The abundance of trees in the savannas and grasslands of South Africa is often highly variable within a landscape. Tree density is increasing in many savanna landscapes and trees are encroaching into many grassland landscapes (Devine et al. 2017), yet, within these treed landscapes, patches of land can often be found where trees are largely absent, with grasses and/or shrubs predominating. The causal mechanisms enabling these treeless patches to prevail over decades, despite trees increasing in density around them, are not known. We hypothesised that differences in soil properties between treed and treeless areas would provide insights into the possible causal mechanisms at play. There are myriad ways in which soil properties influence plant growth and could therefore influence the competitive outcome between different plant growth forms. We suggest, however, that three main mechanisms are likely to be particularly important, with the strength of each mechanism varying from non-existent to strong depending on the soil nutrient availability at a particular site. Firstly, deficiencies in nutrients, such as calcium (Ca) and boron (B), are likely to have a greater negative impact on eudicot species, such as savanna trees, than on monocotyledonous herbaceous plants. This is because eudicots in general require considerably more Ca and B per unit biomass than monocots (Bell 1997; White and Broadley 2003; Tariq and Mott 2007; Wimmer et al. 2015). Secondly, grasses can exert considerable constraint on tree seedlings in savannas (Van Aukon and Bush 1988; Riggins 2009; Porensky and Veblen 2012; Morrison et al. 2019; Tomlinson et al. 2019) and are particularly competitive in nutrient-rich environments (Cohn et al. 1989; Kambatuku et al. 2011; Vadigi and Ward 2012). Thirdly, within a particular landscape, the relatively nutrient-rich soils are likely to attract considerably greater densities of herbivores than the relatively nutrient-poor soils (Braithwaite et al. 1983; Mills and Fey 2005). Notwithstanding the complexity of interactions between soils, herbivores, plants and climate, the greater herbivory pressure on the nutrient-rich soils is likely in savanna environments to constrain tree seedlings more than grasses and other herbaceous plants.

This paper is one of four research notes in this journal volume in which we explore the differences in soil nutrient status between treed and treeless areas in South African grasslands and savannas (Mills et al. 2021a, 2021b; Mills and Kellner 2021). The differences are examined in the context of the three mechanisms presented above. We opted to sample and analyse the pedoderm, namely the top two centimetres of the soil profile (Mills and Fey 2004; Fey et al. 2006), as opposed to soil layers deeper than 2 cm, for two main reasons. Firstly, differences in soil
chemistry across boundaries in vegetation structure are often only readily discernible in the pedoderm, with deeper soil sampling obscuring such differences (Mills and Fey 2004; Wigley et al. 2013). Secondly, the pedoderm usually has a disproportionately large concentration of plant roots compared with deeper soil layers, making underground competition between plants often greatest in this layer (Casper and Jackson 1997; Fynn 2003). We acknowledge that it would be preferable to have a detailed account of all soil physical and chemical properties in topsoils and subsoils at the study sites because all of these properties influence tree and grass growth. There was, however, a trade-off to be navigated between number of sites that can be plausibly sampled and the intensity of sampling at each site. Given the potential importance of the pedoderm in affecting the growth and survivorship of tree seedlings, which in turn would have a major impact on the ultimate vegetation structure of a particular site, we opted to focus on this layer, which also enabled us to maximise the number of sites sampled. Our approach does not downplay the potential importance, once the tree seedlings have established, of other soil properties at depth. It was simply a pragmatic way to make a first step towards understanding why certain areas remain largely devoid of trees in grasslands and savannas which are in general experiencing intense densification of trees.

In this research note, we report on the results from a site in the central Kruger National Park in South Africa. Open grassland, Senegalia savanna and Delagoa Lowveld savanna near Satara Rest Camp are vegetation types in the central Kruger National Park with markedly different structures (Figure 1). Trees are largely absent in the grassland, while abundant in the Senegalia savanna (predominantly Senegalia nigrescens) and Delagoa Lowveld savanna (e.g. Senegalia welwitschii and Euclia divinorum). Given that the grassland and the two savannas experience the same climate, it is likely that the differences in vegetation structure are ultimately a result of differences in soil properties, with factors such as herbivory and fire having a potentially modifying role.

Based on global datasets, satellite imagery analysis and machine learning, soil types at the study site have been classified as Calcic Luvisols and Rhodic Nitisols (ISRIC 2008), with mean clay contents of the three vegetation types ranging from 24% to 29% (Hengl et al. 2017) (Supplementary Figure S1). As a first step towards identifying the soil properties underpinning the differences in vegetation structure, we investigated the chemistry of the pedoderm in the different vegetation types.

Composite pedoderm (0–2 cm) samples, comprising six to eight subsamples within an area of approximately 100 m², were taken in the grassland site (n = 15) and outside of tree canopies in Senegalia savanna (n = 15) and Delagoa Lowveld savanna (n = 15). The samples were air-dried and sieved to <2 mm. pH (KCl) was determined using a 1:2.5 soil:1 M potassium chloride solution. Inductively coupled plasma mass spectrometry was used to analyse extractable: phosphorus (P); potassium (K); calcium (Ca); magnesium (Mg); sodium (Na); sulphur (S); boron (B); manganese (Mn); copper (Cu); and zinc (Zn). Phosphorus, K, Ca, Mg and Na were extracted with 1% citric acid solution (Du Plessis and Burger 1965; Division of Chemical Services 1956). Sulphur and B were extracted using calcium phosphate and hot water, respectively (Beaton et al. 1969; Bingham 1982). Manganese, Cu and Zn were extracted using 0.02 M di-ammonium ethylenediaminetetraacetic acid (Trierweiler and Lindsay 1968; Beyers and Coetzee 1971). The Walkley–Black method (Walkley 1935; Nelson and Sommers 1982) was used to determine organic carbon (C). Statistical differences between the vegetation types were tested using Kruskal–Wallis tests in R (version 3.6.1).

The grassland was significantly enriched (p < 0.05) in P, Ca, Mg and Cu relative to both the savannas (1.8- and 5.8-fold for the Senegalia and Delagoa Lowveld savannas, respectively, for P; 1.8- and 5.7-fold for Ca; 1.7- and 6.0-fold for Mg; and 1.3- and 9.4-fold for Cu). Compared with the Delagoa Lowveld savanna, the grassland also had a higher pH (KCl) (means of 5.23 vs 6.04) and was richer in K (3.0-fold), Mn (6.3-fold), Zn (1.6-fold), B (1.8-fold), Na (4.7-fold) and C (1.7-fold) (Figure 2). Notwithstanding that the effects of individual plant nutrients on the competitive strength of grasses relative to tree seedlings in savannas over long periods are largely unknown, we suggest that some of these differences in soil chemistry listed above result in greater constraint of tree seedlings in the grassland than in the savannas.

It is noticeable that none of the individual nutrients measured at the study site were likely to have had a dominant effect on the vigour of grasses in the grassland relative to the savannas. This is because, apart from B, the mean concentrations of all nutrients measured were above those expected to constrain plant growth (Peverill et al. 2005; Reis et al 2010; Sims and McGrath 2011; Marschner 2012). It is, however, plausible that the relative richness of the nutrients P, Ca, Mg, Mn, Cu and Zn in the grassland results in a ‘constellation of weak forces’ (McNaughton 1983) that enhance the competitive strength of grasses in the grassland relative to the two savannas. The relative deficiency of B in the Delagoa Lowveld savanna is a force working in the opposite direction of all the other weak forces, in that scarcity of B is expected to favour grasses over trees (Bell 1997; Tariq and Mott 2007). We suggest that, despite this opposing force, the relative deficiency of all other nutrients in the Delagoa Lowveld results in reduced vigour of grasses in this vegetation type relative to that in the grassland.

The relative richness of nutrients in the grassland could also be playing a role in vegetation structure at the study site via an effect on herbivory pressure and/or fire frequency. The nutritive value of the grass in the grassland is likely for example to be greater than in the two savannas, resulting in greater herbivory pressure and potentially greater constraint of tree seedlings. This hypothesis is not however borne out by the data on herbivore density (Supplementary Figure S2), which shows a greater concentration of herbivores in the two savannas than in the grassland. Regarding fire, the greater nutrient richness of the grassland may result in greater production of biomass and in turn a greater frequency of fire. The available data on fire frequency for the study site supports this hypothesis to some extent, showing that the grassland has burnt more frequently than the two savannas (Supplementary Figure
However, the difference in fire frequency between the grassland and the Delagoa Lowveld savanna is minor, suggesting that fire does not provide an overarching explanation for the marked variability in vegetation structure across our study site.

Soil properties, such as C, pH (KCl) and soil texture, are additional forces potentially influencing the competitive interplay between grasses and tree seedlings at our study site. The relatively high mean C concentration of 2.0 ± 0.1% in the grassland may, for example, be a contributing factor to the greater availability of nutrients in the grassland than the Delagoa Lowveld savanna. The effect of pH (KCl), by contrast, is unlikely to be of major significance in determining vegetation structure at the study site because the pH (KCl) levels recorded (means of 6.0 ± 0.2 in grassland, and 5.0 ± 0.1 in the Delagoa Lowveld savanna) are unlikely to cause either nutrient deficiencies or toxicities in grasses or tree seedlings. Regarding soil texture, the grassland is predicted through analyses of global datasets and satellite imagery to have a slightly higher clay content than the two savannas. Given that clay content tends to be correlated with nutrient and water-holding capacity, the higher clay content in the grassland may have an enhancing effect on the vigour of herbaceous plants. This effect is however likely to be relatively small given the minor differences in clay content recorded (Supplementary Figure S3).
The differences in nutrient content of the pedoderm between the three vegetation types in our study site are likely to be a function of a complex interplay of factors, including for example geological parent material, colluvial action, dust deposition, deep retrieval of nutrients in the regolith by roots and different leaching rates of nutrients. Vegetation type will have influenced many of these processes. Soils beneath tree canopies, for example, tend

Figure 2: Soil chemical properties of the pedoderm in open grassland (G; \(n = 15\)), Senegalia savanna (SS; \(n = 15\)) and Delagoa Lowveld savanna (DL; \(n = 15\)). Asterisks denote significant differences across sites according to Kruskal–Wallis tests (*** \(p < 0.0001\); ** \(p = 0.001–0.009\); * \(p = 0.01–0.05\)). Different letters indicate significant differences (\(p < 0.05\)) between vegetation types. The lower and upper bounds of the boxes correspond to the first and third quartiles (the 25th and 75th percentiles). Centre lines represent the median. The whiskers represent 1.5 times the interquartile range (IQR). Data beyond the end of the whiskers were deemed outliers and plotted individually. The elements presented are all extractable concentrations as per the methods described in the main text.
to be enriched in nutrients as a result of dust deposition in the canopies and deposition of leaf litter, whilst the high density of roots in the topsoils of grasslands tend to result in a relatively high soil organic C concentration which in turn increases the nutrient holding capacity of the soils and reduces the rate of nutrient leaching. Notwithstanding the influence of such processes at our study site, we suggest that geological parent material has been the primary force determining the variation in soil chemistry and consequently vegetation structure within our study site. This is because the geology across the site varies from a nutrient-poor sandstone to nutrient-rich shales and basalt (Supplementary Figure S3). The grassland is situated several kilometres from a band of sandstone running through the site, whereas the two savannas are immediately adjacent to this band. As a result, the influence of the sandstone on the nutrient composition of the pedoderm is likely to be greater in the savannas than the grassland. This influence could be via water erosion, wind erosion and colluvial action. Further studies on the influence of this band of sandstone on the nutrient content of the pedoderm are likely to yield further insights into relationships between vegetation structures, geology and soil properties in the central Kruger National Park grasslands and savannas.

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