Functional attributes of savanna soils: contrasting effects of tree canopies and herbivores on bulk density, nutrients and moisture dynamics

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Summary

1. Savannas are highly heterogeneous tree-grass mixtures, and the structural variation imposed by a discontinuous canopy cover results in spatial variation in soil properties such as plant-available nutrients, temperature and soil moisture. Many savannas are also dominated by large vertebrate herbivores, which impose a different suite of effects on soil properties related to consumption, excretion and physical disturbance.

2. In nutrient-poor, water-limited systems, variation in soil resource availability may play a fundamental role in structuring plant communities, but the relative and interactive effects of key drivers of heterogeneity have received little attention in savanna ecosystems.

3. We investigated the independent and interactive effects of herbivores and tree canopy cover on multiple soil properties up to a depth of 10 cm, including bulk density, soil C pools, total and plant-available nutrients, moisture dynamics and temperature at two contrasting sites in Kruger National Park, South Africa. We analysed samples from locations under and between adult tree canopies and inside and outside long-term herbivore exclosures using a nested design.

4. We found strong positive effects of tree canopies on total and labile pools of soil C and N and negative effects on plant-available P and soil temperature. Tree canopy effects on soil moisture availability were small but clearly detectable. During precipitation events, trees increased moisture inputs on granite soils but decreased moisture inputs on basalt soils compared to open sites.

5. Conversely, we found mixed evidence for herbivore effects on soil chemistry and temperature, but a clearer effect on soil moisture, with areas outside exclosures experiencing higher soil moisture retention, particularly immediately following precipitation events. Soil bulk density, a driver of both nutrient and soil moisture dynamics, was lower under trees and when herbivores were excluded.

6. Synthesis. Our results suggest that variation in tree cover is the dominant biotic driver of C, N and P dynamics in these savanna systems in the top 10 cm of soil, that herbivores primarily affect soil moisture content, and that canopy and herbivore effects tend to be additive rather than synergistic.

Key-words: functional heterogeneity, grazers, Kruger National Park, microclimates, plant-available nutrients, plant–soil (below-ground) interactions, resource limitation, spatial heterogeneity

Introduction

Savanna vegetation is characterized by a high degree of structural heterogeneity (Scholes & Archer 1997). This heterogeneity is primarily the result of small-scale variation in canopy cover, which in turn exerts control over biophysical processes (Sankaran, Ratnam & Hanan 2008; Brudvig & Asbjornsen 2009). It has been established, for example, that savanna tree canopies diminish understorey solar radiation and temperature and enhance soil moisture availability and nutrient and carbon (C) concentrations, with consequences for herbaceous composition and diversity (Belsky et al. 1989; Vetaas 1992; Brudvig & Asbjornsen 2009). Many savannas, particularly in Africa, are also dominated by large herbivores, which impose their own effects on soils and plants, thus potentially enhancing or counteracting tree canopy effects (Vetaas 1992). When herbivores aggregate under trees, non-additive (i.e. synergistic or antagonistic) canopy–herbivore interactions may result
A key remaining challenge is to understand the relative contributions and interactions of tree canopies and herbivores to soil functional heterogeneity. Unlike grasslands or forests, which are treeless or have essentially closed canopies, respectively, savannas have a discontinuous tree layer over a ground layer of near-continuous grass cover (Scholes & Walker 1993). They are therefore highly patchy in terms of incoming radiation, precipitation (which may be intercepted or concentrated) and in the amount and quality of litter deposition both above- and below-ground. This spatial heterogeneity in the abiotic and biotic environment can in turn influence the underlying grassland matrix and soil (Scholes & Archer 1997). Tree canopy effects can influence soil nutrients and C via competition with grasses for resources (Knoop & Walker 1985; Riginos 2009), through variables that influence decomposition rates (such as soil moisture and temperature) and through leaching (Belsky et al. 1989, 1993). Trees can also redistribute nutrients and water through hydraulic lift (Schulze et al. 1998; Ludwig et al. 2003) and concentrate water flow via stem-flow (Vetaas 1992). Conversely, tree canopies intercept water, a substantial fraction of which may then be lost through evaporation prior to reaching the soil surface, particularly during small precipitation events (Rodriguez-Iturbe et al. 1999). Overall, sub-canopy effects on soil nutrients have generally been found to be positive relative to inter-canopy sites (Belsky et al. 1989; Ludwig et al. 2004; Holdo, Mack & Arnold 2012), but effects on soil moisture have been less well described (Belsky et al. 1993; Belsky & Canham 1994).

The role of herbivores on soil C and N dynamics has been quite widely studied in many grassland systems (Parton et al. 1987; Frank et al. 1994; Biondini & Manks 1996; Johnson & Matchett 2001). Herbivores have been shown to impose considerable effects on soil nutrients in savanna ecosystems when aggregated at high densities, such as in hotspots (McNaughton 1988; McNaughton, Banyikwa & McNaughton 1997; Augustine, McNaughton & Frank 2003) or near water-holes (Naiman et al. 2003), but their overall effects at large scales or at the scale of tree canopies and inter-canopy spaces are often not the focus of investigation. When examined across a range of systems, herbivores can exert either positive or negative (and sometimes neutral) effects on soil N (Milchunas & Landers 1993). Their effects on soil P have been less well-studied, but these may be as or more important than effects on soil N, given the evidence for P limitation or co-limitation of primary productivity in tropical savannas (Penning de Vries, Krul & van Keulen 1980; Chapin & McNaughton 1989; Crane, Morrow & Stock 2008). Herbivores may also potentially influence soil moisture dynamics by causing changes in plant transpiration as a result of grazing, and by altering interception in the herbaceous or tree layer through biomass removal (Coughenour 1984; Frank & Groffman 1998). Trampling, a relatively understudied ecological process (Cumming & Cumming 2003), may also plausibly affect soil hydrological properties by reducing rates of drainage to deeper layers, but generally, the role of herbivores for soil moisture dynamics remains largely unstudied.

In addition to the independent effects of tree cover and herbivore biomass, synergistic interactions between these two variables may occur through a variety of mechanisms. For example, canopy trees attract birds and other animals that may act as vectors for importing nutrients from the surrounding matrix (Vetaas 1992; Dean, Milton & Jeltsch 1999), and may influence the spatial distribution of foraging behaviour of shade-seeking herbivores (Vetaas 1992; Treydte et al. 2010). Shade-seeking herbivores may concentrate nutrients under canopies (Vetaas 1992) or otherwise magnify any baseline effects they may exert on soil moisture dynamics, thus exacerbating any pre-existing canopy effects. By and large, these interactions have not been quantified because of the lack of data for these two drivers at single sites.

Much of the literature on tropical savannas has focused on the direct effects of disturbance and herbivores on vegetation structure (Hoffmann 1999; Archibald et al. 2005; Bond 2005; Bond, Woodward & Midgley 2005; Holdo 2007; Staver et al. 2009). In ecosystems with highly seasonal precipitation, however, soil moisture availability may be the key limiting resource for plant growth (Sankaran, Ratnam & Hanan 2008; February et al. 2013). Terrestrial ecosystems in general are also nutrient-limited (Vitousek & Howarth 1991), and nutrient to carbon ratios in soils play an important role in controlling nutrient availability (Parton et al. 1987). Spatiotemporal variation in nitrogen (N) in particular is widely associated with variation in plant community composition (Bobbink et al. 2010), and has been proposed to influence tree to grass ratios in savannas (Sankaran, Ratnam & Hanan 2008). Given the pervasive nature of resource limitation for vegetation, it is important to understand the factors influencing various resource pools in systems where such pools are likely to show a high degree of spatial heterogeneity. In savannas specifically, a key question is: how do some of the key drivers responsible for the heterogeneity that pervades this biome, such as herbivores and tree canopies, separately and jointly influence spatial variation in nutrient and C pools and soil moisture dynamics?

In this study, we used ~35-year-old enclosures to explore the effects of herbivores, tree canopies and their interactions on nutrient and soil moisture dynamics on two soil types in the lowveld savanna of Kruger National Park (KNP), South Africa. Previous work in this system has examined canopy effects on soil nutrients and forage quality, either in isolation or in relation to fire (Coetsee, February & Bond 2008; Treydte, Grant & Jeltsch 2009; Holdo, Mack & Arnold 2012). A general finding is that trees are strongly associated with elevated C and N soil pools, and that fire effects are primarily indirect, and modulated by tree cover (Coetsee, February & Bond 2008; Coetsee, Bond & February 2010; Holdo, Mack & Arnold 2012). Here, we explored how herbivores and herbivore–tree interactions affect soil nutrient and C stocks and drive soil moisture dynamics. We asked two key questions: (i) How do herbivores affect total and plant-available nutrients and soil C pools, soil moisture availability and soil temperature? (ii) What is the relative importance of canopy versus herbivore effects on soil chemistry, moisture and temperature?
Materials and methods

STUDY SITES

We sampled soils and monitored soil temperature and soil moisture in and around two large long-term herbivore exclosures (Fig. 1) within the boundary of KNP. This park comprises 20 000 km² of tropical to sub-tropical ‘lowveld’ (low-altitude) savanna along the South Africa-Mozambique border in southern Africa. The climate is characterized by a well-defined summer rainy season (spanning the period from late October–May), with mean annual precipitation ranging between <400 mm in the far north and ~800 mm in the South (Venter, Scholes & Eckhardt 2003). There is a marked E–W geomorphological divide, with granitic- and basaltic-derived soils dominating in the W and E respectively (Venter, Scholes & Eckhardt 2003). Soils on granite are nutrient-poor and sandy, and tend to be dominated by relatively unplatable broad-leaved tree species such as Terminalia sericea, whereas soils on basalt are slightly more clay- and nutrient-rich rich and tend to be dominated either by Acacia spp. (in the wetter South) or by Colophospermum mopane (in the hotter, drier North). Fire and large ungulate herbivores are important drivers of vegetation dynamics in the ecosystem (du Toit 2003; van Wilgen et al. 2003; Asner et al. 2009).

The herbivore exclosures (Fig. 1) are more accurately described as ‘enclosures’ constructed for breeding rare antelope, but in essence can function effectively as exclosures for experimental purposes because herbivore density and biomass are much greater outside than inside the enclosure fences, and have been extensively treated as such (Asner et al. 2009; Treyte, Grant & Jeltsch 2009; Levick et al. 2010). In particular, both sites exclude elephants, dominant ecosystem engineers in Kruger (Whyte, van Aarde & Pimm 2003). The Hlangwine enclosure, established in 1971, is 254 ha in size and is located on granitic soils in the south of KNP near Pretoriuskop (Fig. 1). The N’washishhumbe enclosure (290 ha), established in 1976, is situated in the drier North of the park on basaltic soils. It is problematic to make formal comparisons between the two due to the lack of replication and because there are confounding factors other than soil differences (e.g. climate and levels of herbivory), but the two areas serve as fairly representative examples of two dominant habitat types typical of the savanna domain: i.e. ‘broad-leaved’, savanna on nutrient-poor sandy soils and ‘fine-leaved’ savanna on richer soils, often found at the semi-arid end of the rainfall spectrum (Scholes & Walker 1993; Venter, Scholes & Eckhardt 2003). For simplicity, we refer to the two areas as the ‘granite’ (for Hlangwine) and ‘basalt’ (for N’washishhumbe) exclosures hereafter.

SOIL SAMPLING

At the granite exclosure, we selected potential sampling sites at least 200 m apart along the length of the fence in November 2009. We randomly selected a sample of 16 sites from this set. Inside the fence (I sites, with low herbivory), we tagged and mapped with GPS the nearest tree satisfying a minimum set of criteria (>10 m from the access road, >20 cm diameter at breast height; Fig. S1 in Supporting Information). We similarly identified and marked a matching tree outside the fence (O sites, with high herbivory). At each tree, we obtained three soil cores to a depth of 10 cm under the crown of the tree (the ‘under’ or U sample) plus 3 matching cores away from the tree, between the crowns of the target and neighbouring trees (the ‘between’ or B sample). We combined the U and B cores, stored the samples in airtight ziplock bags, and kept them refrigerated prior to transportation to the laboratory in the United States. We collected a fixed, known volume of soil with each core (262 cm³) and weighed the fresh composite sample prior to subsampling and reweighing between 100 and 200 g of soil for shipment and analysis. At the basalt exclosure, we restricted sampling to portions of the fence that had not been burned in several years to avoid confounding effects of fire (the exclosures are divided into blocks and burned in a rotation). Also, the effect of fencing out herbivores is quite dramatic at this exclosure (Asner et al. 2009), as evidenced by an almost complete lack of trees >20 cm d.b.h. outside the fence. In this case, we took the O site as the nearest tree (regardless of size) across the fence from the matching I site. Given that these trees were heavily-browsed and effectively lacked crowns of appreciable sizes, we only collected B samples in most cases.

Strictly speaking, the herbivory effect is unreplicated in this study (given that we only sampled one exclosure per soil type), as landscape-level studies often are (e.g. Asner et al. 2009; Levick et al. 2009). In practice, however, the large size of the exclosures (>6 km of fencing, >250 ha) should allow pairs of sites (inside and outside

Fig. 1. Sampling locations at the herbivore enclosure sites: (a) Hlangwine (granite) and (b) N’washishhumbe (basalt). Labels correspond to trees around which paired under- (U) and between-crown (B) soil samples were taken. Circles identify trees with paired soil moisture and temperature sensors located in U and B locations. Trees with sensors were paired in sites across the fence boundary.
the fence) to be considered as independent samples for practical purposes, provided that they are located far enough from each other to minimize unwanted spatial autocorrelation and to capture a meaningful amount of the landscape heterogeneity present in the system as a whole. To help assess whether this was the case, we examined the scale of spatial autocorrelation across sampling sites for each enclosure by applying Moran’s I (Legendre & Legendre 1998) to the first principal component calculated across five soil variables (total C and N, labile C and N, and Mehlich-P). We found no significant spatial autocorrelation at any of the lag distances tested, including those corresponding to adjacent sites (~200 m). The trend in the pattern of autocorrelation also tended to alternate between being positive and negative as a function of increasing lag distance, which indicates that the enclosures were large enough to capture variation in soil properties across entire catenas, which are dominant mesoscale topographic properties of the landscape, further suggesting that the spatial scope of the enclosures was sufficient to encompass much of the spatial heterogeneity present in this system (Fig. S1).

SOIL MOISTURE AND TEMPERATURE

We collected soil moisture and temperature data at a subset of eight trees (four each inside and out) per enclosure (Fig. 1) over the rainy season, spanning ~200 days between November 2009 and June 2010. We selected trees using a stratified randomization protocol (one individual per group of four consecutive trees inside the fence, paired with its matching tree on the other side of the fence). At each tree, we buried two HOBO soil moisture probes (ECH20 EC-10; Decagon Devices, Pullman, WA, USA) vertically in the top 10 cm of soil, one under the tree canopy (U probe) and one in the nearby intercanopy area (the B probe). Both probes were connected to a single HOBO Micro Station datalogger (Onset Computer Corporation, Bourne, MA, USA) attached to the tree trunk. At each enclosure, we connected a tipping bucket-type rain gauge to one of the dataloggers located inside the fence. For temperature measurements, we buried ibutton temperature dataloggers (DS1921G; Maxim Integrated, San Jose, CA, USA) at a depth of 5 cm next to (but not touching) each soil moisture probe. Soil moisture and rainfall data were logged at 5-min intervals, while temperature data were logged every hour. These sampling schemes allowed us to obtain ~205 days of soil moisture data (November–June) and ~85 days of temperature data (November–February) over the course of the growing season.

LABORATORY ANALYSES

In the laboratory, we passed soil samples through a 2-mm sieve and then subsampled them for determination of gravimetric water content (GWC) (by drying at 105 °C for 48 h) and total C and N. We used our water content data to convert the field-measured soil mass to dry mass. We calculated the bulk density for every sample by dividing its known volume of soil collected by its dry mass. We measured the soil subsample shipped from the field-moist soils and final pools of inorganic N (NH4+ and NO3−) on soil samples extracted with 50 mL of 2 M KCl. We moistened final (incubated) samples to an estimated 60% water holding capacity (determined from a composite soil sample) with a fixed amount of deionized water (Ruess & Seagle 1994). We shook solutions for 2 h and left them overnight before filtering and freezing prior to analysis. We determined inorganic N concentrations in the extracts colorimetrically on an Astoria-Pacific autoanalyzer (Astoria-Pacific, Clackamas, OR, USA). We also determined labile C pool size from the incubations following a method described by Lavollé et al. (2011). We analysed soil-respired CO2 on a LI-COR 6252 CO2 analyser (Lincoln, NE, USA) fitted with a calibrated injection port. We used extractable P from the Mehlich-1 procedure as an index of plant-available soil P (Kuo 1996). We analysed extracts colorimetrically with a microplate spectrophotometer (PowerWave XS Microplate Reader; Bio-Tek Instruments, Winooski, VT, USA).

STATISTICAL ANALYSIS

We used linear mixed models implemented in the R (R Development Core Team 2011) package nlme (Pinheiro & Bates 2000) to test for effects of herbivores (HERB, as captured by fencing) and canopy cover (CAN) on soil bulk density, nutrient concentrations and mineralization rates, and temperatures. We note that it would be more accurate to call the herbivore effect a fencing or removal effect, but find that the former description makes our results easier to follow and interpret. We included two temperature (mean daily temperature Tmean and daily temperature range Trange) and seven soil variables: bulk density, total C and N, in vitro mineralizable N (Nmin and C (Cmin), Mehlich-P, and C:N. We conducted a first set of analyses with N, P and C data expressed on a mass basis (in g kg−1 of dry soil). The initial analysis showed a strong effect of both fencing and canopies on bulk density, at least on granite, so we repeated the analyses an area basis (g m−2 for the top 10 cm of soil) for all variables except C:N, which as a ratio is invariant with respect to mass or area. We log-transformed most soil variables prior to analysis, except for Nmin, which exhibited negative values in several cases (i.e. indicating immobilization), as well as Cmin and the soil temperature variables. We treated fencing and canopy position as fixed effects, and modelled two random effects: an individual tree effect (with paired U and B sampling locations) nested within a site effect (with paired I and O trees), and a site effect. For soil nutrients at the granite enclosure, we tested main effects and interactions among fixed effects. At the basalt enclosure, the near-absence of U samples outside the fence resulted in a highly-unbalanced design and demanded a two-part analysis: a test of canopy effects on I trees, and a test of fencing effects on B sites. Each of these analyses included a single random effect (individual trees in the first case and sites in the second). For the soil temperature data, we initially proposed to leverage the large number of temperature records in our data set into a repeated measures analysis, but an initial analysis showed high temporal autocorrelation in the model residuals over long (>20 days) time lags, even after detrending the data with periodic functions. When such autocorrelation patterns are observed over a few time lags, they can readily be accounted for by modelling the temporal dependency in lme (Pinheiro & Bates 2000). In this case, we opted for the more conservative approach of estimating mean values of Tmean and Trange per datalogger for the duration of the sampling interval, and treating these means as observation units in a linear mixed model. As with the soil nutrient data, the lack of U sites outside the fence on basalt required a two-part analysis of crown and fence effects on separate subsets of the data. After fitting the models, we visually and quantitatively examined plots of residuals versus fixed effects and quantile-quantile normal plots of both residuals and random effects to evaluate departures from normality and
variance homoscedasticity (Pinheiro & Bates 2000). For the few cases in which serious outliers were detected, we repeated the analyses without the outliers to evaluate the robustness of the analysis to the presence of such values.

In addition to testing for fencing and canopy effects, we tested for effects of soil organic matter quality on $N_{0\text{ lab}}$, to examine the extent to which any observed variation in N mineralization can be explained by litter quality effects on decomposition rates. We used two measures of soil organic matter quality: the log of the C:N ratio and the ratio of $C_{\text{lab}}$ to C. We interpreted the latter as the ratio of labile or fast to recalcitrant soil C. We can regression models using $\text{ln}$ with the same random effect structure described above for canopy and herbivore exclusion effects.

**MODELLING SOIL MOISTURE DYNAMICS**

For the analysis of soil moisture dynamics, we initially proposed to follow the approach we adopted for the analysis of the temperature data. This was complicated by two factors. First, unlike temperature, soil moisture is subjected to episodic forcing by rainfall, which leads to a pattern of sudden spikes and decays in moisture content that appear to interact nonlinearly with the fixed effects of interest (e.g. canopy cover). This means that it is difficult or misleading to simply subtract the average soil moisture trend from each sensor and relate the resulting offset value to some independent variable. The problem is exemplified in Fig. S2, where two sensors (a B and a U sensor for the same tree) appear to exhibit quite different temporal patterns, with decay trajectories that cross over time (indicating different rates of decline). The second complication is introduced by gaps in our data, given that temporary failures of some of the soil moisture probes and the rain gauge at one of our sites resulted in significant periods without data for some sensors. Elimination of all days without a complete data set would have substantially reduced our power to make meaningful inferences. As a result of these challenges, we opted for a modelling approach that allowed us to combine a simple, well-established soil moisture dynamics process model (Rodriguez-Iturbe et al. 1999; Liao et al. 2001; Guswa, Celia & Rodriguez-Iturbe 2002) into a Bayesian statistical framework that allowed us to impute probability distributions for missing data points, and thus leverage the entire data set in the analysis.

Our process model essentially identifies three phases or processes in a soil moisture dynamics time series: water input, and ‘fast’ and ‘slow’ output rates (Fig. S2). Inputs are driven by precipitation events (Fig. 2a) and the factors that modify the size of these events, such as canopy interception or stem flow. Outputs are controlled by drainage to deeper soil layers (in our case to depths below 10 cm), evaporation and plant transpiration (or evapotranspiration (ET) when the latter two are considered jointly). Following a precipitation event (which leads to a spike in soil moisture content), there is an initial, fairly rapid drop-off in moisture (the fast output), due mainly to drainage as soils return to their field capacity, followed by a slower draw-down (the slow output), driven mainly by ET. In our model, we incorporated the canopy and fencing effects as potential modifiers of these processes and rates. For example tree canopies can modify inputs by locally diminishing or enhancing incoming precipitation amounts, and/or affect the fast and slow output rates that dominate when soils are above and below field capacity, respectively (a priori we link these rates with drainage to deeper layers and ET, respectively, and revisit these assumptions in the Discussion). We used a state space framework for the analysis. State space models combine a process model (in this case, our soil moisture dynamics model) with an observation or data model (our sensor data). The state space framework allowed us to model both observation error (i.e. measurement or sensor error) and process error. Process error allows for the fact that, even in the complete absence of observation error, soil moisture dynamics will exhibit stochastic variability associated with unmeasured factors (Clark & Bjornstad 2004; Holdo et al. 2009). For example, transpiration might vary seasonally as a result of phenology, leading to temporal drift in soil moisture decay rate, even when soil moisture is measured with great accuracy. State-space models are also ideal for dealing with the second challenge outlined above, i.e. missing data (Clark & Bjornstad 2004), because the model effectively estimates (with error) the underlying ‘true’ soil moisture time series that provides the best fit to the process and observation models, even for time periods that lack observations. This is because the values that occur before and after a gap in the data for a particular sensor, as well as values obtained for other sensors, provide information about the state of the sensor during the interval with missing data. The larger the gap, the greater the uncertainty around these missing values, and the lower the leverage of these imputed points for model inference (e.g. Fig. 2b). Finally, the highly hierarchical nature of our design (i.e. random effects of trees nested within sites, probes nested within trees and repeated measures at the probe level) made the problem amenable to a Bayesian framework, with posterior distributions derived through Markov Chain Monte Carlo (MCMC) methods, implemented in WinBUGS (McCarthy 2007). The soil moisture model, which is explained in detail in Appendix S1, in principle should allow us to tease apart the independent effects of fencing and tree crowns on the inputs and outputs outlined above, because each of these processes can, to varying degrees, be inferred from particular features of the trajectories of maximum and mean daily soil moisture increases and declines. For example, if two sensors start at the same baseline soil moisture, but one exhibits a higher spike following a rainfall event than the other (Fig. S2), we can infer that the sites associated with each sensor modify inputs (e.g. through interception) in different ways. We incorporated the effects of the covariates on the three processes that drive the model by expressing three model variables as linear equations containing the two covariates (Appendix S1). For example, fast outputs are controlled by the saturated conductivity rate (Rodriguez-Iturbe et al. 1999), which in our model, rather than being treated as a fixed parameter, is a simple function of CAN and HERB.

We conducted the soil moisture analysis slightly differently for the granite and basalt sites. We performed a single analysis at the granite exclosure, with additive effects of CAN and HERB on each of the soil moisture dynamics processes. We did not test for interaction effects to avoid overburdening an already-complex model. On basalt, the almost complete lack of canopy cover outside the fence meant that we lacked outside U data. We therefore divided the soil moisture analysis into two parts: an analysis of canopy effects inside the exclosure, and an analysis of fencing effects between B samples. Also, to test the ability of our approach to infer the parameters of the underlying process model, we generated a simulated data set with tree canopy and herbivore effects on inputs and fast outputs (Appendix S1). Our Bayesian approach was able to recover the underlying model parameters (Table S7).

To obtain soil moisture data for the Bayesian analysis, we first calibrated our HOBO sensors with soil samples of known moisture content from the granite exclosure (GWC measured in the lab). We used: (i) soil cores collected to a depth of 10 cm from sites immediately adjacent to each sensor in March 2010, and (ii) containers with soil of contrasting soil moisture content into which we inserted a pair
of soil moisture dynamics. We ignored random effects, and only included one stochastic effect, the process error. Each time series was driven by the actual rainfall time series from our data set. We then compared mean soil moisture availability (computed across the 100 runs) under and between canopy sites and inside and outside the fence.

Results

SOIL BULK DENSITY AND NUTRIENTS

Bulk density in the top 10 cm of soil was lower under canopies than between canopies at both exclosures, while herbivore presence increased bulk density on granite, but not on basalt. On a mass basis, we found no effects of herbivore exclusion (or herbivore by canopy interactions) for either total or labile pools of C and N or for Mehlich-P (Tables S1 and S2). On an area basis, however, the effect of herbivore exclusion on bulk density modified the results on granite, with areas outside the fence (i.e. with higher herbivore biomass) having higher total C and N than areas inside. The canopy effects were consistent regardless of the basis used to express soil chemistry. Canopy effects were common on both soil types, with total and labile C and N tending to be higher under tree crowns (Tables S3 and S4, Figs 3 and 4), and Mehlich- (extractable) P being higher between crowns on basalt (Tables 1 and S2, Figs 3 and 4). Outlier removal only slightly altered the results; in particular, the removal of one prominent outlier in the \( C_{\text{min}} \) analysis on basalt indicated that labile C may be lower outside the enclosure than inside on this soil type (\( F_{1,14} = 16.99, P < 0.005 \)). The canopy effects on C and N were comparable in magnitude: C:N ratios did not vary with canopy position, or as a function of herbivore exclusion (Tables 1 and S1, S2). \( N_{\text{min}} \) was unrelated to either C:N or \( C_{\text{min}} \) ratios on either granite (Table 2, Appendix S1).

SOIL TEMPERATURE AND MOISTURE DYNAMICS

Tree canopies, but not herbivore exclusion, had clear cooling effects (\(-2 \degree C\)) on mean soil temperatures at both sites, and moderated temperature fluctuations at the granite (but not basalt) site (Tables S3 and S4).

The state-space model estimated inputs and outputs (expressed as linear functions of CAN and HERB) for soil moisture availability over the course of the wet season. There was support on both granite and basalt for a negative effect of HERB on fast outputs (which we assume are driven by drainage to deeper layers) to a depth of 10 cm, as inferred from the mean value and credible intervals (which did not include 0) for the coefficient \( \gamma_2 \) (Table 2, Appendix S1). This negative effect means that herbivores reduce the fast output rate compared to a baseline rate given by an intercept \( \gamma_0 \) (Table 2). It also means that outside the enclosure, where...
herbivores occur at a higher population density, the top 10 cm of soil tended to remain wetter shortly after precipitation events compared to soils inside the fence. Conversely, we found a positive effect of CAN on fast output (compared to between-canopy areas) on granite (but not on basalt), suggesting that water flows through the upper soil layer faster under tree canopies than in the open (Table 2). We found no effects of any of the covariates on slow output at either site (Table 2).

We found opposing effects of tree canopies on inputs on the two soil types: tree cover was associated with higher water inputs in the top 10 cm as a result of precipitation events on granite compared to open areas, but lower input rates on basalt. On granite, herbivore exclusion also affected input, but its effects opposed those of canopies: areas outside the exclusion had lower inputs than those inside (Table 2), indicating that herbivores were associated with a reduction in the fraction of incoming precipitation making it into the top soil layer. This effect, while nonzero, was small, however; whereas the opposing effects of herbivores and canopies on fast output were comparable in absolute magnitude, the herbivore effect on input was small compared to the canopy effect (Table 2). All of the results reported so far were consistent regardless of the whether the soil moisture model used site-specific or mean values of bulk density (Tables S5 and S6).

The exception was provided by the fencing effect on input, which was predicted to be positive on basalt (i.e. opposite to what we found on granite) for the model with site-specific bulk density but unimportant when we used mean bulk density values (Tables S5 and S6). We note that our state-space model.
model contains fixed parameters (e.g. field capacity; Appendix S1) that would be expected to vary with bulk density, and we did not examine the effect of this dependence on our model inference. We note that these parameters mainly control when soil moisture output switches between the fast and slow phase, rather than the rate of decay itself (Appendix S1), so we would not expect that allowing these parameters to take sensor-specific values would have a qualitative effect on our conclusions. We note also that we tested for a correlation between mean GWC values per sensor and bulk density at the granite site, and found no relationship between the two variables for the subset of locations with both sensor and bulk density data (N = 16, $R^2 = 0.005$). This suggests that our observed patterns are not simply spurious relationships driven by bulk density effects on sensor readings.

The simulation results indicated that the mean net effects of tree canopies and herbivore exclusion on soil moisture over the course of the wet season were small (mean = 4.8% higher at U vs. B sites and 11.6% higher at U vs. B sites). This suggests that the positive effects of canopies on water inputs at the granite site are largely cancelled out by their effects on the fast output rate, indicating that the main role of tree canopies is to accelerate water turnover through the top 10 cm of the soil rather than to affect overall moisture content.

**Discussion**

**SOIL NUTRIENTS AND BULK DENSITY**

The finding that soil total C and N (as well as labile N, C and P) are affected by tree canopies reinforces previous findings from other studies as well as our own work on canopy-fire interactions in KNP (Belsky et al. 1989; Ludwig et al. 2004; Treyde, Grant & Jeltsch 2009; Holdo, Mack & Arnold 2012). We propose that the observed patterns are primarily due to direct biotic effects of the trees, such as nutrient transport, or to tree–grass interactions. Tree effects on soil nutrient pools could also result from herbivore effects, effects of trees on soil organic matter quality, or be a consequence of microclimatic conditions under tree crowns, such as lower temperatures and higher soil moisture, or combinations of the above (Vetaas 1992; Belsky 1994; Coetsee, Bond & February 2010). Our results are in conflict with some of these proposed processes. We inferred elevated water inputs at granite sites, but not on basalt, where subcanopy areas show similar patterns of elevated C and N pools. Second, despite cooler subcanopy temperatures and slightly lower soil moisture availability, the U sites had higher rates of C and N mineralization than open (B) sites. This suggests that the canopy effect on the nutrient cycle may not be driven through abiotic control of the mineralization process. This is because while mineralization rates increase with soil temperature and moisture (Parton et al. 1987), we found higher labile C and N concentrations where both temperature and soil moisture were lower. Also, we found no relationship between N mineralization and our two indices of soil organic matter quality, suggesting that labile N pools are not controlled by variation in the quality of litter inputs under and between canopies. The lack of herbivore by canopy interactions in our results (to the extent that we were able to test for them) also suggests that canopy effects do not interact with any effects that herbivores may exert on soil nutrients, which in our study were largely absent.

We found no evidence for any effects of long-term herbivore exclusion on labile pools of N or plant-available

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**Fig. 4.** Herbivore exclusion and tree canopy effects on soil variables at the N’wathitshumbe (basalt) exclosure in KNP: (a) bulk density, (b) total soil C, (c) total soil N, (d) Mehlich-P, mineralization rates for laboratory soil incubations of (e) N ($N_{\text{min}}$) and (f) C ($C_{\text{min}}$). There were almost no sites outside the fence in the U category, so only under (U) versus between (B) canopy comparisons inside the fence (I) and inside versus outside (O) fence comparisons (between canopies) are depicted. Lines link samples (U and B) within individual trees for I sites and B sites (I and O) across the exclosure fence. KNP, Kruger National Park.
Positive coefficients for CAN and HERB indicate positive effects of herbivores (O > I) and tree canopies (U > B) on a given process, respectively, compared to baseline values (given by intercepts). Coefficients shown in bold differ from zero. The results are for site-specific bulk density soil moisture conversion factors (see text for details).

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Table 2. Posterior distribution means and lower and upper 95% credible intervals (CI) for canopy (CAN) and herbivore exclusion (HERB) effects on three processes driving soil moisture dynamics

<table>
<thead>
<tr>
<th>Process</th>
<th>Factor</th>
<th>Par</th>
<th>Granite CAN effects</th>
<th>Basalt CAN effects*</th>
<th>Basalt HERB effects*</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>CI</td>
<td>CI</td>
<td>CI</td>
</tr>
<tr>
<td>Fast output</td>
<td>Intercept</td>
<td>$\gamma_0$</td>
<td>2.94</td>
<td>2.86</td>
<td>3.01</td>
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<td></td>
<td>CAN</td>
<td>$\gamma_1$</td>
<td>0.42</td>
<td>0.35</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>HERB</td>
<td>$\gamma_2$</td>
<td>-0.48</td>
<td>-0.56</td>
<td>-0.40</td>
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<tr>
<td>Slow output</td>
<td>Intercept</td>
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<td>-0.47</td>
<td>-0.92</td>
<td>-0.16</td>
</tr>
<tr>
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<td>$\beta_1$</td>
<td>0.01</td>
<td>-0.27</td>
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<tr>
<td></td>
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<td>$\gamma_2$</td>
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<td>0.68</td>
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<tr>
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<td>-1.17</td>
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<td>0.19</td>
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<td></td>
<td>HERB</td>
<td>$\gamma_2$</td>
<td>-0.08</td>
<td>-0.16</td>
<td>0.00</td>
</tr>
</tbody>
</table>

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P. Herbivores are generally assumed to enhance plant-available N because the herbivore decomposition pathway short-cuts the plant litter pathway and returns N to the soil in organic form (urine) or as high-quality (i.e. low C:N) detritus (Frank et al. 1994; McNaughton, Banyikwa & McNaughton 1997; Johnson & Matchett 2001). Although herbivore effects on soil nutrients may be substantial when herbivores are aggregated, for example in hotspots (Augustine, McNaughton & Frank 2003; Naiman et al. 2003), it is less clear what their average effects are at landscape scales, and here we found no evidence for an herbivore effect on soil organic matter quality as measured by C:N ratios inside and outside exclosures. The majority of the Kruger landscape does not experience super-abundant herbivore densities, and sites not close to water (such as our experimental exclosure sites) probably provide a more realistic assessment of the mean impact of herbivores. On basalt, we did find some weak evidence of a herbivore effect on labile C, but the effect was opposite to what we had predicted. We expected that higher nutrient turnover in areas with high herbivore population density might lead to larger pools of labile C and N. It is possible that what appears as a herbivore effect is actually a fire effect (consistent with an effect of fire on labile C on basalt, as reported in Holdo, Mack & Arnold (2012)). It has previously been shown that the basalt exclosure is associated with dramatic differences in tree cover on opposite sides of the fence (Asner et al. 2009; Holdo & Mack 2014). There may be a synergistic interaction with fire at work here, however. Loss of canopy cover outside the fence as a result of elephant activity favours grassland expansion, which can lead to hotter fires (with the caveat that the exclosures also exclude grazers, which tend to reduce fuel loads and may counteract the effects of browsers). These fires may accelerate tree cover loss and/or exert a differential impact on soils inside and outside the exclosure. Overall, we may draw an analogy with previous work on canopy-fire interactions in this system, which suggested that fire effects on soil nutrients are mainly indirect and mediated through effects on canopy cover. At our basalt site, where browsing is intense, herbivores may drive similar changes in tree cover and cause canopy effects (which we studied at the scale of individual trees) to scale up at the landscape level.

As a caveat to the lack of an herbivore association with nutrient pools, one of the most striking patterns in our study was the effect of both canopy cover and herbivore biomass on soil bulk density in the top 10 cm. The higher bulk density outside the fence may be associated with soil compaction as a result of trampling by herbivores. Support for this is provided by the contrasting relationship between bulk soil C and bulk density inside and outside the fence (Fig. S3). On granite (where the bulk density patterns were most prominent), we found a strong negative relationship between bulk density and soil C inside the fence, where herbivore biomass is very low, but this relationship disappeared outside the fence (Fig. S3). On granite (where the bulk density patterns were most prominent), we found a strong negative relationship between bulk density and soil C inside the fence, where herbivore biomass is very low, but this relationship disappeared outside the fence (Fig. S3). Despite the lack of strong effects of the granite exclosure on woody vegetation structure, even decades after the exclosure was constructed (Asner et al. 2009), visible differences were apparent in terms of effects on the ground layer across the fence at this site, with clear evidence of trampling and abundant dung piles outside the exclosure. We note that although the canopy effects on bulk density were consistent across the two soil types, the herbivore effects were only detected on granite, where paradoxically, herbivore effects on vegetation are much less evident (Asner et al. 2009). The bulk density effects are of significance because they influence nutrient pools. Even when two sites contain similar nutrient concentrations on a mass basis, the site with higher bulk density has higher
nutrient availability on a per-area basis for a given depth, and therefore a higher nutrient concentration within the rooting zone (although we must note that bulk density may also potentially affect plant nutrient uptake ability, and therefore it is unclear to what extent concentration differences capture availability differences). Previous studies have largely ignored site variation in bulk density (Belsky et al. 1993; Coetsee, February & Bond 2008; Treydte, Grant & Jeltsch 2009), yet we show that it varies as a function of some of the key drivers in this system. Our study, in conjunction with previous work in KNP (Wigley et al. 2013), underscores the fact that bulk density can vary substantially across space, with important implications for our understanding of soil fertility.

SOIL TEMPERATURE AND MOISTURE DYNAMICS

Previous work conducted in Kenyan savannas (Belsky et al. 1989) found positive net effects of tree canopies on soil moisture. We found that the overall net effect of tree canopies on soil moisture was negligible over the course of the season. We found stronger patterns during and immediately following rainfall events. We found opposing effects of tree canopies on inputs on the two soil types: tree cover was associated with higher water inputs in the top 10 cm as a result of precipitation events on granite compared to open areas, but lower input rates on basalt. This suggests that tree canopies enhance water inputs on granite (for example via the process of stem flow, which may concentrate incoming precipitation near the tree trunk), but reduce them on basalt, most likely due to interception. To reinforce this conclusion, we computed the difference between the maximum and mean daily values of GWC for each sensor in our data set. We interpret this as the size of the initial input in soil moisture that occurs as a result of rainfall events. We then calculated the quantity $\Delta GWC$ by subtracting the former quantity for B sites from U sites for any given tree (only for days in which both sites had data). We treat $\Delta GWC$ as an approximate estimate of the magnitude of the ‘canopy’ effect on soil moisture input. We calculated mean $\Delta GWC$ values across all trees and regressed them against rainfall event sizes (including days with no rainfall).

Our results were consistent with those of the state-space model: at the granite site, canopies are positively associated with inputs, and the size of the effect increased as a function of rainfall (Fig. S4 and Table S8). At the basalt site, the effect was weak, but statistically significant: canopies tended to slightly reduce water inputs in a nonlinear fashion (Fig. S4 and Table S8). As rainfall increased, U sites had progressively lower inputs, but the effect disappeared at higher rainfall. The latter results are consistent with interception effects.

It is difficult at this point to fully explain the contrasting patterns at the two sites, given that they differ in multiple ways (not only geology but plant species composition and climate). The basalt site is significantly drier and hotter than the granite site, and our results are consistent with the observation that canopy interception and evaporation are expected to play a more important role on moisture inputs in arid than mesic sites (Rodriguez-Iturbe et al. 1999). The two sites also differ in terms of tree species composition: our granite site was dominated by *T. sericea* and *Sclerocarya birrea*, while the basalt site is dominated by *C. mopane* and *Combretum imberbe* (Table S9). These two communities may differ in terms of leaf area index and architecture in ways that affect interception and stem-flow. We also considered the possibility of browsing differences contributing to the canopy effect, but we consider this unlikely. Our population of sites with U data consisted of trees inside the exclosure on basalt (where they are protected from browsing damage) and trees from both sides of the fence on granite. Browsing damage at the latter site is minimal (Asner et al. 2009), however, and therefore we consider it unlikely that browsing damage on the subsample of trees at this site explain the differences between the two sites. Despite the uncertainty about the exact mechanisms at play, we are fairly confident that the input differences are driven by canopy-related effects on water entering the system, and not by differences in water use, given the rapid time scales (sub-daily) over which they occur.

Our results also suggest that herbivores exert greater overall effects on soil moisture dynamics than on plant-available nutrients, based on the fact that soil moisture effects were detected while labile nutrient effects were absent. The soil moisture model suggested that high herbivore biomass is associated with smaller rates of fast output following precipitation (and therefore a tendency for incoming moisture to remain in the top 10 cm of soil for longer than would be the case without herbivores), which, following the structure of our model, would lead us to suggest that differences in drainage primarily explain the association between herbivores and soil moisture availability. A potential explanation for this pattern is that it is driven by differences in soil bulk density, with denser soils having a lower saturated conductivity, and therefore lower infiltration rates. On granite at least, there is a clear pattern of increasing bulk density from canopy to intercanopy and across the exclosure fence, matching soil moisture patterns. We observe the soil moisture effect of the exclosure even after accounting for inter-site variation in bulk density, however, suggesting that other unknown factors may be at play. Our model found no effects of any of the covariates on slow output (which we mechanistically associate primarily with ET) at either site (Table 2). Given that our estimated coefficients for this process (e.g. $\beta_0$) had very wide credible intervals (Tables S5 and S6), we believe that the model has low power when it comes to estimating ET effects on soil moisture dynamics. It is conceivable therefore that our herbivore effect may not be a drainage effect, but rather an ET effect that arises from differential grazing on transpiring vegetation (or differences in grass community composition) outside the exclosure. We believe that this is unlikely, however, because the herbivore effects are manifested primarily immediately following rainfall events, when drainage is the dominant mechanisms drawing down soil moisture.

Overall, our study suggests that: canopy cover is a dominant biotic driver of soil C, N and P dynamics in these savanna systems; herbivores appear to affect soil moisture availability to a greater extent than they do soil nutrients; and
canopy and herbivore effects on soil nutrient availability tend to be additive, given the lack of significant interaction effects in our analysis. We suggest that herbivores may shift limitation towards nutrients by slowing down soil moisture drainage from the upper soil layer following precipitation events. Finally, we propose that potentially important canopy effects on soil moisture turnover may be revealed by a closer examination of the various mechanisms that control soil moisture dynamics, even when time-averaged effects are small.

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Data accessibility


References


Herbivore and tree effects on savanna: soils

1181
