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Interactions between C : N : P stoichiometry and soil macrofauna control dung decomposition of savanna herbivores

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Summary

1. Although dung of mammalian herbivores is an important pathway for nutrient return in savanna ecosystems, differences in dung decomposition rates among species have been little studied.

2. We measured the rates of dung deposition and decomposition for various herbivores in a moist Tanzanian savanna and the related differences among species to nutrient concentrations and the activities of soil macrofauna (e.g. different mesh sizes of decomposition bags, or presence and absence of dung beetles).

3. Dung C : N : P stoichiometry varied widely among species, which could in part be explained by differences in feeding strategy (browsers vs. grazers) and digestive physiology (ruminants vs. non-ruminants). Rates of both decomposition and nutrient release were influenced by the C : N : P stoichiometry of dung, with lower relative losses of the least abundant nutrient in the dung. Surprisingly, soil macrofauna increased the relative losses of the least abundant nutrient, thereby stabilizing the ratio of N loss to P loss. Dung beetles increased rates of N and P release from wildebeest dung significantly and also increased N availability in the soil.

4. We conclude that rates of nutrient return in dung depend not only on where herbivores deposit their dung, but also on its C : N : P stoichiometry, the activity of soil macrofauna and interactions between these factors. These factors may therefore influence the relative availabilities of N and P in the soil and hence the functioning of savanna ecosystems.

Key-words: African herbivores, carbon, dung beetles, dung deposition, faeces, nitrogen, nutrient cycling, nutrient release rate, phosphorus, termites

Introduction

By returning nutrients in their excreta, mammalian herbivores strongly influence the processes of nutrient cycling and primary production in savanna ecosystems (Ruess & McNaughton 1987; Blackmore, Mentis & Scholes 1990; Augustine, McNaughton & Frank 2003; van der Waal *et al.* 2011). In African savannas, nitrogen (N) inputs in dung have been found to vary widely, from 0·2 to 50 kg ha^{-1} $year^{-1}$ (Augustine, McNaughton & Frank 2003; Fornara & Du Toit 2008; Cech, Olde Venterink & Edwards 2010; van der Waal *et al.* 2011). Less is known about phosphorus (P) inputs; though, they were estimated to range from 0·03 to 1·0 kg P ha^{-1} $year^{-1}$ in a humid savanna in Tanzania (Cech, Olde Venterink & Edwards 2010). However, these nutrient returns are not necessarily uniform, but may be locally concentrated through the activities of large herbivores (Augustine, McNaughton & Frank 2003; Archibald *et al.* 2005; Riginos & Grace 2008; van der Waal *et al.* 2011).

Most of the N and P in dung is present in an organic form, and rates of release are therefore regulated by factors influencing decomposition, including not only the environmental conditions where the dung is deposited but also its chemical composition, and especially its C : N : P stoichiometry (Anderson & Coe 1974; Ouédraogo, Mando &

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Brussaard 2004). The latter can vary widely among herbivore species, reflecting differences in body size, feeding strategy (e.g. grazers and browsers) and digestive physiology (e.g. foregut and hindgut fermenters, or for comparison ruminants and non-ruminants; Edwards 1991). For example, the dung of browsers has higher N concentrations than that of grazers (Codron *et al*. 2007), which likely results in differences in dung C : N : P ratios. Although some studies have measured dung concentrations of N (Edwards 1991; Codron *et al*. 2007; van der Waal *et al*. 2011) or N and P (De Iongh *et al*. 2011), little is known about how C : N : P stoichiometry varies among species.

In general, nutrients are released more rapidly from dung than from plant litter, and grazing therefore increases turnover (Bakker *et al*. 2004). However, just as different types of plant litter decompose at different rates (Enríquez, Duarte & Sandjensen 1993; Coûteaux, Bottner & Berg 1995; Sterner & Elser 2002), so we might expect the decomposition of dung from different herbivores to vary. Indeed, it has been shown that N and P release rates of plant litter increase with decreasing litter C : N and C : P ratios, respectively (Enríquez, Duarte & Sandjensen 1993; Moore *et al*. 2011), while the ratio of N loss to P loss depends largely on the litters N : P ratio (Güsewell & Gessner 2009).

If the rate of dung decomposition does vary widely, it is likely to have consequences for the relative availabilities of nutrients in the soil and thus for competitive interactions among plants (Olde Venterink & Güsewell 2010) and soil microbes (Güsewell & Gessner 2009). For instance, if N : P ratios in the soil are low, N_2-fixing seedlings might be relatively good competitors because of their ability to fix N, while at high N : P ratios they might prove to be poor competitors because of their relatively high P requirements compared to competing C_4 grasses (Smith 1992; Vitousek *et al*. 2002). Hence, differences in nutrient release rates from dung of different herbivore species could result in changes in plant and/or soil communities.

The soil macrofauna of savanna ecosystems, and especially dung beetles and termites, strongly increase the breakdown of herbivore dung and nutrient release rates (Anderson & Coe 1974; Freymann *et al*. 2008; Nichols *et al*. 2008). Since these animals depend upon nutrients present in dung, we might expect C : N : P stoichiometry to affect their choice of substrate and therefore also rates of turnover of N and P in the ecosystem (Sterner & Elser 2002). However, there appears to have been no studies comparing the interactions between C : N : P stoichiometry and soil macrofauna on dung decomposition.

We investigated the processes of dung decomposition and nutrient release for a range of herbivores living in a moist tallgrass savanna ecosystem in Tanzania. We predicted the following factors:

1. Dung C : N : P stoichiometry would be related to a herbivore's feeding strategy.
2. Rates of dung decomposition and N and P release would increase with decreasing ratios of C : N and C : P.
3. Relative rates of N and P release from dung would depend upon the N : P ratio, with faster N release if N : P were high and faster P release if N : P were low.
4. Release rates of nutrients from dung would be increased by the presence of soil macrofauna.

In addition, we question whether decomposition and nutrient release rates would be influenced by an interaction between dung C : N : P stoichiometry and soil macrofauna. However, our current knowledge is too limited to merit a prediction at this stage.

Materials and methods

STUDY AREA

The study was conducted in the Saadani National Park, on the coast of Tanzania (5°43′S, 38°47′E). The northern part (Mkwaja area: *c*. 470 km^2) was managed as a cattle ranch until 2000, while the southern part (Saadani area: *c*. 210 km^2) has been a wildlife reserve since the 1960s. Although the entire park is accessible to wildlife, the northern part still has a lower density and diversity of large herbivores (Treydte, Edwards & Suter 2005), probably because of its former use as a ranch and the bush encroachment that ensued (Tobler, Cochard & Edwards 2003).

The vegetation in the Saadani National Park is mainly tallgrass savanna, encroached to different degrees by the leguminous tree *Acacia zanzibarica* (S. Moore) Taub. var. *zanzibarica*. Rainfall varies widely, from 500 to 1700 mm year^{-1}, with the mean for the 4-year period preceding and during our study being *c*. 580 mm. Most rain falls during the wet seasons from March until June and from mid-October until mid-November. Mean annual temperature is 25 °C.

Herbivores include large grazers such as African buffalo (*Syncerus caffer*), Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes taurinus*) and Burchell's zebra (*Equus burchellii*), and smaller grazers such as Bohor reedbuck (*Redunca redunca*), savanna cane rat (*Thryonomys* sp.), scrub hare (*Lepus saxatilis*) and warthog (*Phacochoerus africanus*). African elephant (*Loxodonta africana*) is a mixed-feeder in the area, and the most abundant browsers are giraffe (*Giraffa camelopardalis*), bushbuck (*Tragelaphus scriptus*), and the smaller grey duiker (*Sylvicapra grimmia*), Harvey's duiker (*Cephalophus harveyi*) and suni (*Neotragus moschatus*).

ANNUAL DUNG INPUT BY HERBIVORES

Dung deposition was measured at 21 sites in Mkwaja and 22 in Saadani. These sites (30 × 30 m^2), selected as part of a larger study of soil nutrient processes and nutrient fluxes across the savanna landscape, represented gradients of increasing *A. zanzibarica* density from 0 to 2000 trees ha^{-1} (Sitters, Edwards & Olde Venterink 2013; J. Sitters, P.J. Edwards, W. Suter & H. Olde Venterink, unpublished data). In each site, a plot was selected in which we collected all dung of mammalian herbivores every 2 weeks during three periods (five collections in July–September 2009; three collections in January–February 2010; three collections in July–October 2010). There was slight variation in the size of the dung plots with a mean size of 63 ± 1·8 m^2. At the beginning of each of the three collection periods we removed all dung present by walking transects across each plot. The 2-week interval between subsequent collections was chosen as logistically feasible while avoiding significant loss of dung biomass through decomposition. The collected dung was identified with the help of experienced rangers and then dried and weighed. To account for seasonal vari-

ation in nutrient content, we collected fresh pellets (pellets dropped within a couple of hours preceding collection) of the various herbivore species on six occasions between July 2009 and August 2010 to incorporate seasonal variation in dung C, N and P concentrations. These samples were dried and ground, after which total C concentrations were measured on a dry combustion analyzer (CN-2000; LECO Corp., St. Joseph, MN, USA). Total N and P concentrations were measured after Kjeldahl digestion (sodium salicylate method: 120–150 mg dung added to 5 mL of concentrated H_2SO_4 and one Kjeldahl tablet from FOSS for digestion; Tecator Digestion System, FOSS, Effretikon, Switzerland) using a continuous flow injection analyzer (AutoAnalyzer 3; Seal Analytical, Dietikon, Switzerland).

EFFECTS OF HERBIVORE SPECIES AND SOIL MACROFAUNA ON DUNG DECOMPOSITION RATES

A decomposition experiment using the litterbag technique was set out in the field between August 2010 and January 2011. In the Saadani area, we collected fresh dung (pellets dropped within a couple of minutes preceding collection) of giraffe (ruminant browser), buffalo, reedbuck, waterbuck and wildebeest (ruminant grazers), and warthog (non-ruminant grazer). Dung was stored until use in plastic bags, which were kept underground in a shady location. At the beginning of the experiment, 10 g samples of dung were placed in small nylon bags (10 × 10 cm). Half of the bags had a fine mesh (100 μm), which permitted entry of microfauna only, and half had a coarse mesh (5 mm) allowing meso- and macrofauna access to the dung. However, when discussing results of coarse-meshed bags we will refer to the effect of soil macrofauna only, as especially dung beetles and termites have large effects on dung decomposition and nutrient release rates (Anderson & Coe 1974; Freymann *et al.* 2008; Nichols *et al.* 2008). Both mesh sizes permitted entry of bacteria and fungi (i.e. microbes). The experiment was carried out at two locations in the Saadani area: one with low density of *A. zanzibarica* (*c.* 200 trees ha^{-1}) and the other with a high density (*c.* 2000 trees ha^{-1}). Bags were placed on the soil surface and protected from animals by a fence of chicken wire. Half of the bags were collected after 41 and the remainder after 167 days. For all herbivore species except reedbuck we used seven replicates per treatment, location and collection time. For reedbuck, we used five replicates, which were all collected after 167 days, giving us a total of 300 dung bags. After collection we noted any obvious signs of dung beetles (such as spreading/crushing of dung, dead insects) or termites (such as hollowing out of dung), and then dried and weighed the remaining material.

At the start of the experiment we estimated the water content of five subsamples of dung per herbivore species by determining their fresh and dry weight and used this value to calculate the initial dry biomass and relative loss (in percentage) on each collection date. All dung was ground for nutrient concentration analyses. Total C concentrations were measured on a dry combustion analyzer (CN-2000; LECO Corp.), while total N and P concentrations were measured after Kjeldahl digestion (sodium salicylate method: 120–150 mg dung added to 5 mL of concentrated H_2SO_4 and one Kjeldahl tablet from FOSS for digestion; Tecator Digestion System, FOSS) using a continuous flow injection analyzer (AutoAnalyzer 3; Seal Analytical). We calculated C, N and P release rates (in mg kg $dung^{-1}$ day^{-1}) by dividing the total loss of C, N and P by the dry biomass of dung at the start of the experiment, and the number of days in the field. Relative C, N and P losses (in percentage) were based on the biomass and C, N and P concentrations of the remaining dung in comparison with the initial biomass and concentrations.

Flux

EFFECTS OF DUNG BEETLES ON DUNG DECOMPOSITION AND NUTRIENT RELEASE RATES

To investigate the influence of dung beetles in more detail, we performed two additional experiments during January and February 2010 in the garden of our temporary research station in the Mkwaja area. In the first experiment, samples of wildebeest dung – either as five intact pellets or as 5 g of crushed material – were weighed and placed in small cages (20 × 20 × 10 cm^3) covered with mosquito netting (mesh size 1·2 mm). The crushing was intended to establish whether the most important effect of dung beetles was merely to fragment the dung. In half of the cages we added 10 beetles of the genus *Sisyphus* (length 0·5–1 cm), which were collected on fresh dung in the Mkwaja area. Dung was collected after 15, 29 and 47 days and weighed. We used five replicates per treatment and collection time, which yielded a total of 60 cages. Rates of decomposition and C, N and P release were calculated as for the dung decomposition experiment.

The second experiment was designed to estimate the effect of beetles on N and P release rates from dung. For this, we filled 14 plastic pots (0·8 L; 10 cm height) with soil from a nearby tallgrass savanna and placed a small bag containing ion-exchange resin at 7 cm depth in each pot. Each resin bag (25 cm^2) of nylon (60 μm mesh size, Sefar Nitex 03-60/35; Sefar AG, Heiden, Switzerland) contained 2 g mixed-bed ion-exchange resins (Amberlite IRN 150, H^+- and OH^-forms; Sigma Aldrich, Buchs SG, Switzerland). Resins were conditioned by shaking them for 2 h in 2 M KCl solution. We had four control pots containing only soil, five pots containing 10 g of fresh wildebeest dung and five pots containing 10 g of fresh wildebeest dung and 20 dung beetles of the genus *Sisyphus*. The pots were covered with mosquito net and placed in the shade. We added 32 ml of water every 4 days and after 34 days, the resin bags were removed, dried and gently cleaned by brushing. They were later extracted by shaking each bag for 2 h with 50 mL 1 M KCl. The extracts were then analysed colorimetrically for PO_4^{2-}, NO_3^- and NH_4^+ (AutoAnalyzer 3; Seal Analytical).

STATISTICAL ANALYSES

We used one-way analyses of variance (ANOVA) followed by Tukey–Kramer HSD tests to test for differences in dung nutrient concentrations and stoichiometry among herbivore species and functional groups (i.e. ruminant browser, ruminant grazer, non-ruminant grazer). If necessary, data were log-transformed to meet assumptions of normality and homogeneity of variance. We combined the 43 sites in which dung was collected into four tree density classes (0–500, 501–1000, 1001–1500, 1501–2000 trees ha^{-1}) per area, and for each estimated the contributions of herbivores with different digestive physiologies and feeding strategies to annual dung biomass, and N and P inputs.

For the dung decomposition experiment and the dung beetle experiment, we analysed the effects of herbivore species, treatments (i.e. mesh size, location, crushing treatment, dung beetle treatment), collection time, and their interactions (all fixed) with three- or four-way ANOVAs. For multiple comparisons between factor levels, we used Tukey–Kramer HSD tests. Data were log-transformed to meet assumptions of normality and homogeneity of variance. For both experiments, model assumptions were not fulfilled even after data transformation, so we performed nonparametric Euclidean distance-based ANOVAs with permutation tests (Anderson 2001). Results using the traditional and nonparametric ANOVAs were similar. We were not able to retrieve two dung samples from the dung beetle experiment due to removal of the dung by termites. Generalised linear models (GLMs) were used to investigate the effects of initial dung nutrient ratios and soil fauna on relative losses of N and P and on the ratios of C to N loss, N to P loss and C to P loss, including both initial dung nutrient ratios

Donnée prise dans l'excel "Dung nutrient overview"

Table 1. Dung C, N, P concentrations and ratios (mean ± SE) for the most common herbivore species in Saadani National Park. Herbivore species were grouped per digestive physiology and feeding strategy (based on Kingdon 1997; Cerling, Haiis & Passey 2003; Codron *et al.* 2007) and differences between dung C, N and P concentrations and ratios were determined with one-way ANOVAS between herbivore species or digestive physiology and feeding strategy group

Herbivore species	Digestive physiology and feeding strategy	*n*	C (mg g^{-1})	*n*	N (mg g^{-1})	P (mg g^{-1})	C : N	C : P	N : P
Bushbuck	Ruminant browser	6	417 ± 16^{abc}	21	$18{\cdot}9 \pm 1{\cdot}2^{abcd}$	$3{\cdot}32 \pm 0{\cdot}27^{abcd}$	$25{\cdot}0 \pm 2{\cdot}8^{def}$	164 ± 15^{bcd}	$6{\cdot}09 \pm 0{\cdot}43^{cdef}$
Giraffe	Ruminant browser	35	449 ± 2^{a}	50	$29{\cdot}3 \pm 1{\cdot}2^{a}$	$3{\cdot}34 \pm 0{\cdot}12^{abcd}$	$16{\cdot}1 \pm 0{\cdot}9^{f}$	142 ± 7^{cd}	$9{\cdot}10 \pm 0{\cdot}32^{bcd}$
Grey duiker	Ruminant browser	10	433 ± 7^{ab}	10	$23{\cdot}9 \pm 1{\cdot}9^{ab}$	$3{\cdot}87 \pm 0{\cdot}47^{a}$	$19{\cdot}6 \pm 2{\cdot}1^{ef}$	125 ± 13^{cd}	$6{\cdot}76 \pm 0{\cdot}77^{bcdef}$
Red duiker	Ruminant browser	2	427 ± 7^{ab}	2	$18{\cdot}1 \pm 1{\cdot}8^{abcd}$	$2{\cdot}95 \pm 0{\cdot}15^{abcd}$	$23{\cdot}8 \pm 2{\cdot}0^{def}$	145 ± 5^{cd}	$6{\cdot}13 \pm 0{\cdot}31^{cdef}$
Suni	Ruminant browser	2	420 ± 10^{abc}	2	$21{\cdot}9 \pm 1{\cdot}8^{abc}$	$1{\cdot}63 \pm 0{\cdot}13^{cde}$	$19{\cdot}3 \pm 2{\cdot}0^{ef}$	259 ± 15^{b}	$13{\cdot}6 \pm 2{\cdot}2^{a}$
Buffalo	Ruminant grazer	10	348 ± 16^{f}	23	$10{\cdot}9 \pm 0{\cdot}6^{efg}$	$2{\cdot}36 \pm 0{\cdot}25^{abcde}$	$30{\cdot}5 \pm 2{\cdot}4^{cde}$	153 ± 11^{bcd}	$5{\cdot}25 \pm 0{\cdot}37^{ef}$
Hartebeest	Ruminant grazer	3	403 ± 20^{abcde}	3	$8{\cdot}6 \pm 1{\cdot}7^{fg}$	$3{\cdot}00 \pm 0{\cdot}89^{abcd}$	$52{\cdot}9 \pm 15{\cdot}0^{b}$	153 ± 30^{cd}	$3{\cdot}58 \pm 1{\cdot}24^{f}$
Reedbuck	Ruminant grazer	30	389 ± 3^{bcdef}	41	$17{\cdot}1 \pm 0{\cdot}5^{abcde}$	$3{\cdot}70 \pm 0{\cdot}13^{ab}$	$21{\cdot}9 \pm 0{\cdot}8^{def}$	103 ± 5^{d}	$4{\cdot}79 \pm 0{\cdot}19^{ef}$
Waterbuck	Ruminant grazer	35	379 ± 2^{cdef}	52	$14{\cdot}5 \pm 0{\cdot}6^{bcde}$	$2{\cdot}92 \pm 0{\cdot}14^{abcd}$	$29{\cdot}1 \pm 1{\cdot}3^{cde}$	145 ± 6^{cd}	$5{\cdot}28 \pm 0{\cdot}23^{ef}$
Wildebeest	Ruminant grazer	40	358 ± 4^{ef}	46	$13{\cdot}5 \pm 0{\cdot}5^{cdef}$	$3{\cdot}47 \pm 0{\cdot}22^{abc}$	$27{\cdot}3 \pm 1{\cdot}1^{de}$	119 ± 5^{d}	$4{\cdot}76 \pm 0{\cdot}35^{ef}$
Cane rat	Non-ruminant grazer*	5	423 ± 4^{abc}	17	$7{\cdot}5 \pm 1{\cdot}0^{g}$	$1{\cdot}02 \pm 0{\cdot}19^{e}$	100 ± 9^{a}	925 ± 147^{a}	$9{\cdot}29 \pm 0{\cdot}87^{bc}$
Scrub hare	Non-ruminant grazer*	6	408 ± 7^{abcd}	17	$14{\cdot}2 \pm 1{\cdot}2^{cdef}$	$1{\cdot}53 \pm 0{\cdot}22^{de}$	$34{\cdot}8 \pm 4{\cdot}0^{bcd}$	510 ± 44^{a}	$10{\cdot}2 \pm 0{\cdot}9^{ab}$
Warthog	Non-ruminant grazer	11	368 ± 8^{def}	28	$13{\cdot}4 \pm 0{\cdot}9^{def}$	$2{\cdot}70 \pm 0{\cdot}21^{abcde}$	$34{\cdot}1 \pm 2{\cdot}2^{bcd}$	138 ± 16^{cd}	$5{\cdot}45 \pm 0{\cdot}40^{def}$
Zebra	Non-ruminant grazer	4	414 ± 3^{abc}	10	$12{\cdot}2 \pm 1{\cdot}0^{def}$	$3{\cdot}54 \pm 0{\cdot}57^{ab}$	$45{\cdot}7 \pm 1{\cdot}3^{bc}$	213 ± 12^{bc}	$4{\cdot}01 \pm 0{\cdot}42^{f}$
Elephant	Non-ruminant mixed-feeder	7	447 ± 4^{a}	17	$13{\cdot}5 \pm 0{\cdot}7^{cdef}$	$1{\cdot}84 \pm 0{\cdot}17^{bcde}$	$34{\cdot}4 \pm 1{\cdot}4^{bcd}$	221 ± 25^{bc}	$7{\cdot}88 \pm 0{\cdot}61^{bcde}$
	Ruminant browsers	5	429 ± 6^{a}	5	$22{\cdot}4 \pm 0{\cdot}9^{a}$	$3{\cdot}02 \pm 0{\cdot}38^{a}$	$20{\cdot}8 \pm 1{\cdot}6^{b}$	167 ± 24^{b}	$8{\cdot}34 \pm 1{\cdot}43^{a}$
	Ruminant grazers	5	375 ± 10^{b}	5	$12{\cdot}9 \pm 1{\cdot}5^{b}$	$3{\cdot}09 \pm 0{\cdot}23^{a}$	$32{\cdot}3 \pm 5{\cdot}3^{b}$	135 ± 10^{b}	$4{\cdot}73 \pm 0{\cdot}31^{a}$

Values not sharing the same superscript letter are significantly different (Tukey-Kramer HSD test, $P < 0{\cdot}05$). Note that the number of dung samples (*n*) analysed for C concentration differed from the number analysed for N and P concentrations. For non-ruminant mixed-feeder we only had data on elephant and non-ruminant grazers were not grouped together due to additional variations in their digestive systems (see asterisk in table).

*These species are coprophagous.

and mesh size as factors. We used Chi-square tests to test for any differences between locations in proportions of big mesh-sized dung bags attacked by soil macrofauna.

For the ion-exchange resin bag experiment we analysed the effects of either dung beetle treatment or herbivore species with one-way ANOVAS followed by Tukey–Kramer HSD tests. All analyses were performed with the open source R (R Development Core Team 2011).

Results

DUNG C : N : P STOICHIOMETRY AND ANNUAL DUNG INPUT BY HERBIVORES

We found large interspecific differences in C, N and P concentrations and C : N : P stoichiometry of dung (Table 1). Dung of the giraffe and grey duiker, both ruminant browsers, had relatively high N and P concentrations and low C : N ratios, whereas dung of hartebeest, ruminant grazer, had a very low N concentration and high C : N ratio. Dung of cane rat and scrub hare had exceptionally low N and/or P concentrations and correspondingly high ratios of C to these nutrients. Comparisons among functional groups showed that dung C and N concentrations were significantly higher for ruminant browsers than for ruminant grazers, and the N : P ratio tended to be higher ($P = 0{\cdot}06$). However, there was also considerable variation in nutrient concentrations and ratios within functional groups.

Total dung deposition was lower in the Mkwaja area than in the Saadani area (Fig. 1a), reflecting the lower herbivore density. Most of the dung collected in Saadani was from ruminant grazers, but in Mkwaja there were similar contributions from ruminants and non-ruminant grazers. Annual inputs of N and P in dung were 0·8 and 0·14 kg ha^{-1}, respectively, in the Mkwaja area, and 2·0 and 0·34 kg ha^{-1} in the Saadani area (Fig. 1b,c). In both areas, the highest dung inputs were at sites with low densities of *Acacia* (0–500 trees ha^{-1}), especially for browsing herbivores in Saadani.

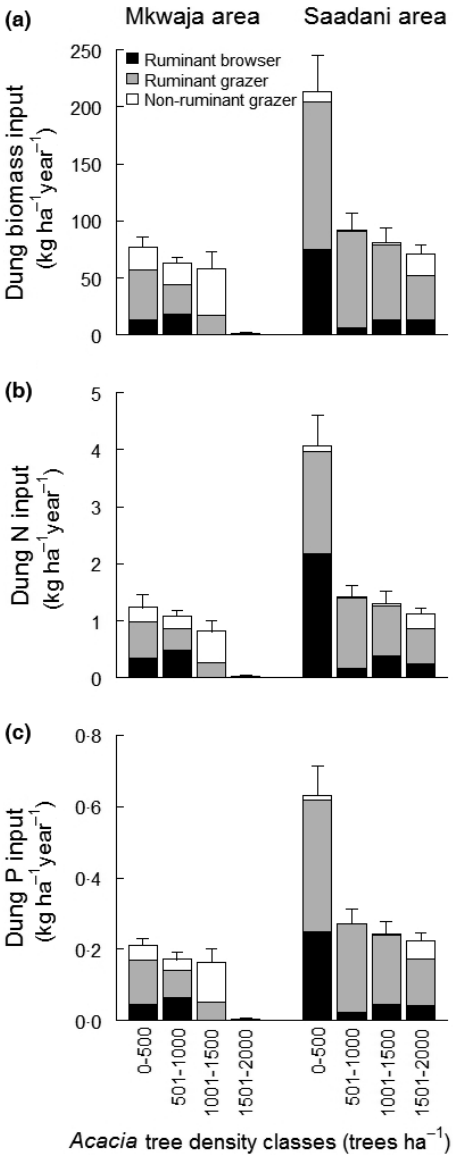

Fig. 1. Contribution of herbivores with different digestive physiologies and feeding strategies (i.e. ruminant browser, ruminant grazer, non-ruminant grazer) to annual dung biomass (a), N (b) and P (c) inputs in the two savanna areas. Dung was collected in 43 sites across two *Acacia* tree density gradients (one in each area), which were then combined into four tree density classes containing (i) 0–500 ($n = 6$ for Mkwaja; $n = 9$ for Saadani), (ii) 501–1000 ($n = 8$; $n = 6$), (iii) 1001–1500 ($n = 4$), and (iv) 1501–2000 trees ha^{-1} ($n = 2$; $n = 3$).

EFFECTS OF HERBIVORE SPECIES AND SOIL MACROFAUNA ON DUNG DECOMPOSITION RATES

In the dung decomposition experiment, all factors – herbivore species, mesh size, collection time, and location – significantly influenced relative biomass losses and release rates of C, N and P (Table 2). Mesh size and collection time were the main factors affecting relative biomass loss and C release rates, while N and P release rates were mainly affected by herbivore species, followed by collection time, and the interaction between herbivore species and collection time (see *F*-ratios in Table 2). The highest N release rates were from dung of giraffe and reedbuck, the dung types with the lowest dung C : N ratios (and for giraffe also the highest N : P ratio). Similarly, the highest P release rate was from wildebeest dung, which had the lowest C : P and N : P ratios (Fig. 2e–h; see Table S1 (Supporting information) for C, N, P concentrations and ratios from dung used in the experiment; see Fig. S1 for the first collection time). For relative biomass loss and C release rate, the effect of species was low (Table 2), which resulted in few significant differences when mesh sizes were analysed separately (Figs 2a–d and S1).

Biomass loss from bags was approximately proportional to time, being much greater after 167 days than after 41 days (Table 2; compare Fig. 2a,b with Fig. S1). However, release rates of C, N and P were relatively much higher during the first 41 days (Figs 2c–h and S1),

Table 2. ANOVA results (*F*-ratios and significance levels) for the effects of herbivore species, several treatments and collection time on relative biomass loss (in percentage) and C, N and P release rates (in g kg dung^{-1} day^{-1} for C and in mg kg dung^{-1} day^{-1} for N and P) of dung from the dung decomposition experiment and the dung beetle experiment

Test factor and source of variation	d.f.	Relative biomass loss	C release rate	N release rate	P release rate
Dung decomposition experiment					
Herbivore species (S)	5	3·6**	3·3**	181·7***	31·6***
Mesh size (M)	1	38·2***	59·2***	29·6***	10·6**
Collection time (T)	1	80·4***	29·9***	136·8***	12·8***
Location (L)	1	NS	10·6***	17·0***	10·4**
S × M	5	2·5*	NS	NS	NS
S × T	4	NS	NS	70·5***	21·6***
S × L	5	3·6**	NS	NS	NS
M × T	1	25·9***	8·8**	NS	NS
M × L	1	NS	8·7**	5·3*	NS
T × L	1	NS	5·6*	4·5*	NS
S × M × T	4	NS	NS	NS	NS
S × M × L	5	NS	NS	NS	NS
S × T × L	4	NS	NS	NS	NS
M × T × L	1	5·9**	NS	NS	NS
S × M × T × L	4	NS	NS	NS	NS
Dung beetle experiment					
Beetle treatment (B)	1	NS	30·4***	6·7*	6·7**
Crushing treatment (C)	1	NS	5·1*	NS	NS
Collection time (T)	2	NS	NS	NS	5·2**
B × C	1	NS	7·5*	7·1**	11·3**
B × T	2	NS	NS	NS	NS
M × T	2	NS	NS	NS	NS
B × C × T	2	NS	NS	NS	NS

d.f., degrees of freedom.
Significance levels: *$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$, NS: $P > 0{\cdot}05$.

especially for giraffe dung. Unlike other species, waterbuck dung retained P during the first period, causing a significant interaction between herbivore species and collection time (Table 2).

Overall, losses of biomass and C, N and P were faster from bags with a coarse than with a fine mesh (Table 2; Figs 2 and S1). For C and N, this difference was most pronounced at sites with a low tree density (see two-way interaction effects; Table 2; Figs 2c–f and S1), reflecting the fact that more bags at this site were attacked by larger invertebrates (Chi-square test, $P = 0{\cdot}005$; see Fig. S2). For biomass loss and C release rate, the effect of time was also larger for the coarse-meshed bags, with higher C release rates during the first period (Figs 2a–d and S1).

Relative N loss after 167 days was related negatively to initial C : N ratio of dung (GLM, F-ratio = 24·7, $P < 0{\cdot}001$, Fig. 3a) and positively to initial N : P ratio (GLM, F-ratio = 41·4, $P < 0{\cdot}001$, Fig. 3b). Relative P loss depended on the initial dung C : P ratio (GLM, F-ratio = 14·9, $P < 0{\cdot}001$), but not on the initial dung N : P ratio (Fig. 3c,d). Because N and P were lost at different relative rates, the ratio of N loss to P loss increased with initial dung N : P ratio (Fig. 3g; GLM, F-ratio = 14·1, $P < 0{\cdot}001$).

Relative losses of both N and P were always higher from coarse- than from fine-meshed bags (Fig. 3). The ratio of N loss to P loss became more equal when soil macrofauna had access to the dung, as they increased the relative loss of N from dung with lower N : P ratios and decreased it at higher N : P ratios (Fig. 3f; GLM, interaction between initial dung N : P ratio and mesh size, F-ratio = 7·2, $P = 0{\cdot}008$). No such pattern was found for the ratio of C to N loss or the ratio of C to P loss, although the ratio of C to N loss tended to increase with initial dung C : N ratio (Fig. 3e,f).

EFFECTS OF DUNG BEETLES ON DUNG DECOMPOSITION AND NUTRIENT RELEASE RATES

The presence of dung beetles increased C, N and P release rates significantly, while crushing the dung only increased C release (Table 2; Fig. 4). Crushing had no effect in the absence of beetles and tended to have a negative effect when beetles were present (Table 2; Fig. 4). Furthermore, N release rates increased when dung beetles were present (one-way ANOVA, F-ratio = 4·1, $P = 0{\cdot}047$), while the treatment with dung alone had no significant effect (Fig. 5). P release into the soil showed the same pattern, but was not significant.

Discussion

To our knowledge this is the first study to compare the C : N : P stoichiometry of dung for a wide range of

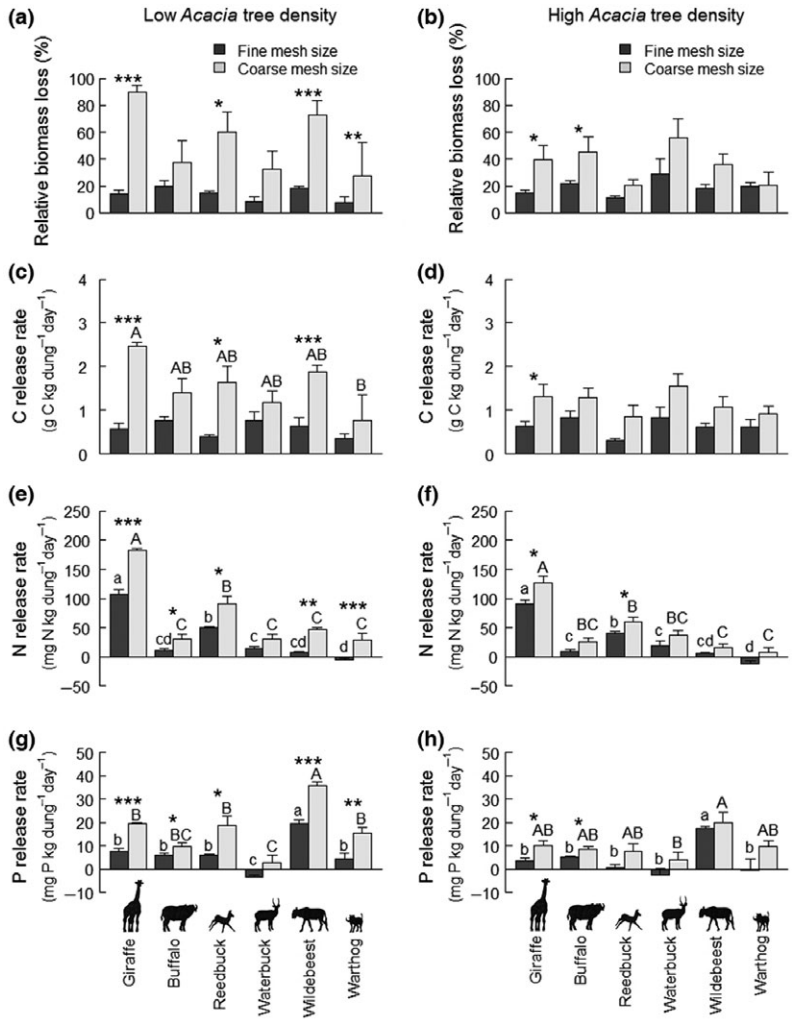

Fig. 2. Relative biomass loss (a, b), and C (c, d), N (e, f) and P release rates (g, h) of dung from different herbivore species after 167 days in the field, at two locations (low *Acacia* tree density: *c*. 200 trees ha^{-1}; high *Acacia* tree density: *c*. 2000 trees ha^{-1}), and when placed in dung bags with a fine (100 μm; dark-grey bars) or coarse mesh size (5 mm; light-grey bars). The coarse-meshed dung bags allowed access by soil macrofauna. Bars show mean relative biomass loss or nutrient release rates per herbivore species (±SE; $n = 7$ or $n = 5$ for reedbuck). Bars within a location not connected by the same letter indicate significant differences between herbivore species; lowercase letters are for fine-meshed dung bags, uppercase letters for coarse-meshed dung bags. Asterisks indicate differences in relative losses or release rates between mesh size for a certain herbivore species with *($P < 0{\cdot}05$), **($P < 0{\cdot}01$) or ***($P < 0{\cdot}001$). No letters or asterisks indicate no significant differences between herbivore species or mesh size.

African mammalian herbivores. Our analyses reveal considerable interspecific variation, much of which can be linked to differences in feeding strategy and digestive physiology (Table 1). One of the greatest contrasts was between the dung of ruminant browsers (e.g. giraffe and grey duiker) and ruminant grazers (e.g. buffalo and hartebeest). Similarly, the exceptionally low N and/or P concentrations in the dung of cane rat and scrub hare might be related to the efficient internal recycling of N and P through a coprophagous feeding strategy.

In general, our results are supported by data from other studies. Thus, our finding of higher N concentrations in the dung of browsers compared to grazers (Table 1) is consistent with a negative correlation between grass intake and dung N concentrations reported by Codron *et al*. (2007). Similarly, a relationship between body size and nutrient concentrations in dung – reflecting a tendency for diet quality to decrease with body size – has been reported in several previous studies (Edwards 1991; Codron *et al*. 2007; De Iongh *et al*. 2011). However, most comparisons – both in our work and in the literature – are based upon rather few, often related herbivore species (4–5; see Table 1); therefore, before drawing firm conclusions about the influence of functional group upon nutrient stoichiometry of dung, data for a larger and more diverse range of herbivores will be needed in combination with phylogenetic corrections.

As predicted from studies of plant litter decomposition, rates of dung decomposition and nutrient release depended strongly on C : N : P stoichiometry (Enríquez, Duarte & Sandjensen 1993; Coûteaux, Bottner & Berg 1995; Sterner & Elser 2002; Ouédraogo, Mando & Brussaard 2004). Thus, dung with high N concentrations and low C : N ratios, as from the ruminant browser giraffe, had the highest N release rates, whereas dung with low C : P ratios, especially from ruminant grazers such as reedbuck and wildebeest, had high P release rates (Figs 2 and 3). We note that the C, N and P contents in the dung used for the dung decomposition experiment (see Table S1) differed somewhat from those in a larger sample of material collected over several seasons (Table 1), especially dung from wildebeest used in the experiment had higher P concentrations than normal, which may reflect where the herd was feeding when the material was collected.

The relative rates at which N and P were lost from dung depended on the initial N : P ratio; thus, P was lost

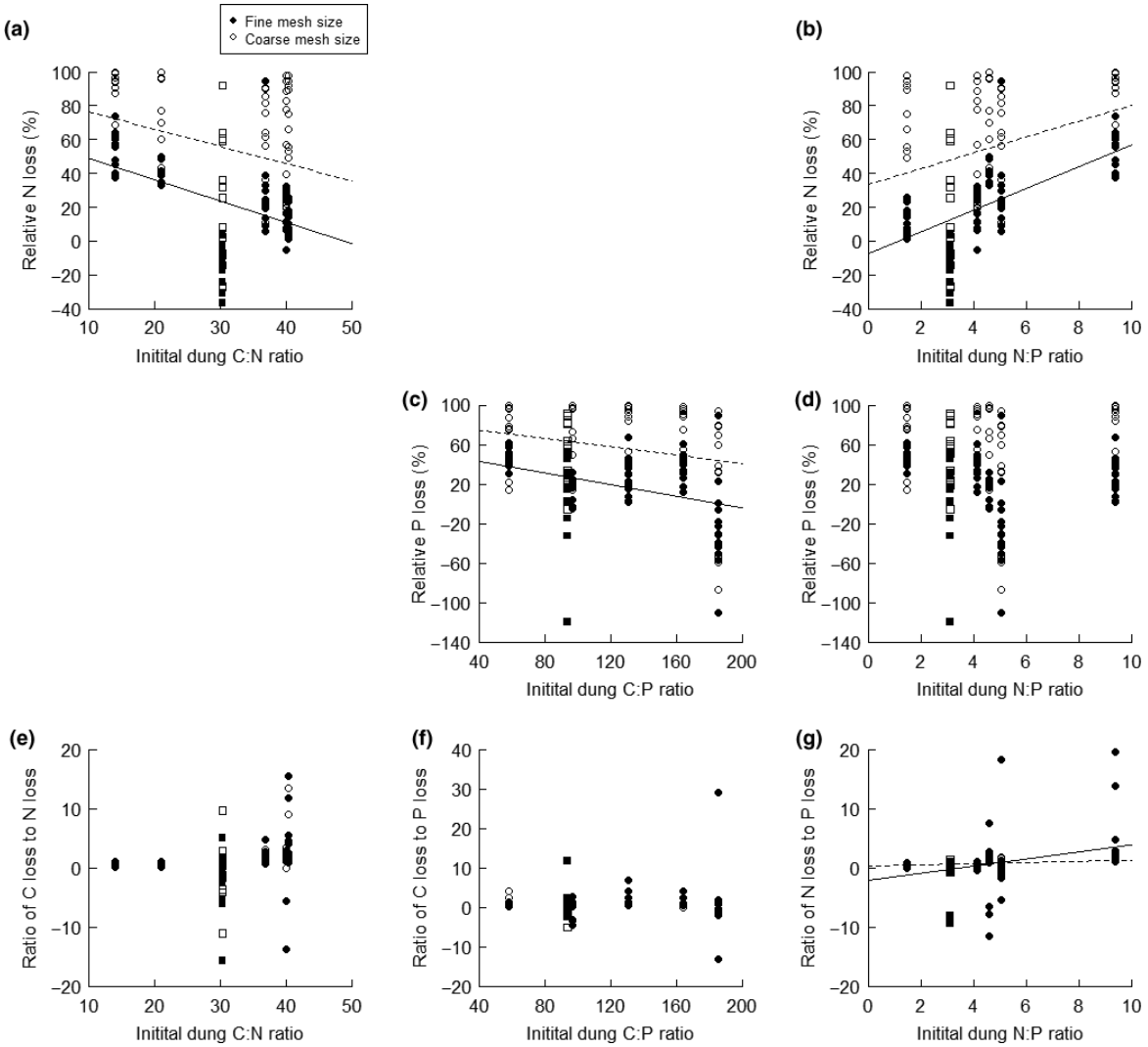

Fig. 3. Relative losses of N (a, c) and P (b, d) from dung of several herbivore species (circles: ruminants; squares: non-ruminants) expressed as percentages of the initial concentrations and plotted against initial dung C : N, C : P or N : P ratios. Also shown are the ratios of C loss to N loss (e), C loss to P loss (f) and N loss to P loss (g) plotted against initial ratios. Variations on the horizontal axes are due to variation among species. The data are for dung samples placed for 167 days in the field in either fine- or coarse-meshed bags. Linear regression lines were drawn where significant ($P < 0{\cdot}05$; more statistical details in text); solid lines represent measurements from the fine-meshed bags and dashed lines from the coarse-meshed bags.

relatively faster from dung with a lower N : P ratio, while N was lost faster from dung with a higher N : P ratio (Fig. 3g). The resulting changes in the ratio of N loss to P loss were mainly driven by differences in the rate at which N was lost (Fig. 3b,d) and, as far as we know, have not been reported before for dung, although the patterns are consistent with N and P release from decomposing plant litter that differed in N : P stoichiometry (Güsewell & Gessner 2009; Moore *et al.* 2011).

We conclude that differences among species in the stoichiometry of dung are likely to have strong local effects upon N and P cycling and upon the availabilities of these nutrients to plants or microbes. This conclusion is supported by the small additional experiment (Fig. 5), and by results from Nichols *et al.* (2008), showing that nutrients released from dung do reach the soil. Thus, dung of giraffe, for example, is likely to increase relative N availability, while wildebeest dung will increase relative P availability; in contrast, waterbuck dung might even decrease P availability, at least in the first weeks (since the observed negative net P release can only be explained through P adsorption from the environment; see Fig. S1).

The importance of the soil macrofauna in dung decomposition was demonstrated in the field using dung bags of different mesh size and in a garden experiment by adding dung beetles to wildebeest dung (Table 2; Figs 2 and 4). In both cases, the presence of soil macrofauna considerably increased the N and P release rates from dung of all herbivores (Table 2; Figs 2e–h and 4b,c). Moreover, the soil macrofauna promoted the loss of the least abundant

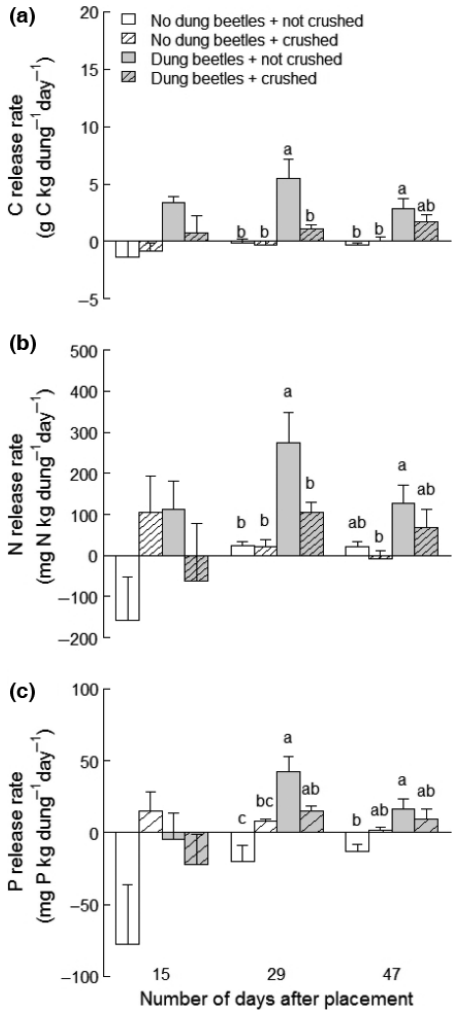

Fig. 4. Effect of dung beetles (white bars: absent, grey bars: present) and crushing treatments (open bars: non-crushed dung, lined bars: crushed dung) on C (a), N (b) and P release rates (c) of wildebeest dung after 15, 29 and 47 days. Bars show mean relative losses (±SE) and bars not connected by the same letter indicate significant differences between treatments per collection time; no letters indicate no significant differences between treatments.

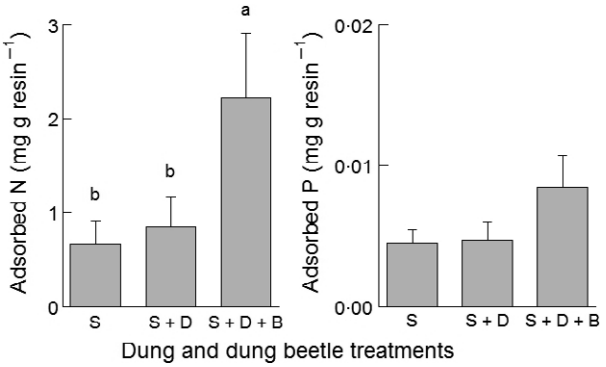

Fig. 5. Mean dung N and P release rates into the soil (±SE) after 34 days, measured through adsorption to ion-exchange resins, per dung and dung beetle treatment, where S = control with only soil (n = 4), S + D = soil and wildebeest dung (n = 5), S + D + B = soil, wildebeest dung and dung beetles (n = 5). Letters indicate significant differences between treatments for adsorbed N; adsorbed P showed no significant differences between treatments.

nutrient, and appeared to stabilize the ratio of N loss to P loss (Fig. 3g). This novel finding cannot be explained simply in terms of the nutrient requirements of dung beetles and termites, and may be related more to their need for energy. For example, Holter & Scholtz (2007) found that dung beetles in savannas apparently maximize the concentration of assimilable C by feeding selectively on small dung particles. Similarly, we found that dung beetles preferred dung of the non-ruminants zebra and elephant, which had the highest C : N and C : P ratios (see Table S1 and Appendix S1). Thus, the preference of dung beetles for non-ruminant dung may in part be due to its C : N : P stoichiometry, and not only to factors such as water and fibre content (Edwards 1991; Paetel 2001). Also, termites have developed strategies to overcome possible C : N : P imbalances between their food and stoichiometric requirements, which are likely related to adding N or selectively eliminating C. For example, they have been shown to obtain extra N through N_2-fixation and release a surplus of C through production of methane gas, both achieved with the aid of symbiotic bacteria (Higashi, Abe & Burns 1992). Overall, dung C : N : P stoichiometry seems to play an important role in the proportions of nutrients utilized by soil macrofauna, though more studies are needed, preferably with dung from a larger number of species, for instance, on the potential facilitating role of feeding macrofauna on the release of microbially immobilized C, N or P and how macrofauna might interact with the different stages of decomposition.

The annual returns in our study area of 1–4 kg N ha^{-1} and 0·2–0·6 kg P ha^{-1} (Fig. 1) represent important internal nutrient pathways comparable in magnitude to annual inputs through wet atmospheric deposition (3·8–5·3 kg N ha^{-1} and 0·2–0·3 kg P ha^{-1}; J. Sitters, P.J. Edwards, W. Suter & H. Olde Venterink, unpublished data). Thus, the dung of mammalian herbivores plays an important role in the spatial distribution and cycling of nutrients in savanna (Ruess & McNaughton 1987; Augustine, McNaughton & Frank 2003; Fornara & Du Toit 2008; van der Waal *et al.* 2011). In our field site, nutrient release rates were probably highest in the open areas (at 0–500 trees ha^{-1}), since these received larger amounts of both browser dung (high N release) and ruminant grazer dung (high P release; Fig. 1). In other areas, however, local or regional differences in N or P release from dung could be expected because of different proportions of these functional herbivore groups.

Previous studies have estimated nutrient inputs from dung by multiplying biomass deposition rates by nutrient concentrations in dung (Augustine, McNaughton & Frank 2003; Fornara & Du Toit 2008; Cech, Olde Venterink & Edwards 2010; van der Waal *et al.* 2011). However, these studies take no account of possible differences in N and P

release rates among species and may therefore lead to misleading conclusions about the rates at which nutrients become available to plants or microbes. For example, if we multiply deposition rates by nutrient concentrations, we find that the N input from giraffe dung in our study was twice as high as from wildebeest (see Table S2). Taking N release rates of these two dung types into account, however, we see that the actual N release of giraffe dung in the first 41 days was 6–9 times higher, depending on invertebrate activity, whereas the release of P was higher from wildebeest dung, even though the total P inputs from the two herbivores were similar (Table S2).

We conclude that heterogeneity of N and P turnover through herbivore dung in savanna ecosystems depends not only upon the distribution of dung across the savanna landscape (Augustine, McNaughton & Frank 2003; van der Waal *et al.* 2011), but also on its C : N : P stoichiometry, on the presence of soil macrofauna and on interactions among these factors. Together, these factors may exert a strong influence upon the relative availabilities of N and P in the soil and thus upon the functioning of savanna ecosystems.

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Data accessibility

Data deposited in the Dryad repository: http://doi.org/10.5061/dryad.73b8m (Sitters *et al.* 2014).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Dung beetle preference for herbivore dung.
Fig. S1. Relative biomass loss and nutrient release rates of dung from several herbivore species.
Fig. S2. Proportion of dung bags attacked by soil macrofauna.
Table S1. C : N : P stoichiometry of dung of several herbivore species.
Table S2. Total dung N and P inputs of several herbivore species.