	9800	intermediate
23	bison	32.388700	4.578883	1600	1600	fresh
23	Konik	32.388700	4.578883	5400	5400	fresh
23	Konik	52.388767	4.578550	2750	2750	fresh
23	bison	52.388767	4.578550	24200	24200	intermediate
23	deer	52.388767	4.578550	1	1	old
23	Konik	52.388767	4.578550	2400	2400	old
23	deer	52.388467	4.578550	10	10	fresh
23	deer	52.388467	4.578550	35	35	old
23	bison	52.388467	4.578550	9400	9400	intermediate
23	Konik	52.388467	4.578550	3100	3100	fresh
23	Konik	52.388467	4.578550	2000	2000	old
23	Konik	52.388517	4.578217	3250	3250	old
23	bison	52.388517	4.578217	9300	9300	intermediate
23	bison	52.388517	4.578217	5200	5200	old
23	deer	52.388517	4.578217	3	3	old
23	Konik	52.388517	4.578217	1100	1100	old
23	bison	52.388750	4.578333	8000	8000	intermediate
23	deer	52.388750	4.578333	5	5	old
23	Konik	52.388750	4.578333	1500	1500	old
23	bison	52.388750	4.578333	10100	10100	intermediate

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
23	deer	52.388917	4.578550	4	4	old
23	Konik	52.388917	4.578550	3100	3100	fresh
23	Konik	52.388917	4.578550	3000	3000	old
23	bison	52.388917	4.578550	13400	13400	old
23	bison	52.388917	4.578550	8000	8000	intermediate
23	deer	52.388917	4.578550	3	3	old
23	Konik	52.388833	4.578133	3750	3750	fresh
23	deer	52.388833	4.578133	5	5	old
23	bison	52.388833	4.578133	10000	10000	intermediate
23	Konik	52.388833	4.578133	4000	4000	fresh
23	bison	52.388983	4.578450	8400	8400	old
23	Konik	52.388983	4.578450	9000	9000	fresh
23	bison	52.388983	4.578450	1900	1900	intermediate
23	Konik	52.388983	4.578450	1600	1600	old
23	deer	52.389067	4.578600	23	23	old
23	bison	52.389067	4.578600	2000	2000	old
23	Konik	52.389067	4.578600	6200	6200	fresh
24	bison	52.387433	4.574917	2970	2970	intermediate
24	Konik	52.387433	4.574917	940	940	fresh
24	Konik	52.387450	4.575183	2920	2920	old
24	bison	52.387450	4.575183	2200	2200	intermediate
24	Konik	52.387450	4.575183	4900	4900	fresh
24	deer	52.387450	4.575183	8	8	old
24	bison	52.387533	4.575633	4080	4080	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
24	rabbit	52.387533	4.575633	10	10	old
24	Konik	52.387533	4.575633	2720	2720	old
24	Konik	52.387533	4.575633	1250	1250	fresh
25	bison	52.387833	4.579533	16930	16930	fresh
25	Konik	52.387833	4.579533	8700	8700	fresh
25	bison	52.387833	4.579533	2000	2000	intermediate
25	Konik	52.387833	4.579533	2090	2090	old
25	bison	52.387833	4.579533	1140	1140	old
25	rabbit	52.388083	4.579683	10	10	old
25	Konik	52.388083	4.579683	3780	3780	old
25	bison	52.388083	4.579683	2050	2050	intermediate
25	bison	52.388083	4.579683	3210	3210	old
25	deer	52.388050	4.579050	174	174	fresh
25	Konik	52.388050	4.579050	940	940	old
25	Konik	52.387883	4.578883	9760	9760	old
25	bison	52.387883	4.578883	4870	4870	old
25	bison	52.387883	4.578883	5640	5640	fresh
25	bison	52.387717	4.579300	5960	5960	fresh
36	Konik	52.381633	4.577833	1620	1620	old
36	bison	52.381633	4.577833	5910	5910	fresh
36	Konik	52.381517	4.578267	800	800	old
36	bison	52.381517	4.578267	3820	3820	old
36	rabbit	52.381517	4.578267	15	15	old
36	Konik	52.381517	4.578267	3000	3000	old
36	bison	52.381517	4.578267	1170	1170	fresh

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
36	Konik	52.381917	4.578383	1610	1610	old
36	rabbit	52.381917	4.578383	88	88	old
45	rabbit	52.38362	4.56802	340	340	old
45	Konik	52.38362	4.56802	50	50	old
45	bison	52.38362	4.56802	4330	4330	old
45	deer	52.38362	4.56802	6	6	old
45	rabbit	52.38343	4.56771	80	80	old
45	bison	52.38343	4.56771	46	46	old
45	deer	52.38346	4.56809	9	9	old
45	rabbit	52.38346	4.56809	110	110	old
45	bison	52.38346	4.56809	2.74	2.74	old
45	Konik	52.38346	4.56809	26	26	old
46	rabbit	52.383767	4.56995	130	130	old
46	Konik	52.383767	4.56995	2001	2001	old
46	bison	52.38396	4.57081	20540	20540	old
46	rabbit	52.38396	4.57081	40	40	old
46	Konik	52.38396	4.57081	61	61	old
46	rabbit	52.38362	4.57042	60	60	old
46	Konik	52.38362	4.57042	74	74	old
46	bison	52.38362	4.57042	41	41	old
46	bison	52.38369	4.57128	58	58	old
46	Konik	52.38369	4.57128	34	34	old
47	bison	52.384133	4.574733	3900	3900	old
47	rabbit	52.384133	4.574733	430	430	old
47	Konik	52.384050	4.574583	3570	3570	old
47	bison	52.384050	4.574583	8590	8590	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
47	rabbit	52.384050	4.574583	330	330	old
47	deer	52.384050	4.574583	10	10	old
47	Konik	52.384050	4.574583	3170	3170	old
47	rabbit	32.383917	4.574650	240	240	old
47	bison	32.383917	4.574650	6270	6270	old
47	Konik	32.383917	4.574650	190	190	old
47	deer	32.383917	4.574650	16	16	old
47	bison	52.383950	4.575150	4790	4790	old
47	Konik	52.383950	4.575150	3230	3230	old
47	bison	52.383950	4.575150	6050	6050	old
47	Konik	52.383950	4.575150	350	350	old
47	bison	52.383950	4.575150	1200	1200	fresh
47	deer	52.383950	4.575150	13	13	old
53	bison	52.386800	4.569533	8800	8800	old
53	rabbit	52.386800	4.569533	40	40	old
53	deer	52.386800	4.569533	24	24	old
53	Konik	52.386800	4.569533	5.7	5.7	old
53	bison	52.386700	4.569100	8850	8850	old
53	Konik	52.386700	4.569100	3250	3250	old
53	Konik	52.386583	4.568500	1530	1530	fresh
53	bison	52.386583	4.568500	1930	1930	old
53	deer	52.386583	4.568500	76	76	old
53	rabbit	52.386583	4.568500	410	410	old
53	bison	52.386317	4.568817	1300	1300	fresh
53	rabbit	52.386317	4.568817	40	40	old
53	bison	52.386317	4.568817	4730	4730	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
53	Konik	52.386317	4.568817	3180	3180	old
53	deer	52.386317	4.568817	33	33	old
53	bison	52.386533	4.569617	6090	6090	old
53	Konik	52.386533	4.569617	3280	3280	old
53	Konik	52.386533	4.569617	460	460	fresh
53	rabbit	52.386533	4.569617	10	10	old
64	rabbit	52.392067	4.563133	70	70	old
64	rabbit	52.392067	4.563133	4	4	fresh
64	Konik	52.392167	4.562967	45	45	old
64	deer	52.392167	4.562967	20	20	fresh
64	bison	52.392167	4.562967	6350	6350	old
64	bison	52.391983	4.562850	96	96	old
64	rabbit	52.391983	4.562850	40	40	old
64	deer	52.391683	4.563217	20	20	fresh
64	rabbit	52.391683	4.563217	210	210	old
64	bison	52.391683	4.563217	98	98	old
64	Konik	52.391683	4.563217	3440	3440	old
64	bison	52.391683	4.563217	2870	2870	intermediate
64	Konik	52.392233	4.563650	90	90	old
65	bison	52.391800	4.559050	12680	12680	old
65	rabbit	52.391800	4.559050	40	40	old
65	bison	52.391633	4.559200	6200	6200	old
65	Konik	52.391633	4.559200	40	40	old
65	Konik	52.391633	4.559200	1640	1640	fresh
65	deer	52.391633	4.559200	22	22	fresh
65	rabbit	52.391417	4.559183	20	20	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
65	bison	52.391417	4.559183	2800	2800	old
65	bison	52.391667	4.558683	7800	7800	old
65	rabbit	52.391750	4.558033	110	110	old
65	bison	52.391750	4.558033	91	91	old
69	Konik	52.392900	4.941117	9590	9590	
69	bison	52.392900	4.941117	50210	50210	
69	Konik	52.392900	4.941117	1480	1480	
69	rabbit	52.392900	4.941117	320	320	
69	deer	52.392900	4.941117	16	16	old
69	deer	52.392600	4.564750	13	13	
69	rabbit	52.392467	4.564517	110	110	
69	bison	52.392467	4.564517	1100	1100	
69	rabbit	52.392650	4.564167	80	80	
69	bison	52.392650	4.564167	3040	3040	
69	Konik	52.392650	4.564167	2970	2970	
74	rabbit	52.393817	4.557317	110	110	old
74	rabbit	52.393817	4.557317	10	10	fresh
74	rabbit	52.393633	4.557533	20	20	fresh
74	rabbit	52.393633	4.557533	110	110	old
74	rabbit	52.393583	4.557150	20	20	old
77	rabbit	52.39495	4.55451	240	240	old
77	deer	52.39495	4.55451	6	6	old
77	Konik	52.39495	4.55451	3900	3900	old
77	bison	52.39495	4.55451	1550	1550	old
77	deer	52.39466	4.55421	12	12	old
77	bison	52.39466	4.55421	3470	3470	old

Quadrat	Species	Latitude	Longitude	Weight (grams)	Weight (grams)	Age
77	Konik	52.39466	4.55421	1140	1140	old
77	rabbit	52.39466	4.55421	160	160	old
77	bison	52.394600	4.554800	2270	2270	old
77	rabbit	52.394600	4.554800	140	140	old
77	rabbit	52.394600	4.554800	5	5	fresh
77	bison	52.394417	4.554117	1230	1230	old
77	rabbit	52.394417	4.554117	30	30	old