DAVIS EXPEDITION FUND

REPORT ON EXPEDITION / PROJECT

Expedition/Project Title:	Effect of invasive cactus *Opuntia stricta* on mammalian herbivore abundance and on the herbaceous community in Laikipia, Kenya
Travel Dates:	09.07.2018 – 07.08.2018
Location:	Mpala, Laikipia, Kenya
Group Members:	Iris Berger (only member grant awarded to), Brogan Costello, Giorgia Ferretti
Aims:	Tropical Biology Association field course: first two weeks quire fieldwork and analysis skills through workshop and lectures, second two weeks: conduct independent project

Outcome (a minimum of 500 words):-

Effect of invasive cactus *Opuntia stricta* on mammalian herbivore abundance and on the herbaceous community in Laikipia, Kenya

Iris Berger, University of Edinburgh, UK

Brogan Costello, National University of Ireland, Galway

Giorgia Ferretti, University of Lausanne, Switzerland

Abstract

Invasive species negatively affect the native flora and fauna in various systems all over the globe. In Laikipia, Kenya, invasive cactus *Opuntia stricta* has spread widely, and there is concern that African savanna herbivores of conservation concern may be negatively impacted by its presence. Here, we asked whether *O. stricta* reduces mammalian herbivore abundance, and how this negative effect may be mediated: directly, through physical obstruction, or indirectly, through altering the herbaceous community which ultimately impacts herbivores. We also considered the influence of tree density which affects the foraging behaviour of herbivores through the predation-risk perceived. In a "red-soil"-savannah in Laikipia, we sampled 34 20m x 20m plots with varying densities of *O. stricta*, where we recorded the volume of all cacti, the abundance of different tree species and the relative abundance of different grass species along four transects within the plot. A Structural Equation Model was generated, and results showed a negative effect of the invasive cactus on the herbivores distribution with 42% of the variance explained by the model. The presence of the cactus exhibited a positive effect on certain grass species which may be non-palatable, as grasses influenced dung abundance negatively. The model suggests that the presence of *O.stricta* reduces the abundance of herbivores in the area because of both physical obstruction and alteration of the herbaceous community. Therefore implementation of management schemes are required to reduce the spread of *O.stricta* and better control current invasions.

INTRODUCTION

Levels of biological invasions have grown exponentially in the past 25 years, and they have such large impacts that they are now considered a part of global change (Wan, Wang and Yu, 2017). This increase is largely thought to be due to anthropogenic activities, with increased worldwide trade. Introductions may be both intentional and accidental (Mack, 2003). Invasive species have large economic and environmental impacts and are known to reduce biodiversity and general plant health (McNeely, 2006; Kumschick et al., 2012). There are also large costs associated with their removal and control, much of which is difficult to fund through lack of research and "difference in opinion" (Shackleton *et al.*, 2017).

The family Cactacae is extremely popular in a horticultural context and is one of the most widely sold families, particularly in temperate regions (Walters et al, 2011). *Opuntia stricta* is an example of one of these cacti, which has been introduced but is now considered invasive across many countries. It was originally introduced to act as fencing against cattle, however, it has now become invasive in some African countries, Australia, and India (Foxcroft & Rejmánek, 2007). Within its introduced range it has escaped cultivation and is spreading to rangelands (Strum et al. 2015), conservation areas (Vila et al. 2003) and agricultural lands (Vila and Gimeno, 2003). It produces a large amount of seeds which tend to be spread by baboons feeding on their fruit, aiding its escape out of its introduced range (Foxcroft and Rejmanek, 2007). However, it can also spread through vegetative propagation and this is aided by its ability to remain succulent for several months once a portion has been removed from its parent plant; this means it is still capable of rooting after it has been broken off (Novoa et al., 2015).

Areas that have been fragmented or transformed for cultivation purposes are extremely susceptible to biological invasions; this is of particular concern for pastoralists whose crops and/or livestock may be affected by the invasion (Fensham, 1998). Shackleton et al. (2017) investigated the local perception of *O. stricta* in Laikipia, Kenya, where they found that the local population had an overwhelmingly negative perception of *O. stricta.* With many of the belief that it had negative impacts on livestock and agricultural land, as well as costing them money every month, with little to no benefits being listed for the species. The presence of *O. stricta* may therefore affect mammalian herbivore populations by reducing their ability or willingness to graze in invaded areas. This effect can be via direct obstruction (the cacti are extremely painful when they attach to herbivores) or via reduction in forage biomass, particularly herbaceous above-ground net primary productivity. In order to assess the relative importance of direct and indirect effects of *O. stricta* on mammalian herbivore

abundance, we used Structural Equation Models (SEM) which allow for the examination of different causal pathways (Grace et al., 2010; Riginos and Grace, 2008).

The aim of this study was to investigate if the presence of invasive cactus, *Opuntia stricta,* has an influence on mammalian herbivore presence in a "red-soil" savanna habitat on a local scale. We predicted that: (1) Higher levels of *O. stricta* will reduce the abundance of mammalian herbivore dung (as a measure of the levels of herbivores present). (2) A higher density of trees will reduce dung abundance (i.e. the presence of mammalian herbivores) through reducing visibility and thus increasing the predation-risk (as previously demonstrated by Riginos and Grace, 2008). (3) The presence of *O. stricta* will alter the herbaceous community (grass diversity and abundance), for example through competition for resources or by altering soil composition.

MATERIALS AND METHODS

Study site

To estimate the influence of the invasive species *O.stricta* on herbivores density, we compared invaded areas to non-invaded areas at the Mpala Research Centre (36°52' E, 0°17' N), MRC, in Laikipia, Kenya (Figure 1). MRC is managed for domestic cattle production and wildlife conservation, where common wild herbivores include: grazers, mostly plains zebras (*Equus burchelli*), and browsers, mostly giraffes (*Giraffa camelopardalis*), dik-dik (*Madoqua kirkii*), and kudu (*Tragelaphus strepsiceros*), and mixed feeders, mostly elephants (*Loxodonta africana*) and impala (*Aepyceros melampus*). Common large predators include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and spotted hyenas (*Crocuta crocuta*).
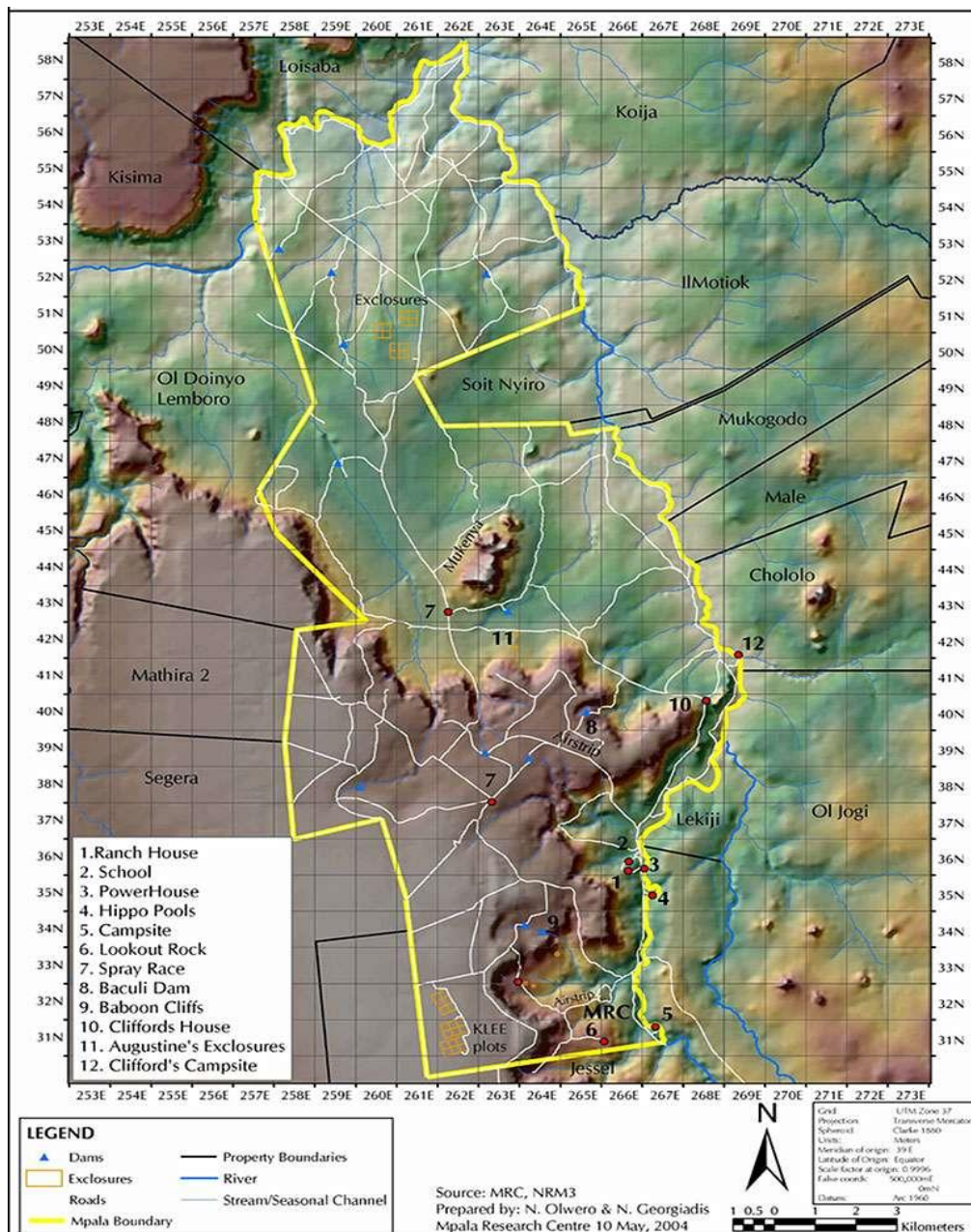
Figure 1: Map of Mpala Research Centre. Site with presence of *Opuntia stricta* located at point 4 ("Hippo Pools") and the site without the invasive species located at point 5 ("Campsite").

Data collection

Data were collected between July 27th and August 1st 2018, where 34 plots of 20 m x 20 m were selected (18 with the presence of *O. stricta*, and 16 without). Plots were randomly selected along the Ngare Nyiro river (no further than 300m) to have a constant vegetation structure and soil composition,

with all plots placed on "red soil". All the plots were a minimum of 30 m apart, and the *O.stricta*-invaded sampling area was 3.5 km away from the *O.stricta*-absent sampling area.

In each plot, we sampled four line transects in parallel to the perimeter, each spanning 20m and being 5m from the next transect. At every meter, the plant (grass, forb or tree) beneath the meter mark was recorded, giving a total of 80 points per plot. If it was a grass, then we identified the species. If no plant material was beneath the measuring tape, then we recorded the point as "bare". We identified all trees in the plot and categorized them into three height classes: <1 m, 1–2 m, and >2m.

We counted all dung piles of wild mammalian herbivores of every age class as long as we could identify the species. Riginos and Grace (2008) found dung densities of common wild herbivore species in this area to be correlated with the relative densities of the same species based on four years of aerial surveys, implying that dung counts are relatively reliable estimate of terrestrial vertebrate densities. Since ground visibility (i.e. the height and density of vegetation) may affect the ability of accurately recording all dung piles in a plot, we rated the ease of recording dung piles from one to three (decreasing ground visibility).

We measured the height, and two diameters in 90 degree angles of all *O.stricta* in a given plot. Additionally, we estimated the distance from the closest point of the plot to the river and from the next road, and we counted the number of animal trails found within the plot.

Data analysis

We approximated *O. stricta* volume using the formula:

$$height\ (cm) \times \frac{diameter\ 1\ (cm)}{2} \times \frac{diamter\ 2\ (cm)}{2} \times \pi$$

Subsequently, we summed the volume of all cacti in a plot to obtain the total cacti volume.

We calculated the percentage of basal cover from the ratio of points with vegetation to the total number of points along the transects in a given plot. The Shannon-Wiener Diversity Index was calculated for the grass community in each plot, of which the exponential is the true alpha diversity (Table 1).

Table 1. Formula of the diversity indices used to calculate alpha diversity. Notations used: S = total number of species in the community; p_i = proportion of S made up of the ith species

Diversity	Index	Formula	True Diversity	Reference
Alpha H_α	Shannon	$H' = -\sum_{i=1}^{S} p_i \ln p_i$	$\exp(H_\alpha)$	(Shannon, 1948)

Statistical analysis: bivariate analyses

We log-transformed the dung abundance data so that it was normally distributed, and subsequently performed a linear regression model. In the full model, the total volume of all cacti, the distance of the plot to the river, the distance of the plot to the road, the number of animal trails, the number of trees (of all three size classes), the rating of ground visibility, the alpha diversity of the grasses recorded, and the percentage of ground cover of a given plot were included as predictor variables. Non-significant terms were excluded from the model, starting with the least significant one. This resulted in a final model with the total cacti volume and the percentage of plant basal cover as the predictor variables, and the number of dung of all herbivore species (impala, zebra, giraffe, kudu, elephant, buffalo, dik-dik, and hare) combined as the response variable.

Statistical analysis: structural equation modelling

We used structural equation modelling (SEM) analyses to consider some of the effects that *O. stricta* may have on herbivores and the herbaceous community. SEM allows for the examination of possible causal pathways among intercorrelated variables, the associations among variables while statistically controlling for other model variables, and the likelihood of alternative models given the data collected (Bollen 1989; Grace et al., 2010; Eisenhauer et al., 2015).

We developed a structural equation meta-model which represents general theoretical premises without specifying statistical detail (Figure 2). Our a priori propositions are: (1) *O. stricta* may influence the abundance of herbivore dung either directly (for example through physical obstruction) or indirectly through affecting the herbaceous vegetation (for example by benefiting non-palatable grass species through allelopathy). (2) Trees may affect the abundance of dung (for example through reducing visibility which may increase the predation-risk). (3) Dung abundance (as a proximation for herbivore density on a local scale) is not likely to affect tree density, cactus density, or the herbaceous community in the short term.
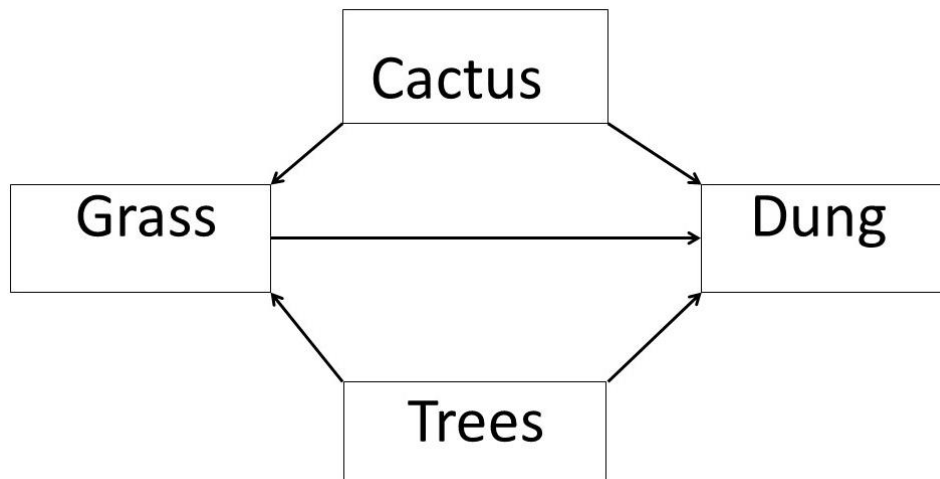
Figure 2: Metamodel of how herbivore dung may be affected by cactus, grass, and trees. Cactus may directly influence herbivore dung, or indirectly through influencing grasses which affect dung.

Since the number of terms in the model should be minimized (especially when the sample size is small), we grouped trees into four classes: Acacia species <2m, Acacia species >2m, Broadleaf species <2m, and Broadleaf species >2m. Only the most common grass species were kept in the model, namely: *Aristida* sp., *Chloris gayana, Chloris roxybaghiana, Cynodon sp., Dactyloctenium aegyptia,* and *Eragrostis racemosa.* Furthermore, we grouped giraffes and kudus together due to their similar foraging behaviour (large browsers). We explored three different models: (1) a full model with cacti, trees, grasses and dung of all species as the composite variables ("full model"), (2) a model with browsers, cacti and trees ("browser model"), and (3) a model with grazers, cacti and grasses ("grazer model"). The final model was chosen based on its highest R^2 value (i.e. the model that explained the most variation in the data recorded).

We conducted all statistical analyses in R version 1.1.442 (R Core Team, 2018).

RESULTS

Bivariate Analysis

The dung of each herbivore species decreased with increasing total cacti volume, although the strength of the effect varied with impala, buffalo, kudu and hare exhibiting the most negative response (Figure 3). Elephant and giraffe dung was found largely irrespectively of cacti volume. Whilst the negative response of dik-dik and zebra dung to cacti volume did not appear to be strong, we only recorded large quantities of dung when there were no cacti, or the overall cacti volume was small (Figure 3).
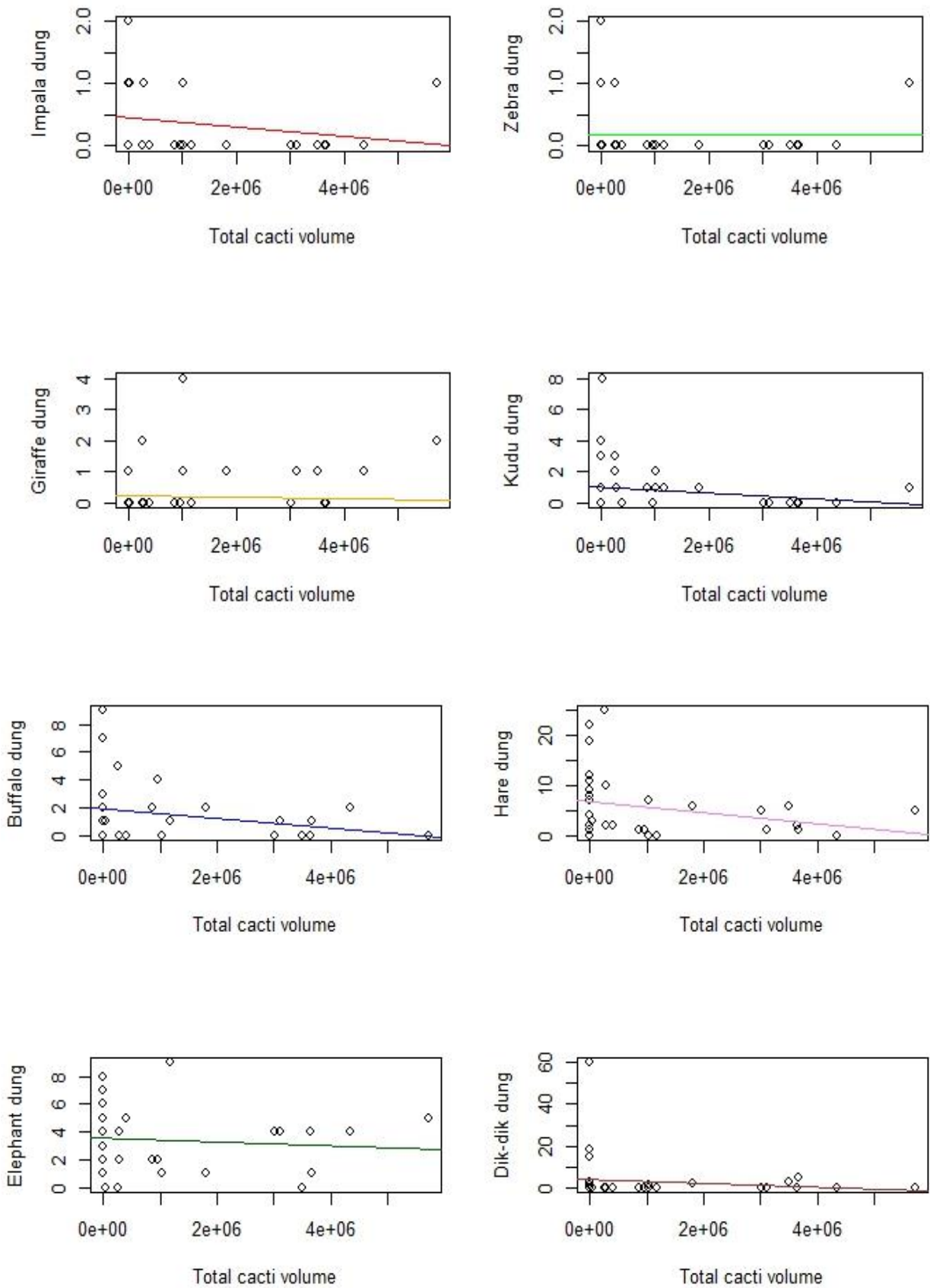
Figure 3: The abundance of dung of each of the different herbivore species (impala, zebra, giraffe, kudu, buffalo, hare, elephant and dik-dik) in relation to the total cacti volume per plot. The regression

lines depict a negative trend in all species, albeit the strength of the varies between the species, with buffalo, hare, kudu, and impala exhibiting the most negative response.

The abundance of dung piles recorded for all herbivore species decreased with increasing total volume of the cacti per plot (lm, $F_{2,31}$ = 4.49, coefficient -1.225e-07, p= 0.042; Figure 4) and with increasing percentage of plant basal cover (lm, $F_{2,31}$ = 12.72, coefficient = -2.122e-02, p < 0.005).
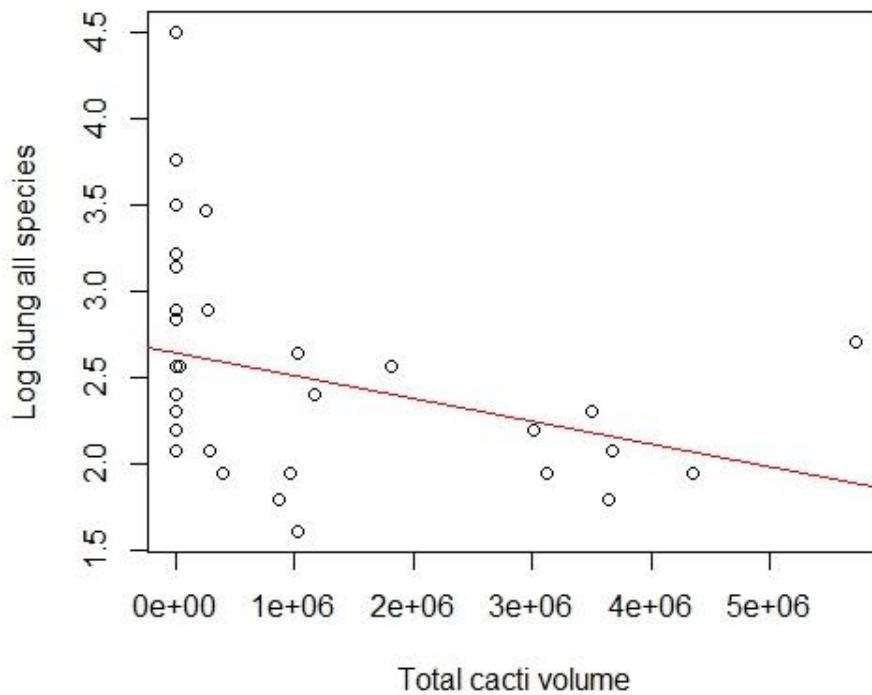
Figure 4: *The abundance of dung (log-transformed) decreases with increasing number of the total volume of cacti per plot.*

Structural equation modelling

In the full model (with grass, trees, cacti, and dung of all species included as composite variables), 42% of the variance was explained by the model (R^2 = 0.42), which was the highest overall R^2 value found for any model (Figure 5). In comparison, the model with grass, grazer dung, and cacti had an R^2 of 0.37 (grazer model; Figure 6) and the model with browser dung, cacti, and trees had an R^2 of 0.17 (browser model, Figure 7).

In the full model, 40% of the variation in "dung" was explained by the model (Figure 4). Cactus *O. stricta* had a negative direct effect on herbivore dung, suggesting that fewer herbivores (as approximated by their dung) were found in areas where cactus was abundant (Figure 5). Cactus abundance had positive influence on the latent variable "grass" which is influenced by the most common grass species recorded and the percentage of plant basal cover. Grass, as well as trees had a

negative effect on herbivore dung (Figure 5). Thus, cactus negatively influenced dung (i.e. herbivores) two-fold: directly, and indirectly through positively influencing grass which negatively affects dung, with direct and indirect influences of approximately the same strength. Trees negatively influenced dung, where Acacia species >2 m had a strong negative effect on trees, whereas broadleaf trees >2 m had the opposite effect.

The negative direct influence of cactus on dung was greater in the grazer model than in the full model and the browser model (beta coefficients of -0.523, -0.256 and – 0.014 respectively). Thus, *O. stricta* had a stronger direct negative influence on grazers than browsers. The negative influence of grass on dung was – 0.212 in the full model and - 0.068 in the grazer model. The negative effect of trees on dung was – 0.465 in the browser model. Hence, *O. stricta* appears to negatively affect browsers mainly indirectly through influencing the tree community (albeit it should be noted that the overall R^2 of the model is relatively low). In contrast, grazers are relatively unaffected by the changes the cacti have on the herbaceous community but experience direct negative effects.
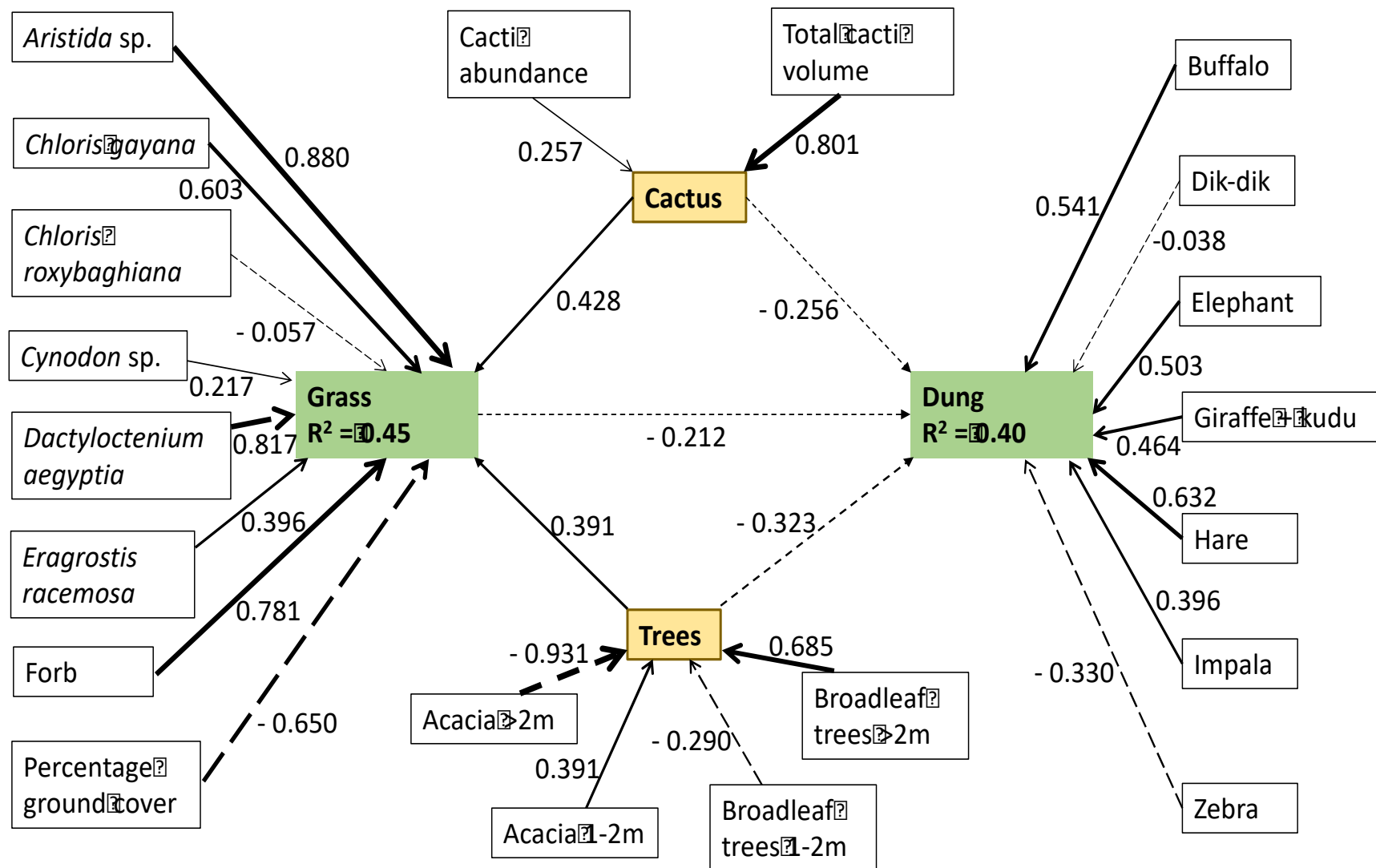
Figure 5: Result of the full SEM where variations in cactus, tree and grass community characteristics are used to explain the presence of herbivores as approximated by the abundance of dung. Solid arrows (i.e. beta, inner model) relating composite variables (trees, grass, cactus and dung) represent positive effect of one variable on another, while dashed arrows represent a negative effect. The strength of the effect of a variable on another is represented by the thickness of the arrow. The same applies to the outer-model, where the influence of variables (e.g. different herbivore species on dung) is depicted (gamma). The variance of grass and dung explained by the model is given by R^2 values.
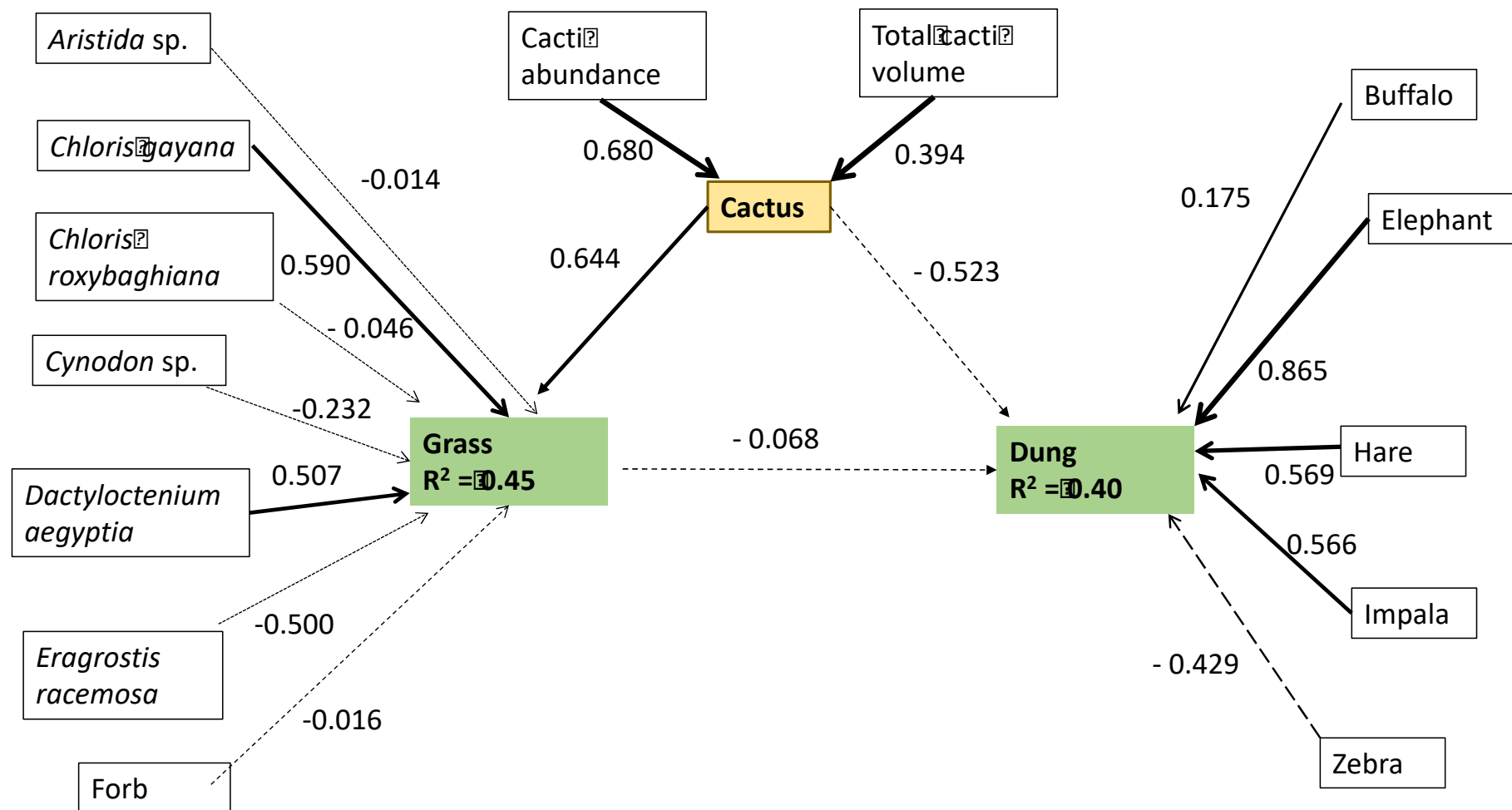
Figure 6: The results of SEM with grazer dung, grass, and cactus as the composite variables (grazer model). Cactus and grass are used to predict dung of which 40% of its variation is explained by the model ($R^2 = 0.40$).
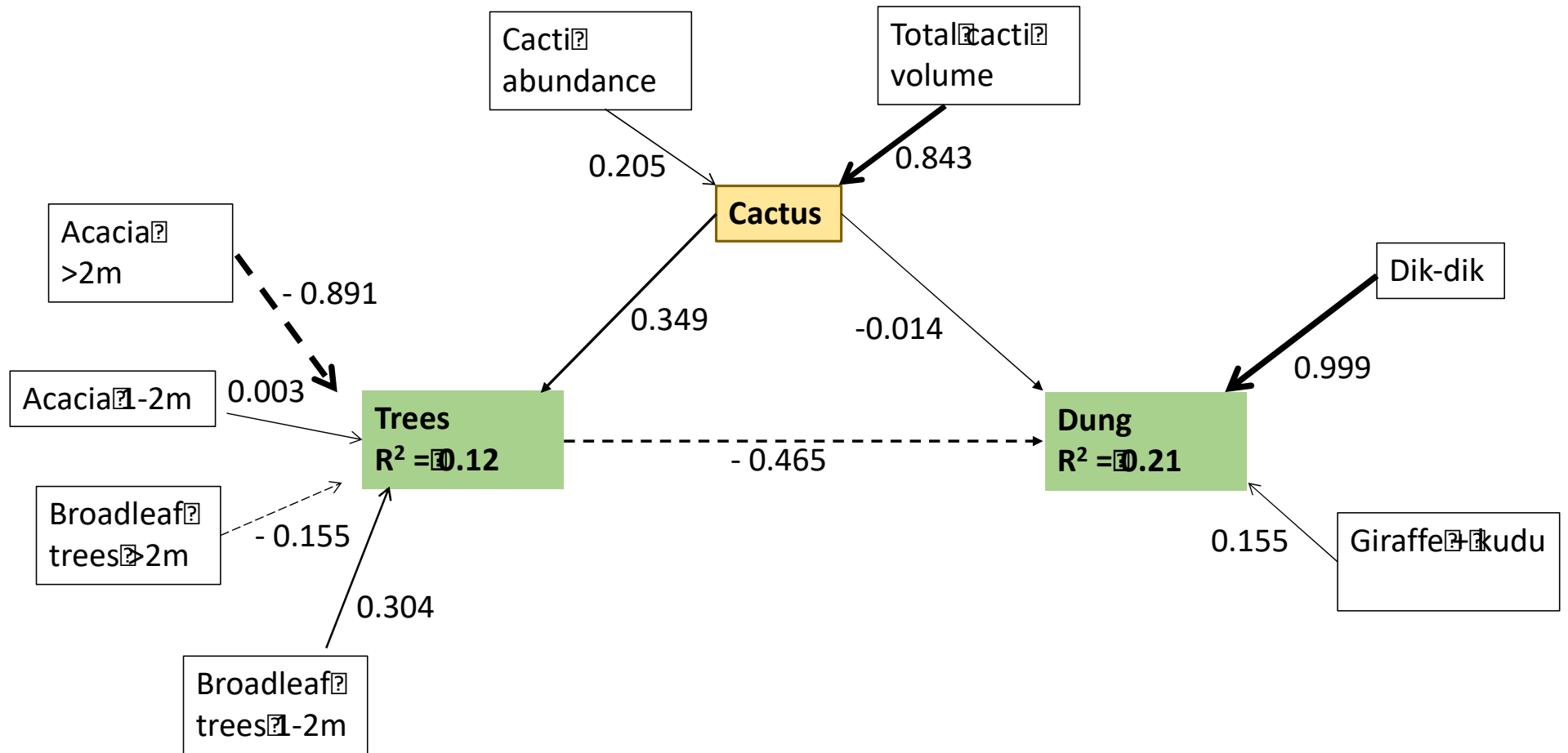
Figure 7: Results of SEM with browser dung, trees, and cactus as the composite variables (browser model). Cactus and trees are used to predict dung of which 21% of its variation is explained by the model ($R^2 = 0.21$).

DISCUSSION

Opuntia stricta invasion can have wide impacts on biodiversity (Shackleton et al, 2017) and animal health (Ueckert et al. 1990; Hanselka and Paschal, 1991). Previous studies concluded that the cactus impact grazing capabilities of livestock, through invasion of agricultural land and therefore reduction in palatable grass species and grazing habitats (Shackleton et al, 2017). Similarly, in this study, the presence of *O. stricta* showed negative impacts on the abundance of dung of African savanna herbivores, suggesting a reduction in their presence in cactus-invaded areas (Figure 4). This could be due to the physical obstruction *O. stricta* imposes on herbivores, including through its mechanical defences (direct effect).

This trend could also explain the positive effect that cactus exhibited on grass by reducing herbivory in the area. This effect was also observed in previous studies, where *O. stricta* was thought to act "as a nurse plant, supporting and protecting native plant species" (Shackleton et al., 2017; Taylor and Whitson 1999). It could also be supposed that non-palatable species are more abundant in these areas because of alterations to soil chemistry which may occur during the invasion process and favour non-palatable species. Additionally, altered soil chemistry may augment palatability of some grass species. Grass species composition may also change seasonally with herbivore preference varying. Thus, longer observation periods may provide alternative explanations, seeing that during wet season herbivores may be more selective due to the abundance of species available, may not be the same during the dry season.

The negative impact of trees on dung could be explained by herbivores' tendency to avoid densely wooded areas due to reduced visibility which implies increased predation risk (Riginos and Grace, 2008). This effect may be mainly mediated through large broad-leafed trees which are relatively un-palatable and have a strong negative effect on visibility. In contrast, (large) Acacia trees have less dense canopies and provide better foraging opportunities. This could explain why broad-leafed trees contributed to the overall negative influence of trees on herbivore dung, whereas large Acacia trees counteracted that effect (i.e. positively affected trees).

Seasonal changes may also affect this result, with the timing of this study taking place at the end of the wet season there is an abundance of food, thus, there is less pressure to forage in non-suitable areas. These phenomena may therefore also alter with changing seasons so longer observation periods could be undertaken in future studies. The negative effect of grasses on dung could also be explained by the same phenomena, additionally, the reduced visibility in high grass areas (and thus reduced

likelihood of recording all dung piles) can affect this result. This could be rectified in future studies by repeating the observation after the area has been mowed to improve visibility.

The differing effects of cactus on herbivores (i.e. dung) may be a result of varying body size amongst the herbivores. For example, elephants and giraffes appear to show no notable response to increased cactus volume, possibly due to their larger size in comparison to smaller herbivores such as impala or hare which showed a higher negative response to increasing cactus volume.

The direct negative effect of *O. stricta* on dung obtained in the browser model was remarkably lower than in the grazer model (Figure 6 – 7). This can be explained by the preference of browsers for (often high) tree species, where cacti pose at most limited obstruction. Furthermore, the browser model depicts that negative influence of trees on dung is roughly 33 X greater than the direct effect of cactus. Hence, the increased predation-risk created by a high tree density masks any direct effect cactus may have. The positive effect cactus has on trees could be facilitated through *O. stricta* reducing grazer abundance which could enhance tree regeneration, where this potentially higher tree density may negatively affect herbivores.

Grazers feed in closer proximity to the cactus and may thus be prevented to forage optimally through reducing access to palatable grasses. The effect of grass on grazer dung is 7.7 X greater than the effect of grass on dung, suggesting that the direct effect cactus has on grazers is more important than the changes *O. stricta* causes in the herbaceous community.

Overall, it can be inferred that *O. stricta* has a negative impact on herbivores, both directly, and indirectly through affecting the herbaceous community. However, further studies could be used to measure these impacts on a species-specific level, of which we only conducted exploratory analyses. Management of this invasive species is therefore important especially in terms of agriculture as it has been found to impact animal distribution and health.

REFERENCES

Bollen, K. A. (1989). Structural equations with latent variables. John Wiley and Sons, New York, New York, USA.

Eisenhauser, N., Bowker, M.A., Grace, J.B., Powell, J.R. (2015). From patterns to casual understanding: Structural equation modeling (SEM) in soil ecology. *Pedobiologia,* 58:65-72.

Fensham, R. J. (1998). The grassy vegetation of the darling downs, south-eastern queensland, australia. Floristics and grazing effects. *Biological conservation, 84*(3): 301–310.

Foxcroft, L. ., & Rejmánek, M. (2007). What helps Opuntia stricta invade Kruger National Park , South Africa : Baboons or elephants ? *Applied Vegetation Science*, *10*: 265–270.

Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M. (2010). On the specification of structural equation models for ecological system. *Ecologocal Monographs,* 80:67-87.

Hanselka, C.W., Paschal, J.C. (1991). Pricklypear cactus: a Texas rangeland enigma. *Rangelands* 13:109–111.

Kumschick, S., Bacher, S., Dawson, W., Heikkila, J., Sendek, A., Pluess, T., Robinson, T.B., KuhnI. (2012). A conceptual framework for prioritization of invasive alien species for management according to their impact. *NeoBiota* 15:69–100.

Mack, R.N. (2003). Global plant dispersal, naturalization, and invasion: pathways, modes and circumstances. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington, pp 3–30.

McNeely, J. (2006). As the world gets smaller, the chances of invasion grow. *Euphytica,* 148:5–15.

Novoa, A., Roux, J. J. Le, Robertson, M. P., Wilson, J. R. U., Richardson, D. M. (2015). Introduced and invasive cactus species : a global review.

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

Shackleton, R. T., Witt, A. B. R., Piroris, F. M., & Wilgen, B. W. Van. (2017). Distribution and socio ecological impacts of the invasive alien cactus Opuntia stricta in eastern Africa. *Biological Invasions*, *19*(8): 2427–2441.

Strum S.C., Stirling G., Kulusi Mutunga S.K. (2015). The perfect storm: landuse change promotes Opuntia stricta's invasion of pastoral rangelands in Kenya. *J Arid Environment*, 118:37–47.

Taylor W.R., Whitson T.D. (1999). Plains prickly pear cactus control. University of Wyoming, Cooperative Extension Service, Bulletin No. B-1074.

Ueckert, D.N., Livingston, Jr. C.W., Huston, J.E., Menzies, C.S., Dusek, R.K., Petersen, J.D., Lawrence, B.K. (1990). Range and sheep management for reducing pear-moth and other prickly pear-related health problems in sheep flock. Sheep and Goat, Wool and Mohair, Research Report. Texas Agricultural Experiment Station. San Angelo, Texas, USA.

Vila, M., Burriel, J.A., Pino, J., Chamizo, J., Llach, E., Porterias, M., Vives, M. (2003). Association between Opuntia species invasion and changes in land-cover in the Mediterranean region. *Glob Change Biology,* 9:1234–1239.

Vila, M., Gimeno I. (2003). Seed predation of two alien Opuntia species invading Mediterranean communities. *Plant Ecology,* 167:1–8.

Walters M., Figueiredo E., Crouch N.R., Winter P.J.D., Smith G.F., Zimmermann H.G., Mashope B.K. (2011). Naturalised and invasive succulents of southern Africa. Belgium: Abc Taxa.