

Interconnected effects of shrubs, invertebrate-derived macropores and soil texture on water infiltration in a semi-arid savanna rangeland

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Abstract

Many semi-arid savannas are prone to degradation, caused e.g. by overgrazing or extreme climatic events, which often lead to shrub encroachment. Overgrazing by livestock affects vegetation and infiltration processes by directly altering plant composition (selective grazing) or by impacting soil physical properties (trampling). Water infiltration is controlled by several parameters, such as macropores (created by soil-burrowing animals or plant roots) and soil texture, but their effects have mostly been studied in isolation. Here we report on a study, where we conducted infiltration experiments to analyze the interconnected effects of invertebrate-created macropores, shrubs and soil texture (sandy soil and loamy sand) on infiltration in two Namibian rangelands. Using structural equation modeling, we found a direct positive effect of shrub size on infiltration and indirectly via invertebrate macropores on both soil types. On loamy sands this effect was even stronger, but additionally, invertebrate-created macropores became relevant as a direct driver of infiltration. Our results provide new insights into the effects of vegetation and invertebrates on infiltration under different soil textures. Pastoralists should use management strategies that maintain a heterogeneous plant community that supports soil fauna to sustain healthy soil water dynamics, particularly on soils with higher loam content. Understanding the fundamental functioning of soil water dynamics in drylands is critical because these ecosystems are water-limited and support the livelihoods of many cultures worldwide.

Keywords: hydrology – soil function – invertebrate macropores – shrub-encroachment – soil texture – infiltration

Introduction

Drylands are characterized by low and erratic annual precipitation and inherently low vascular plant cover, making them highly vulnerable to disturbance. About 50% of global drylands are currently degraded (Collins *et al.*, 2014; Cook *et al.*, 2015; Fu & Feng, 2014). Degradation is often caused or driven by one or several related factors of anthropogenic origin (Reynolds *et al.*, 2007). These include climatic changes, which will likely exacerbate degradation and lead to an expansion of global drylands by 23% by the end of this century (Huang *et al.*, 2015) (but see Schlaepfer *et al.*, 2017). The risk of further degradation is predicted to be greatest in semi-arid drylands where both human population pressure and sensitivity to degradation are of intermediate values (Safriel *et al.*, 2006). In these sensitive semi-arid drylands such as savannas and grasslands, degradation can lead to shrub encroachment (D'Odorico *et al.*, 2011) and eventually to desertification through a loss of perennial grass cover (Middleton & Thomas, 1992). Shrub encroachment can be defined as the increase in density, cover and biomass of indigenous shrubs (Eldridge *et al.*, 2011). There is strong evidence that shrub encroachment leads to changes in biodiversity of multiple taxonomic groups, including birds (Sirami *et al.*, 2009), mammals (Blaum *et al.*, 2007) and arthropods (Blaum *et al.*, 2009; Hering *et al.*, 2018), which may further feedback to the degradation process.

Anthropogenic land-use practices that lead to the dramatic transition of grass-dominated savanna to a shrub-encroached state include overgrazing (Skarpe, 1991), natural fire suppression (Van Langevelde *et al.*, 2003) and exclusion of browsers (Cumming, 1982; Roques *et al.*, 2001; Weltzin *et al.*, 1997). Overgrazing by livestock can lead to serious changes in vegetation cover and soil water dynamics (Fynn & O'Connor, 2000; Hudak, 1999; Skarpe, 1990). Trampling by cattle compacts the top soil, which leads to a decrease in hydrological functioning and increased run-off and erosion (Warren *et al.*, 1986; Yong-Zhong *et al.*, 2005). In addition, the selective grazing of perennial grasses may lead to a decline in soil porosity by a decrease in root channels and macropore-creating invertebrates. However, shrubs and in particular larger shrubs can prevent the movement of livestock by providing a physical barrier. This exclusion of livestock trampling may lead to lower bulk density and higher water infiltration under larger shrub canopies compared to smaller canopies and the interspaces between shrubs, thereby favoring large

shrubs in terms of water competition and leading to a higher overall heterogeneity of soils hydrological function. There is evidence that the effects of livestock and shrub encroachment counteract in terms of infiltration capacity of soils (Marquart *et al.*, 2019). Understanding how livestock affects soil water dynamics depending on shrub size distribution may help to prevent further degradation (Eldridge *et al.*, 2013). This understanding is of great importance for dryland ecosystems, as they support about 50% of the global livestock pool and even if already shrub-encroached, livestock farming often is the only possible agricultural utilization (Millennium Ecosystem Assessment, 2005).

Recent studies showed that infiltration rates are spatially heterogeneous on the landscape scale with a strong decrease from conserved grasslands with few scattered shrubs to degraded shrub-encroached rangelands (Chartier *et al.*, 2011; Parizek *et al.*, 2002). However, on a finer scale, infiltration rates were equal or only marginally higher in plant interspaces on grasslands, compared to shrub steppes, and equal or higher under shrub canopies compared to grass canopies (Bhark & Small, 2003; Eldridge *et al.*, 2015). Thus, the small distance between individual grass tussocks leads to a greater connectivity of infiltration in grasslands than degraded shrublands with a large fraction of bare soil (Bhark & Small, 2003; Eldridge *et al.*, 2015). Furthermore, shrub canopies intercept rainfall which is lost to evaporation, and redistribute a considerable fraction (~10% depending on species) to the shrub's base by stemflow, which directly infiltrates through root-channels (Abrahams *et al.*, 2003; Martinez-Meza & Whitford, 1996; Vetaas, 1992). Even though infiltration rate under shrub canopies is higher compared to open soil, this high infiltration into macropores can lead to rapid water saturation followed by earlier runoff under shrubs, compared to unvegetated plots (Neave & Abrahams, 2002). However, there is no binary distinction between sub-canopy and open soil regarding infiltration, but rather a gradually decline with distance from the stem, where the canopy approximately covers the central one-third of the shrubs' zone of influence (Dunkerley, 2000).

The higher infiltration rate under vegetation is mainly caused by a larger number of macropores, i.e. soil pores with a diameter $>70\mu\text{m}$ that favor preferential flow of water to unsaturated sub-surface soil layers and counteract runoff (Eldridge & Freudenberger, 2005). For example, in Namibian Kalahari rangelands under shrub canopies we recorded about three times as many macropores, created by soil burrowing

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animals, compared to degraded patches with open soil (Marquart *et al.*, in revision). Macropores in drylands are often of biogenic origin, created by dead plant roots or soil disturbing fauna. There is a number of publications on the effect of invertebrate derived macropores on infiltration processes for different insect groups, e.g. Formicidae (Cerdà *et al.*, 2009; Eldridge, 1993) and Isoptera (Bargués Tobella *et al.*, 2014; Mando *et al.*, 1996; Sarr *et al.*, 2001), in several dryland systems. However, most studies were performed by analyzing the effect of a single macropore building species on infiltration and only within a single ecosystem, making it difficult to transfer the results to a broader scale (but see Colloff *et al.*, 2010). Furthermore, soil texture has a great influence on the soil's water retention capacity and thereby infiltration rate (Ma *et al.*, 2016). Thus, the impact of macropores on soil water dynamics might vary greatly among ecosystems with different soil types. In addition, most studies excluded other related factors, known to influence infiltration. These factors include plant litter, which has been shown to be positively correlated to infiltration (Blackburn, 1975; Meeuwig, 1970), soil crusts (communities of non-vascular plants dominated by lichens, mosses and liverworts), whose effect depend on their complexity (Faist *et al.*, 2017), and climatic conditions (Belnap, 2006).

Understanding the interconnected effects of soil surface parameters, soil fauna, vegetation and hydrology is crucial to make target-orientated recommendations regarding shrub control. In recent years many pastoralists from countries in southern Africa started to apply a wide range of management practices to counteract shrub-encroachment, e.g. prescribed fires, chemical or manual bush control, brush packing and reseedling of perennial grasses. It is still not clear which of these practices are successful under which farming system and environmental conditions (Harmse *et al.*, 2016; Throop & Archer, 2007; van den Berg & Kellner, 2005).

Here, we examined the interacting effects of invertebrate-derived macropores and shrub size on infiltration at two Namibian semi-arid livestock rangelands differing inter alia in soil texture. Namibian savannas are hot spots of climate, land-use and socio-economic change that function as model-region for many savannas worldwide. Many semi-arid rangeland systems, including a large fraction of Namibian savannas, are prone to a decrease of total annual precipitation and an increase in extreme rain events. These climatic changes might have severe consequences, as transition from grassy savannas to dense

shrublands and a loss in net primary productivity of rangelands and forage quality, which is likely to lead to increased competition for natural resources by land users (Namibia Ministry of Environment and Tourism, 2011).

In this study we determined two hydrological parameters: Sorptivity and steady state infiltration. Sorptivity is a measure of the capacity of the soil to absorb or desorb water by capillarity, which can be determined at the early stage of the infiltration process, when the soil is not saturated and the movement of water into the soil from the surface is to a large extent controlled by the matric potential of the soil. Once the soil becomes saturated, nearly all soil pores are filled with water and the matrix potential approaches a value of zero. The movement of water in the soil becomes mainly controlled by the gravitational force, as water drains through larger pores. At this stage, the infiltration rate reaches a steady-state and is approximating the saturated hydraulic conductivity of the soil.

We determined both infiltration parameters under two different conditions: First when water was conducted by all soil pores (infiltration under ponded conditions) and second when infiltration was restricted to only matrix-pores (infiltration with a negative tension). Comparing these two conditions, we could draw conclusions regarding the effect of macroporosity on infiltration processes. We then linked the measured infiltration to shrub presence and size and the area of invertebrate created macropores, among other parameters, as litter and biocrust cover. The presence of shrubs in a given savanna with similar edaphic and climatic conditions thereby gives us selective insights on the effect of shrub encroachment per se, while shrub size as a proxy for age relates to the process of encroachment. We tested the following hypothesis: Total infiltration (under ponding) is enhanced by shrub presence (1) and increases with shrub size (2), as shrubs positively affect macroporosity (3) (via dead roots and improved habitat for soil-borrowing invertebrates) and might act as a physical barrier, preventing the movement of cattle, thereby sparing the sub-canopy soil from trampling. With an increase of macropores created by invertebrates, infiltration also increases (4) and the strength of this effect varies among the two ecosystems differing in soil texture (5). In drylands, water is the main limiting factor for plant establishment (Hadley & Szarek, 1981; Rodriguez-Iturbe *et al.*, 1999) and a transition from healthy soil-

water dynamics to physically degraded or sealed soils will lead to severe impacts on vegetation and thereby reducing stocking capacity and maximum yield (Schlesinger *et al.*, 1990).

Methods

Study sites description

The study was undertaken at eight sites within two locations where the savanna plant communities represent a large extent of Namibian semi-arid rangelands. The two locations mainly differ in annual rainfall, vegetation cover and soil texture (Fig. 1A). The soil type at both locations is classified as Ferralic Arenosols.

The first location was the commercial livestock farm Ebenhazer in the western Kalahari, Omaheke region (23°13'14.6"S 18°26'49.5"E). The landscape is defined by parallel running dunes with scattered calcareous pans and soil texture is classified as sand (Appendix A). Soil has a low organic matter content of 0.89±0.33% (mean and standard deviation of 10 topsoil samples). Mean annual precipitation in this area is 267 mm, but precipitation is highly variable (Annual precipitation coefficient of variation = 95 mm). Mean annual temperature is 19.6° C with daily averages ranging from 2.4° C in winter to 32.9° C in summer (Fick & Hijmans, 2017). Livestock comprised mostly cattle and sheep with 0.04 – 0.08 livestock units / ha.

The vegetation is described as *Vachellia luederitzii* - *Vachellia erioloba* tree savanna (Rooyen & Rooyen, 1998). The most common woody species are *Vachellia erioloba*, *Senegalia mellifera* and *Vachellia hebeclada*. The grass layer mainly consists of the perennial species *Stipagrostis uniplumis*, *Aristida stipitata*, *A. meridionalis*, and the annual species *Schmidtia kalahariensis*, *Eragrostis cylindriflora*, *E. biflora* and *Pogonarthria fleckii*. Vegetation ranges from grass-dominated areas with scattered shrubs to shrub-encroached states near historical and recent water holes (Fig. 1B). Shrub cover in the study areas was between 15-22 % (personal observation and satellite data).

The second location was the governmental cattle breeding farm Okomumbonde (20°26'48.5"S 17°20'41.0"E) on the foothills of the Greater Waterberg Landscape Conservation Area. This farm is

heavily bush-encroached with barely any less degraded sites, that were not artificially debushed (Fig. 1C). The most common woody plants are *Grewia flava*, *S. mellifera*, and *V. luederitzii*. Shrub cover in the study areas was approximately 50% (personal observation and satellite data). Soil texture is classified as loamy sand (Appendix A). The organic matter content of the soil is $1.26 \pm 0.67\%$ (mean and standard deviation of 10 topsoil samples without biocrust). Mean annual temperature in this region is 20°C with a mean temporal annual range of 26.7°C . Average annual precipitation is 365 mm with also a high seasonality of precipitation (95 mm) (Fick & Hijmans, 2017). Land use is dominated by cattle raising for breeding purposes but also goat and sheep farming in some areas of the farm.

At both locations, all measurements were conducted on sites encroached by *S. mellifera*. The field work was carried out throughout April 2017 at the end of the rainy season to ensure activity of soil-disturbing invertebrates and environmental conditions where water infiltration would naturally occur. Soil conditions, as tested in our experiments would naturally occur approximately between January and beginning of May.

Study design and infiltration measurements

At both locations, four 50m x 50m study sites were randomly chosen within areas encroached by *S. mellifera* shrubs and low perennial grass cover in the interspaces. Study sites were located at least 1 km apart and spanned across several paddocks (Fig. 1B&C). Within each study site we selected 10 paired plots (2 locations x 4 sites x 2 pairs x 10 replicates: $n = 160$) (Fig. 1D). Each pair consisted of one plot placed under the canopy of a *S. mellifera* shrub midway between the stem and edge of the canopy, and a matched plot on the nearest interspace at least 2 m from any shrub canopy (Fig. 1E). The minimum distance among the 10 paired plots at each site was 10 m. The 10 paired plots within each site were chosen to emulate a gradient in shrub size, by recording height and two canopy diameters along perpendicular axes on the horizontal plane, for each shrub (see Appendix). This approach was chosen to test for both the effect of shrubs' presence and size on the hydrological parameters: sorptivity and steady-state infiltration, each under ponding (with constant head of water of +10mm) and under tension (with a set suction equivalent to a 40mm water column (hereafter -40mm)). The measurements were conducted

with two disk permeameters used simultaneously and placed in close proximity (i.e. a distance of 50 cm to provide independent measurements). The first (tension) permeameter ($\varnothing=20\text{cm}$) was placed on a thin bed of sieved sand to provide uniform contact with the surface soil, while the second (ponded) permeameter was placed on a steel ring ($\varnothing=23\text{cm}$) to support a constant pond of water. The pressure of the tension permeameter was adjusted to -40mm with a Mariotte's tube, to exclude pores with a diameter greater than $70\text{ }\mu\text{m}$, only measuring water flow through micropores of the soil matrix. The ponded infiltrometer, on the other hand, allowed us to measure infiltration rates through pores of all sizes (Perroux & White, 1988). These include biogenic macropores ($\varnothing>0.7\text{mm}$) created e.g. by plant roots or soil burrowing animals, as ants and termites. Measurements were run until the infiltration rate reached steady state, but for at least 12 minutes. We measured sorptivity for the first five minutes of the infiltration process and steady-state infiltration once the infiltration rate became constant, for both pressures.

We also calculated a macroporosity index, as the ratio of sorptivity under ponding and tension ($\text{MI} = \text{sorptivity}_{+10\text{ mm}} / \text{sorptivity}_{-40\text{ mm}}$). This index reveals the extent to which macropores contribute to total water flow (White, 1988). It is indicative of conductive, functional soils with high levels of biological activity (Perroux & White, 1988).

Additional measures of factors influencing infiltration

In addition to the infiltration measurements, we measured three soil attributes: (1) the percentage of the soil surface area within the ponded reading that was covered by detached plant material (litter), (2) the percentage of the soil surface area that was covered by biocrusts, and (3) the number and size of pores produced by invertebrates on the soil surface (macropores). To measure macropores, we carefully removed the litter and topsoil with a spatula after conducting the hydrological measurements and counted the number of pores and measured their maximum diameter using vernier calipers. Biocrusts only occurred on the loamy sand soil at location Okomumbonde.

Statistical analysis

In a first step, we used full factorial linear mixed models to analyze the interacting effects of location (Ebenhazer vs. Okomumbonde Farm), shrub presence (canopy vs. open soil) and area of surface macropores on the hydrological values: sorptivity and steady-state infiltration under both tension and ponding. The four sites per location were included as a random effect with the 10 shrub-open pairs nested within the factor site. Prior to analysis, all hydrological values were \log_{10} -transformed and macropore area was square-rooted to meet the requirements for linear models by stabilizing the residuals. Model selection based on F-tests comparing the nested models resulted in the minimal adequate models. As the variability of ponded infiltration measurements was much higher on loamy sand than sandy soil, we analyzed the interaction effect of shrub presence and macropore area in separate models for both locations. Analysis was conducted in R Version 3.5.1 (R Core Team, 2018). Our models were fitted using REML and p-values were derived using Kenward-Roger approximations for degrees of freedom. The requirements (homoscedasticity, normality, etc.) for general linear mixed models were visually tested. The significance level of all test statistics was $p=0.05$.

In a second step, we applied structural equation modeling (SEM) to analyze the effect strength of connections between the infiltration variables (steady-state infiltration and sorptivity under ponding and tension and the macroporosity ratio), shrub size, macropore area, litter and biocrust cover. SEMs use variance and co-variance matrices to iteratively estimate unknown parameters of the model as variances of endogenous parameters, path coefficients and total effects (the sum of all direct and indirect effects of one variable on another). Thus, using SEMs allowed us to simultaneously analyze how the relationships between multiple connected variables exert on soil water infiltration processes. Another advantage of SEMs is the use of latent variables – unobserved variables, which are defined by their effects on observed variables. In our models, we included three latent variables: total and matrix infiltration defined by sorptivity and steady-state infiltration under ponding and tension, respectively, and a shrub size variable which is defined by the three measured shrub size variables: shrub height, and the two canopy diameters. In SEMs, the understanding of the tested system determines a priori the respective causal relationships of the model. We assumed that the hydrological measures would be directly affected by shrub size, area of invertebrate created macropores, litter and biocrust cover. Furthermore, shrub size would have indirect effects on the hydrological measures by affecting litter, biocrust cover and macropore area.

For a better comparison of effect strengths and to improve normality of the data, values were z-transformed (standardized) prior to analysis. Robust standard errors and a Satorra-Bentler scaled test statistic was used for analysis, as shrub size variables were by default not normally distributed. All SEM analysis were performed using the lavaan package (version 0.5-22) in R (version 3.5.1) (R Core Team, 2018; Rosseel, 2012).

Results

All averaged hydrological values were lower on loamy sand at the Okomumbonde rangelands than on sandy soils from the Ebenhazer farm (Fig.2). This difference, however, was only marginal for total infiltration under ponded conditions (micro- and macropores) below shrub canopies (Fig.2B & D).

The presence of shrubs remarkably increased sorptivity (early) and steady-state (late) infiltration under ponded conditions. This effect was more pronounced on loamy sand (mean steady-state infiltration: under canopy: 107.9mm h^{-1} , open soil: 30.5mm h^{-1} ; Sorptivity: under canopy: $246.3\text{mm h}^{-0.5}$, open soil: $92.3\text{mm h}^{-0.5}$), compared to measurements on sandy soil sites (mean steady-state infiltration: under canopy: 114.5mm h^{-1} , open soil: 75.9mm h^{-1} ; Sorptivity: under canopy: $261.1\text{mm h}^{-0.5}$, open soil: $187.6\text{mm h}^{-0.5}$; location–shrub interaction for sorptivity: $F_{1, 78.4}=17$, $P<0.001$; Steady-state infiltration: $F_{1, 78.4}=18.7$, $P<0.001$).

The effect of microsite (shrub vs open) on infiltration under tension (only micropores) was opposite between the two locations. On sandy soil, sorptivity and state-state infiltration were lower under shrub canopies than open soil (mean steady-state infiltration: under canopy: 8.4mm h^{-1} , open soil: 9.9mm h^{-1} ; Sorptivity: under canopy: $12.8\text{mm h}^{-0.5}$, open soil: $16.5\text{mm h}^{-0.5}$). For the loamy sand soils only steady-state infiltration, but not sorptivity was slightly increased below shrubs (under canopy: 2.5mm h^{-1} , open soil: 1.7mm h^{-1}), but was still over all low (Fig. 2A & C) (location–shrub interaction for sorptivity: $F_{1, 77}=7.3$, $P<0.01$; Steady-state infiltration: $F_{1, 77}=14.7$, $P<0.001$).

Furthermore, we found that a higher area of invertebrate-built surface macropores increased infiltration under ponded conditions (Fig. 3). Contrary to the shrub effect, this effect was stronger on loamy sand soil for both early stage (location–macropore area interaction: $F_{1, 150.4}=8.4$, $P<0.01$) and late stage infiltration ($F_{1, 151}=10.2$, $P<0.01$), compared to the sandy soil (Fig. 3). On sandy soil sites, early stage infiltration was only increased by the macropore area under shrub canopies (shrub–macropore area interaction: $F_{1, 55.9}=4.4$, $P<0.05$) but not on open soil (Fig. 3A). Late stage infiltration was equally increased by macropores on both microsites, however to a lesser extent (Fig. 3C) (macropore area: $F_{1, 69}=6.0$, $P<0.05$).

Our structural equation models revealed that infiltration in our two survey areas was not only controlled by shrub occurrence but also macropore area and biocrust cover. On the sandy soil, shrub size was the main driver, positively affecting total infiltration, while decreasing matrix infiltration (Fig. 4A). The higher standardized total effect (STE=0.53) of shrub size on total infiltration (Table 1) was mainly mediated by a significant positive effect upon macropore area (Fig. 4A). Our SEM did not find a positive direct effect of macropore area on the ponded infiltration measures, however the model predicted this pathway only barely non-significant ($P=0.055$). On loamy sand soils, shrub size was still the most important driver of total infiltration but had no effect on matrix infiltration (Fig. 4B). The effect of macropore area was much stronger compared to sandy soil measurements, but still resulting in only 37% of the STE of shrub size. Biocrusts, which were absent on the sandy soil sites, were the only factor controlling matrix infiltration with a negative STE of -0.38.

In both systems the macroporosity index was positively controlled by shrub size (STE: Ebenhazer (sandy soil) = 0.57; Okomumbonde (loamy sand soil) = 0.48).

Discussion

This study compared the related effects of shrubs and invertebrate-derived macropores on hydrological measures in two Namibian semi-arid savannas, differing amongst others in soil texture. We found clear evidence that presence and size of shrubs play a vital role in the hydrology of these ecosystems. On sandy

soils, shrubs play an important role in soil water dynamics. On loamy sand soils this effect is even more enhanced, while the importance of invertebrate created channels for the infiltration process becomes increasingly relevant. This is particularly important in the light of shrub encroachment through degradation and climate change since high shrub densities can increase infiltration compared to degraded non-encroached grasslands (Neave & Abrahams, 2002). In these water-limited ecosystems, shrubs might thereby buffer the soil degradation process. Management options counteracting shrub-encroachment should be chosen, among other factors, regarding soil texture and its infiltration capacity. Furthermore, conserving a high diversity and abundance of soil fauna should be accounted for to maintain sustainable soil-water dynamics in these semi-arid rangeland ecosystems, especially with loamy sand soils.

We observed increased infiltration under shrub canopies, compared to open soil, which is in accordance with a large number of studies from global semi-arid ecosystems (Bhark & Small, 2003; Eldridge *et al.*, 2015; Lyford & Qashu, 1969; Vandandorj *et al.*, 2017). As this increase was only to be found under ponded conditions when all soil pores, independent of size, were capable of conducting water, we trace this effect rather to higher macroporosity under shrubs, than to other factors, such as changed bulk density or soil texture. This result is further supported by our calculated macroporosity ratio, being positively affected by shrub size. Biologically generated voids mainly created by soil burrowing arthropods or dead plant roots are to a large extent found beneath vegetation structures, as perennial grasses or shrubs (Colloff *et al.*, 2010). Total early and late stage infiltration under shrub canopies was about similar at both locations, while infiltration rates were less than half in interspaces on loamy sand, compared to sandy soil. However, shrubs do not only affect the infiltration capacity of sub-canopy soils, but also beyond the diameter of their canopy (Dunkerley, 2000). Our study could not find any comparable effect, as we did not observe any correlation between infiltration in interspaces and size of the paired shrubs. Nevertheless, it is obvious that a high density of large shrubs leads to an increased area with a high infiltration capacity on the catchment scale.

Our results indicate that presence of larger shrubs plays a relatively more important role regarding soil water dynamics, when soil becomes more fine-textured. Shrubs might function as important vegetation structures which can intercept excess overland flow. This function is particularly relevant in southern

African drylands where low annual precipitation occurs as a few heavy rain events, which are predicted to become less frequent and smaller in their total amount (Kirtman *et al.*, 2013; Tadross *et al.*, 2005). However, it should be noted that in areas with hillslopes, microtopography under shrub canopies may prevent that overland flow reaches the shrubs (Parsons *et al.*, 1992). Moreover, Neave and Abrahams (2002) found that runoff occurred earlier under shrub canopies on loamy sand, compared to sandy loam interspaces at high rainfall intensities. However, this strong increase in runoff under shrub canopies only lasted for a short period until reaching equilibrium with the likewise high infiltration rate, compared to interspaces. Therefore, these results do not contradict the idea that shrubs function as precipitation and runoff sinks, especially if one considers that the effect of shrubs extends beyond the area of the canopy (Dunkerley, 2000).

In degraded savannas large shrubs are needed to maintain adequate soil-water dynamics with reduced runoff, associated gully-erosion, and ground water recharge rates—the latter relying on the infiltration of rare but heavy rain events. The positive effect of shrubs, however, also to some extent depends on the prevalent soil texture.

Our results show a positive effect of shrub size on the area of visible surface macropores on the sandy location and a tendency ($P=0.08$) on the loamy sand location. This is in accordance with a previous study at this location, analyzing a high number of larger plots, where we found a three-fold higher number of surface-macropores under shrub canopies, compared to open soil or grasses (Marquart *et al.*, in revision). In savannas with sparse vegetation, vegetated patches are fertility islands in the otherwise nutrient poor environment, caused by a higher amount of dead plant matter and animal excretions, thereby enhanced decomposition and nutrient pools (Schlesinger *et al.*, 1990). Soil burrowing invertebrates, as termites and ant species profit from the favorable environmental conditions and increased food availability, i.e. a high amount of litter and seeds. With an increase in subterranean arthropod numbers, a higher number of tunnels are constructed, which in turn feedback on soil properties that might lead to greater infiltration rates (Léonard & Rajot, 2001; Mando *et al.*, 1996). Unfortunately, it was not possible to identify the origin of the measured macropores to species or genus levels, but a large fraction was clearly derived by Formicidae and Isoptera, which are known to enhance infiltration (e.g. Eldridge, 1993; Mando *et al.*, 1996). Our study found invertebrate macropores to be a strong driver of infiltration on loamy sand sites,

as well in the single effect linear models, as in our structural equation models. The macropore effect on sandy soils, however seemed to be less pronounced, but more strongly connected to shrub size. Previous studies investigating the impact of macropores on infiltration in sandy soil systems found no, or even negative effects (Mettrop *et al.*, 2013; Wang *et al.*, 1996). Interestingly, our results suggest that due to differences in soil properties under shrub canopies (e.g. Pugnaire *et al.*, 1996), macropores play a minor but significant role in the initial infiltration process, when the soil is not yet saturated. This effect of invertebrates macropores might have implications for heavy rain events after a prolonged period of drought by increasing water catchment in shrubs' zone of influence. Apart from increasing infiltration, soil burrowing invertebrates have been found to improve ecosystem functioning, e.g. by increasing soil turnover, decomposition and nutrient concentrations in the soil (Jouquet *et al.*, 2006). It is therefore of great importance to maintain a preferably heterogeneous environment with scattered shrubs and grass patches to create a suitable habitat for these organisms, as abundance and diversity of most arthropod groups peak at intermediate shrub cover (Blaum *et al.*, 2009; Hering *et al.* 2018).

Surprisingly, matrix infiltration decreased with increasing shrub size on sandy soil. This might seem counter-intuitive at first, as we expected that livestock would predominately increase compaction of interspace soil by trampling (Mead & Chan, 1992), because shrubs would act as a physical barrier thereby preventing the movement of cattle onto the sub-canopy soil (Travers *et al.*, 2018). But quite the opposite might have been the case, given that large shrubs provide protection from intense solar radiation and cattle actively move to shaded patches to avoid heat stress (Tucker *et al.*, 2008). Another explanation may be a higher fraction of fine soil particles, emerging from dust being trapped under larger shrub canopies (Pugnaire *et al.*, 1996).

Even if the negative effects of shrubs, namely water-loss by canopy interception, are considered, our study still clearly shows that large shrubs play a crucial role in healthy soil water dynamics, especially in degraded drylands. This result should be considered in common management practices in degraded semi-arid rangelands with sparse perennial grass cover, where area-wide shrub clearing is applied to increase pastoral production. The redistribution of rainfall on shrub canopies into through-fall and stemflow reduce the kinetic energy of raindrops and lead to less soil sealing, compared to open soil

(Wainwright *et al.*, 1999). Removing large quantities of shrubs from savannas with sparse grass cover might therefore result in increased runoff. Land-users should be advised to retain primary large shrubs in the system and maintain a preferably heterogeneous plant community. On a landscape level, soil water dynamics are in general improved in savannas with a high perennial grass cover (e.g. Chartier *et al.*, 2011; Parizek *et al.*, 2002), thus an appropriately reasonable shrub density should be considered in relation to the degradation status.

Larger shrubs positively affect the amount of plant litter and the number of surface-macropores. Therefore, we would expect these vegetation structures to be a main factor enhancing soil burrowing invertebrate community. This would have a positive effect on macroporosity not only limited to soil directly affected by shrubs, but also on a broad scale. The importance of biogenically created macropores increases, when the soil becomes finer textured and thereby less permeable to water. A high abundance and diversity of soil borrowing invertebrates might therefore represent a possibility in compensating decreasing infiltration capacity due to soil sealing through degradation processes, at least in some ecosystems. Arthropod fauna is of course connected with vegetation and thereby also affected by shrub encroachment, but management measures, as incorporating dead plant matter in degraded areas or reseeding perennial grasses, could positively affect arthropod community and thus improve soil water infiltration and nutrient uptake.

Targeted measures to combat degradation do not only have positive consequences for flora and fauna, but also for about 38% of global human population sustained by these ecosystems. A solid knowledge of all processes leading to dryland degradation is therefore of vital importance to sustain ecosystem functioning and ensure the livelihoods for millions of people.

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Conflict of Interest Statement

The authors declare that they have no conflict of interests.

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Table 1:

Standardized total effects of the different variables on the five hydrological measures. A minus sign represents non-significant total effects. Values in parenthesis indicate a tendency ($0.1 > P > 0.05$).

Attribute	Ebenhazer (sandy soil)			Okomumbonde (loamy sand)		
	Matrix infiltration	Total infiltration	Macropore ratio	Matrix infiltration	Total infiltration	Macropore ratio
Shrub size	-0.36	0.53	0.57	-	0.72	0.48
Macropore area	-	(0.19)	(0.17)	-	0.27	(0.16)
Litter cover	-	-	-	-	-	-
Biocrust cover	na	na	na	-0.38	-	-

Figure captions

Figure 1:

(A) Map of Namibia with annual rainfall (shades of grey indicate isoclines at 50-mm intervals). The two study locations are indicated by squares. (B&C) Sentinel-2 image of the two study locations: (B): Okomumbonde with loamy sand and (C): Ebenhazer with sandy soil (August 2019, only Band 8: Near Infrared Reflectance: darker color indicates higher vegetation density; derived with QGIS 2.18.26). The squares indicate the eight 50 m x 50 m study sites (not to scale). (D) Schematic representation of one study site with 10 different sized shrubs indicated by circles. At each shrub the paired plots are shown as two squares. (E) Schematic representation of one paired plot. The shrub canopy is indicated by the large circle; The small paired circles with two shades of gray represent the locations of the tension and ponded permeameter measurements, which were either sited in the middle between the stem and canopy edge, or in 2 m distance from any canopy edge.

Figure 2:

Back-transformed means (\pm SE, $n=40$) for sorptivity ($\text{mm h}^{-0.5}$) and steady-state infiltration (mm h^{-1}) under -40mm tension (A&B) and under $+10\text{mm}$ of ponding (C&D) for the two rangelands (differing inter alia in soil texture) and microsites (i.e. under shrub canopies and on open soil).

Figure 3:

The effect of invertebrate created macropores (square-root transformed area) on sorptivity and steady-state infiltration (\log_{10} transformed) under $+10\text{mm}$ of ponding on sandy soil (A&C) and loamy sand (B&D). Different microsites are represented by triangles (under shrub canopies) and circles (open soil).

Figure 4:

Structural equation models depicting the effects of macropore area, litter cover, biocrust and shrub size on total infiltration and matrix infiltration on sandy soil (A) and loamy sand (B). Measured variables are indicated by box shaped borders and latent variables are bordered by circles. The value and sign of the standardized path coefficients indicate the strength of the effects between variables. Negative

relationships are shown as red and broken arrows and positive are black and solid arrows. Non-significant pathways are shown as thin arrows without a corresponding path coefficient.

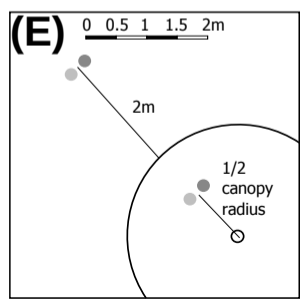
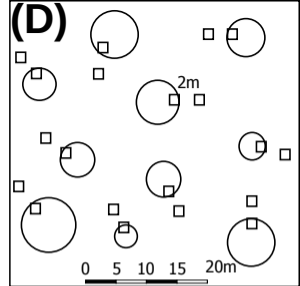
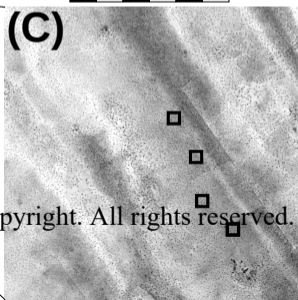
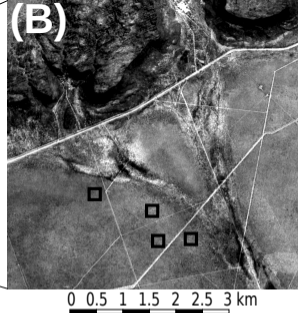
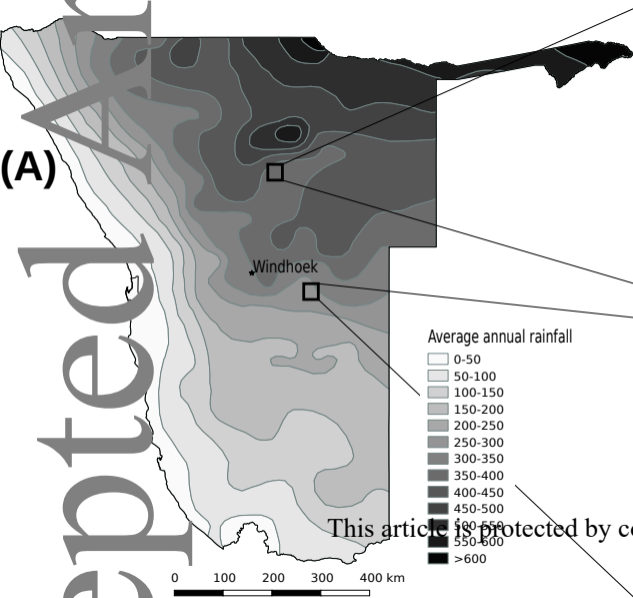
Appendix A:

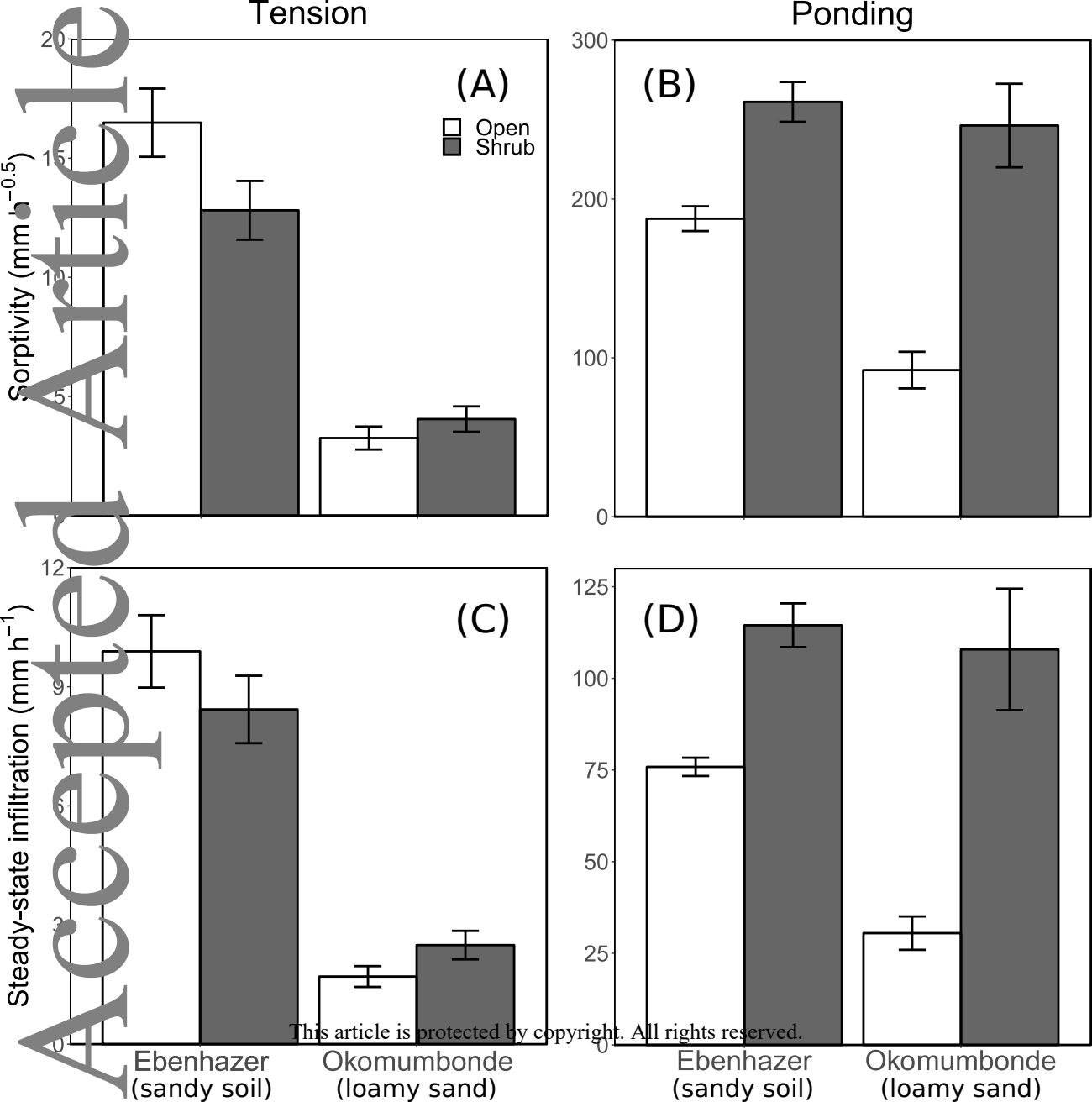
Average grain size fractions (\pm SD) from sieving analysis of six 100g soil samples randomly obtained from 10cm depth from our study sites at both locations.

Appendix

Mean shrub height and diameter in cm with standard deviation of the mean, and minimum and maximum measures for the eight study sites.

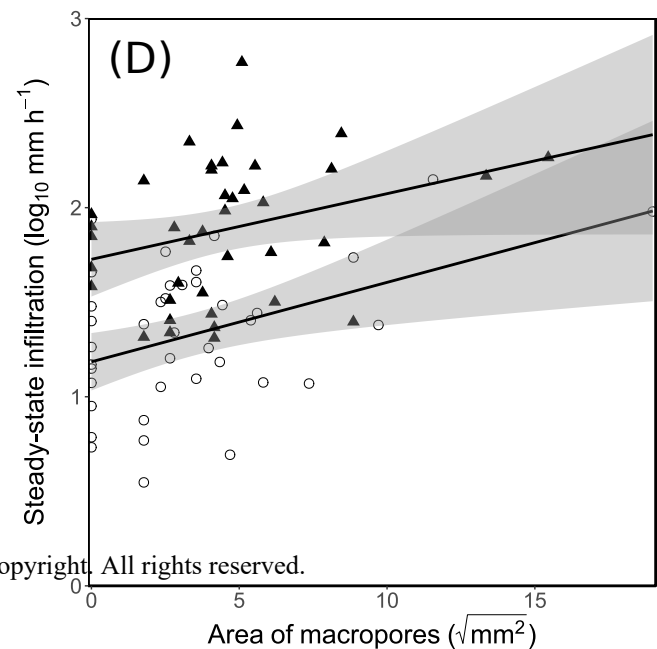
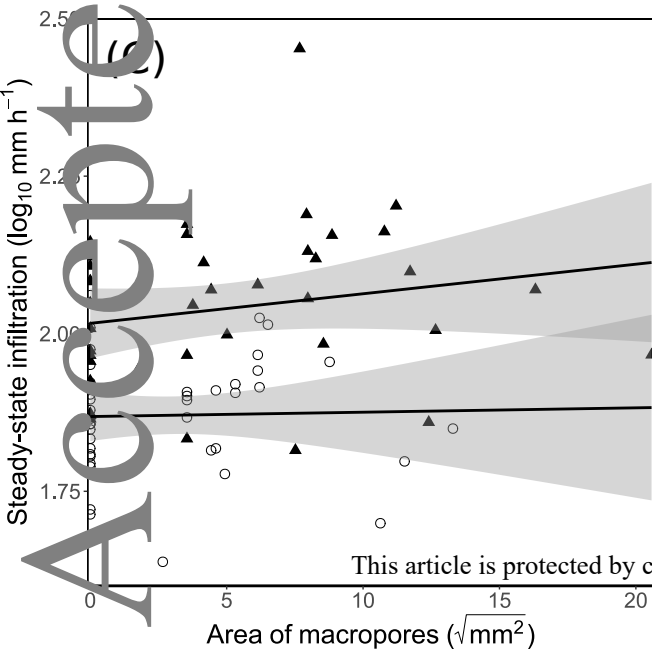
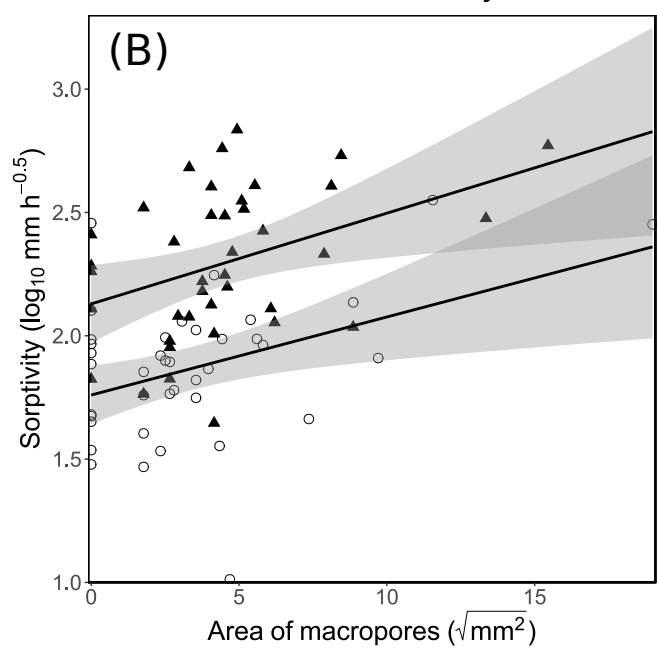
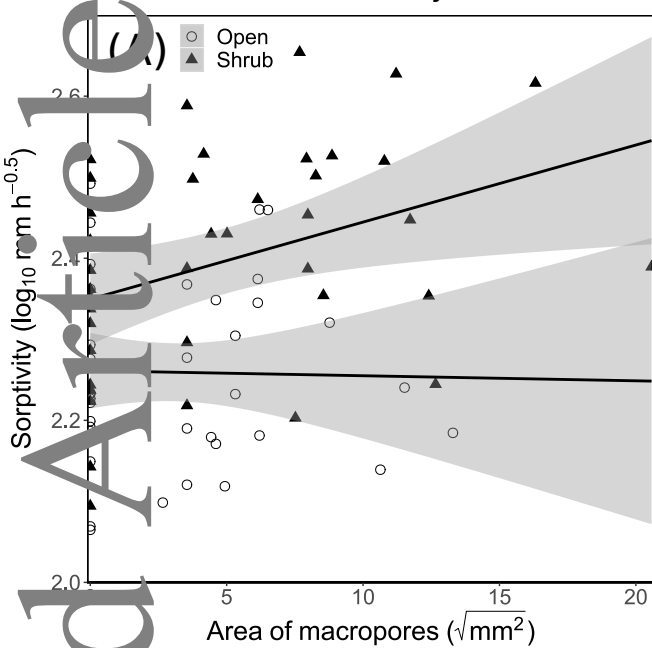
Site	Ebenhazer (sandy soil)								Okomumbonde (loamy sand)							
	Height				Diameter				Height				Diameter			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
1	140	103.1	35	400	256	207.2	75	800	154.8	89.3	23	350	151	105.5	27.5	400
2	188.5	126	50	400	316	242.9	102.5	785	224.5	188.3	25	600	238.1	191.9	26	600
3	142	138.8	50	470	263.6	279.6	90	975	189.9	142.2	16	500	167.8	117.2	20.5	395
4	118	112.8	30	350	190.9	173.5	65	555	174.4	93	50	300	195.8	128.3	45	385





Ebenhazer (sandy soil)

Okomumbonde (loamy sand)



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