# Habitat and bedrock modify the relationship between plant and herbivore species richness in a South-African savanna

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**Abstract**

How grazing interacts with environmental conditions in determining grass species richness and abundance in savanna is still insufficiently understood. Quantifying the impact of herbivores on ecosystems can provide some insights into these relationships. In Kruger National Park, South-Africa, we recorded grass species and estimated their covers in 60 plots 50 × 50 m in size, selected to account for varying proximity to water and nutrient availability. Thus, we located plots (i) near perennial rivers, near seasonal rivers, and on crests that are distant from all waterbodies, and (ii) on nutrient-rich basaltic and nutrient-poor granitic bedrock. The presence and abundance of large herbivores was recorded by 60 camera traps located in the same plots. Grass cover decreased significantly with herbivore abundance and differed between habitats and bedrock types, with plots at crests showing the highest cover and plots near perennial rivers the lowest grass cover; on basalts grasses reached higher cover than on granites. The relationship between herbivore abundance and grass species richness changed with the type of bedrock; it was positive on basalts but negative at granite plots. Similarly, the relationship between herbivore species richness and grass species richness was positive on crests and on basalts, but negative near seasonal rivers and on granites; near perennial rivers the relationship was non-significant. We suggest that the positive relationship between herbivore richness or abundance and grass species richness, which is more pronounced on basalts, is due to herbivores supressing dominant grass species. This may increase microsite heterogeneity and therefore support grass species richness. In contrast, the decrease in grass species richness with herbivore species richness at seasonal rivers indicates that the high impact over-rides the resistance of some species to grazing and trampling.

## Introduction

The savanna ecosystem is typically formed by a patchy mosaic of trees, shrubs and herbs, characterized by the dominance of grasses that create a more or less continuous ground cover (Walker 1987). The structure and abundance of savanna vegetation are driven by four main determinants: water availability, soil properties, fire, and herbivory (Huntley and Walker 2012, Bond 2019). Water and nutrient supply control primary production (Scholes 1990, Skarpe 1991), while fire and herbivory act as consumers of accumulated biomass (Archibald and Hempson 2016). However, although many experiments addressed complete or partial herbivore exclusion (Olff and Ritchie 1998, Staver and Bond 2014, Anderson et al. 2007), it has been pointed out that quantification of the herbivore impact under different nutrient and water availability in savanna ecosystems is still missing (Staver et al. 2021).

Large herbivores differ in their dietary niches, typically divided along the browser-grazer continuum, where three dietary guilds are defined: grazers, browsers, and mixed-feeders (Hofmann and Stewart 1972, Owen-Smith 1997, du Toit 2003). Grazers feed primarily on bulk/roughage that is mainly composed of grass, while browser diets consist of leaves and branches of woody species and forbs where the concentration of nutrients is higher. Mixed-feeders combine both food sources according to their changing availability and palatability during the dry and rainy seasons (Hofmann and Stewart 1972, du Toit et al. 2003, Codron et al.

2007). Grasses are therefore directly affected by grazers and mixed-feeders. Associated activities of animals such as trampling, wallowing, urinating, defecating, and digging also need to be considered when exploring the plant-herbivore relationships in savanna vegetation (Cumming 1982), especially in areas where animals aggregate and/or spend longer periods (Veldhuis et al. 2018). Large herbivores also reduce the woody layer that competes with understory species (Cumming 1982, Bond 2019). Large mammalian herbivores have been estimated to consume about half of the plant production in African savannas with intact faunas (Phillipson 1973), and herbivores have been shown to use ~57% of the grass biomass in exclosure experiments (Staver et al. 2021). The effect of herbivores on grasses is most evident under heavy grazing, which often concentrates at water sources (Thrash et al. 1993, Pringle 2004). Abundance and diversity of vegetation can be affected up to several hundreds of meters from the water source (Olivier and Laurie 1974, Thrash 1998a, Todd 2006, Smit and Grant 2009). Therefore, rivers in savanna systems can be hypothesized to affect vegetation in at least two ways: (i) higher soil moisture supports deep-rooting plants, and this effect interacts with (ii) an increased impact of animals that come to the water. On the other hand, herbivore abundance is driven by forage quality that is higher in nutrient-rich sites, such as fertile soils in termite mounds or grazing lawns (Mayengo et al. 2020).

Soil moisture and nutrients are essential drivers of grass biomass (Dye and Spear 1982, Zambatis 2003). Water supply controls both the growth rate and the length of the growing period, while soil nutrients, among which phosphorus and nitrogen are the most important, influence the growth rate (Scholes 1990). Soil nutrients are primarily determined by the character of bedrock – nutrient-rich soils weather from basic igneous bedrock, such as basalt, gabbro, or dolerite, while nutrient-poor soils from acidic bedrock, like granite, sandstone, or gneiss (Venter et al. 2003). Soil type also influences soil moisture by its water-holding capacity and water penetration during heavy rain; in clayey soils derived from basalts, the runoff is quicker and water does not reach the deeper soil horizons (Colgan et al. 2012). Coarse-textured sandy soils allow for greater infiltration and deeper percolation of rainwater than heavier-textured soils, consequently increasing moisture storage in the subsoil. Fine-textured soils that are high in clay content are much more xeric (Dye and Spear 1982). These differences influence plant species richness and diversity of all functional groups, shrubs, forbs, and grasses (Jacobs and Naiman 2008, Hejda et al. 2022). In the Kruger National Park, South Africa, plant communities on granites are richer in species than those on basalts (Hejda et al. 2022), where soils are more fertile but create less favourable conditions for most plant species due to rapid desiccation and mechanical stress caused by deep cracks in soil that damage fine roots (Muvengwi et al. 2018).

It has been reported that plant species diversity in savannas, including that of grasses, is often positively affected by free-ranging large herbivores (Olff and Ritchie 1998, Anderson et al. 2007, Díaz et al. 2007, Jacobs and Naiman 2008, Staver and Bond 2014). Grass diversity is expected to be highest under intermediate herbivore pressure because under high pressure, only species adapted to disturbance survive, as demonstrated by papers studying the effect of artificial water points or conducted in smaller game reserves (Thrash et al. 1993, Todd 2006, Smit and Grant 2009, Fenetahun et al. 2021), while at low densities or when herbivores are excluded, a few dominant grass species tend to prevail (Olff and Ritchie 1998, Anderson et al. 2007). By this mechanism, grazing affects competitive relationships among grass species. There are two possible scenarios: (i) the preferentially grazed species decrease because their biomass is being removed (Walker 1987), or (ii) they increase due to the suppression of other species in the plant community that are intolerant of grazing (McNaughton 1979, Hempson et al. 2015). The former mechanism is typical for heavy grazing by livestock or in game reserves, where it can lead to the replacement of palatable perennial grasses with unpalatable annuals (Werger 1977, Skarpe 1991). The latter option is likely to manifest in grazing lawns formed by short, palatable grasses with a high content of nutrients that provide a high-quality forage (McNaughton 1984, Cromsigt and Te Beest 2014, Hempson et al. 2015). Therefore, the intensity of grazing and herbivore species composition shape traits of species forming the grass community, such as small stature, high shoot density, and presence of belowground meristems to avoid herbivory pressure (Augustine and McNaughton 1998, Díaz et al. 2007), or high nitrogen leaf content in fast growing species in grazing lawns adapted to grazing (Arnold et al. 2014). Many plant species in African savannas are tolerant of grazing due to a long evolutionary history with herbivores (Cumming 1982). However, hypotheses diverge regarding what is expected to stimulate grass

productivity (Staver et al. 2021). The grazing optimization hypothesis suggests that intermediate levels of herbivory should have the largest stimulating effect on productivity (McNaughton 1979, Hilbert et al. 1981), whereas alternative models indicate that productivity is most stimulated by intense but episodic grazing (Oesterheld and McNaughton 1991, Ritchie and Penner 2020). Studies have shown that the impact of free-ranging herbivores, unlike those in game reserves where animals do not migrate, is affected by migrations, which may change the abundance of herbivores and their species composition (Bakker et al. 2006).

Finally, the herbivore effect on grass abundance and species richness may interact with environmental settings such as nutrients and water availability (Milchunas at al. 1988, Veldhuis et al. 2014). The effect of herbivory on species richness is usually more pronounced in more nutrient-rich and productive ecosystems (Olff and Ritchie 1998, Bakker et al. 2006) or in burnt sites (Eby et al. 2014). However, some comprehensive large-scale studies only found an effect of herbivory, regardless of nutrient conditions. Borer et al. (2014) and Koerner et al. (2018) found that herbivore-induced change in plant dominance was the best predictor of plant diversity regardless of site productivity worldwide. Grazing pressure can lead to severe overgrazing and decreased grass diversity under arid and nutrient-poor conditions (Milchunas et al. 1988, Bakker et al. 2006). In contrast, under high water and nutrient supply, a similar level of grazing can cause a suppression of dominant species and increase grass species richness (Belsky 1992, Proulx and Mazumder 1998, Ritchie and Olff 1999).

To provide an insight into the relationship between plants and herbivores in an African savanna, we explored the interaction of grazing, varying water availability, and soil properties influencing plant communities dominated by grasses in the Kruger National Park, South Africa. Specifically, we asked (i) what is the relationship between either grass species abundance or grass species richness and the abundance and species richness of large herbivores, and (ii) how these patterns change with regard to water availability manifest by location of study sites at perennial rivers, seasonal rivers and dry crests on granite vs. basaltic bedrock.

## Material and methods

### Study area

The study was performed in the Kruger National Park (KNP), located in the Limpopo and Mpumalanga Provinces in north-eastern South Africa. It extends 360 km from north to south and 65 km from east to west and covers almost 20,000 km$^2$, which makes it one of the largest protected areas in Africa. The park has seven perennial rivers: Sabie, Olifants, Crocodile, Letaba, Shingwedzi, Luvuvhu, and Limpopo, which flow from west to east (du Toit et al. 2003). The park has variable environmental conditions; altitude ranges between 140–780 m a.s.l, and annual precipitation between 450–750 mm. Bedrock is mainly acidic and nutrient-poor in the western half of the park (granitoids), and alkalic and more nutrient-rich in the east (mostly basalts). Grasses are represented by ~230 species in the KNP (Gertenbach 1983), ranging from a short pioneer species of low nutritional value, such as *Aristida* spp. or *Pogonarthria squarrosa* to tall species of a high nutritious value, such as *Panicum maximum* , *Digitaria eriantha* or *Themeda triandra*. There are 19 vegetation types in KNP based on a phytosociological classification (Mucina and Rutherford 2006), of which 13 were covered by our plots; most represented were SVl3 Granite Lowveld (13 plots), SVmp4 Mopane Basalt Shrubland (12 plots), SVl5 Tshokwane-Hlane Basalt Lowveld (10 plots), and SVmp5 Tsende Mopaneveld (nine plots; Hejda et al. 2022). The average cover of woody and grass species was 45% and 31%, respectively (see Hejda et al. 2022 for further details on vegetation cover and plant community composition).

### Experimental plot design

Data were collected within the MOSAIK (Monitoring Savanna Biodiversity in Kruger National Park) project, which explores the patterns and interactions among plant, insect, bird, and mammal communities (see Hejda et al. 2022). Data were collected along a gradient of water availability and on two types of bedrock. Water supply was accounted for by locating the plots in three habitats: (i) near a perennial river or another permanent water source, such as artificial water points or dams, (ii) near a seasonal river with a lack of water during dry periods, and (iii) on dry crests, at least 5 km from any source of water (Fig. 1). These habitats types affect groundwater availability for animals as well as soil moisture for deep-rooting perennial species. The plots were grouped into triplets by habitats, with plots within the triplet being closer to each

other (~ 7–13 km apart) than to other plots outside the triplet. The plots were located on two contrasting bedrocks, basalt and granite, which weather into soils that differ in nutrients, water retention capacity, and texture (Venter et al. 2003, Mucina and Rutherford 2006). We established 60 permanent plots 50 × 50 meters that were equally distributed among the three habitats (20 in each) and two bedrocks (30 in each) (Fig. 2). As we focused on the shrubby savanna, we placed our plots outside the riparian gallery forests, and the presence of trees in the plots was generally very low if any.

*Plant data*

Vegetation was sampled in the plots during the peak growing season (see also Pyšek et al. 2020, Hejda et al. 2022). Surveys were done during two rainy seasons, from 16 January to 4 February 2019 (33 plots) and 17 January to 3 February 2020 (27 plots); the plots sampled in each year were equally stratified among habitats and bedrocks. All plant species (for simplicity, intraspecific taxa such as subspecies are further also referred to as 'species') were recorded in each 2,500 m$^2$ plot, separately for the shrub and herb layer. Their abundance was visually estimated using the Braun-Blanquet cover-abundance seven-grade scale (Mueller-Dombois and Ellenberg 1974). To quantify the occurrence of species in plots, the Braun-Blanquet scores were transformed to percentage values as follows: 5 = 87.5%, 4 = 62.5%, 3 = 37.5%, 2 = 15%, 1 = 2.5%, + = 1.0%, r = 0.02% (van der Maarel 1979).

For each plot, we calculated (i) **grass species richness** , i.e., the total number of grass species recorded in the plot, and (ii)**grass cover** as the sum of the ground covers of all grass species present in the plot; the grass cover ranged between 1% and 103% (because leaf layers may overlap across species, summary values over 100% are possible).

Grass traits were extracted from van Oudtshoorn (2018), namely: maximum culm length; maximum leaf length; maximum leaf width; perenniality (as a continuous variable: 1 = annual, 2 = weak perennial, 3 = perennial); grazing value (as a continuous variable: 1 = low, 2 = medium, 3 = high); grazing status (decreaser, increaser I, increaser II, increaser III). Species were classified as annuals if they grow for one season, weak perennials if they grow for two to five seasons, and perennials if persisting longer than five seasons. Decreasers are palatable grasses that decrease under over- or undergrazing, increasers I are unpalatable grasses growing in underutilized veld, increasers II are common in dry and overgrazed grasslands, and increasers III are unpalatable climax grasses of overgrazed veld (van Oudtshoorn 2018). Climax status that describes the species' position on the succession continuum was also converted to a continuous variable (1 = pioneer, 2 = pioneer/subclimax, 3 = subclimax, 4 = subclimax/climax, 5 = climax).

The nomenclature of plant species follows van Oudtshoorn. (2018).

*Herbivore data*

The presence of animal species was estimated by camera traps located in the same plots where the vegetation sampling was performed (one in each plot, n = 60). Bushnell Essential E3 camera traps with low glow IR flash were used to collect data on herbivores. The camera traps were set to take three images in the interval of three seconds once the camera was triggered, from which only one was used for the analysis. The next trigger was delayed by one minute after the last snapshot. When more individuals of the same species occurred in one image, we considered them a single record. In this paper, we use data from a total of 140 days from both dry (June – August 2018) and rainy (December – February 2019) seasons.

From this camera-based dataset, we extracted records of large herbivores (elephants, equids, rhinoceroses, and bovids) that are reported to influence grass species composition (Cumming 1982, du Toit 2003). We considered both grazers and mixed feeders, i.e. species that feed on grass (Table 1); for simplicity, we use the term 'herbivore' for both groups. For each plot, we calculated (i) **herbivore species richness** , expressed as the total number of herbivore species recorded over the monitoring period, and herbivore species abundance, corresponding to the total number of records of a given species. The sum of records of all grazing species (Table 1) served as a proxy for (ii)**herbivore abundance.** Further, we also estimated the total herbivore biomass per plot, calculated as species abundance × mean species biomass summed up

across all species. The species biomasses were taken from Kingdon et al. (2013) and Kingdon and Hoffmann (2013a, b) and calculated as a mean of the ranges given for male and female biomass. We are aware that the term 'abundance' as we use it does not correspond to the exact numerical abundance of species populations per plot, but we suggest that it is an informative measure of the total herbivore feeding pressure in a plot.

*Data analysis*

Univariate analyses: grass cover and species richness

The relationship between herbivore abundance and species richness, habitat, bedrock, and their mutual two-way interactions (predictors) on grass cover and species richness (response variables) were explored by the linear mixed-effect models – LMMs (Table 1). Data on abundance and species richness of herbivores were merged for both seasons, as separate models for dry, wet and both seasons merged gave similar results (not shown). Triplet identity, which reflected the spatial clustering of the plots, was set as a random variable. For grass cover and species richness, we used LMMs with normal distribution; the response variable grass species richness was square-root transformed to improve normality and homogeneity of variance. Herbivore abundance was log-transformed in LMM to reduce the skewness of data. To test possible non-linear effects of herbivore abundance and herbivore species richness, we added their quadratic terms to the models; however, as they were not significant, they were not included in the final models. The significance of the terms in LMM models was obtained via *anova* function. The marginal coefficient of determination $R^2$, which represents the variance explained by the fixed effects, was computed using *r.squaredGLMM* function from the "MuMIn" package (Bartoń 2022). Marginal $R^2$ for individual terms (predictors) was computed by comparing models with and without the particular term, obtained by model backward simplification. Here we present only $R^2$ for significant terms. Regression lines in figures were plotted based on simplified LMM models that contained only the predictor and response variables shown on the given graph. Regression estimates (marginal means and their confidence intervals) presented in graphs (Fig. 5, 7 and 8) were computed by *ggpredict* function from the "ggeffect" package (Lüdecke 2018). The differences among individual habitats in the simplified models with only the predictor and response variables were further tested by the post-hoc Tukey HSD pairwise comparison of estimated marginal means (Lenth 2021). In addition to the R-base packages, we further used the packages "nlme" (Pinheiro et al. 2021) for fitting the linear mixed-effect models, and package "emmeans" was used for subsequent multiple comparisons among significant terms (Lenth 2021). Graphs were plotted using the "tidyverse" (Wickham et al. 2019), "grid" and "ggpubr" (Kassambara 2020) packages. All computations were done in the programme R 4.2.0 (R Core Team 2022).

Multivariate analyses: grass community composition and mean grass traits

In the first group of analyses, grass species covers were response variables, and (i) the total number of records and the species richness of herbivores , or (ii) the number of records of individual herbivores were predictors (Table 1). To filter out the effect of habitat, bedrock, and spatial arrangement given by the mutual position of permanent plots, we set them as covariates in all analyses. Spatial effects (autocorrelation of plots) were identified by the PCNM analysis (ter Braak and Šmilauer 2012), where GPS coordinates represented the plot position, from which a matrix of spatial PCoA vectors was calculated; here we used the scores of the first three PCoA vectors as spatial covariates. Because plots were grouped in triplets in the field, we used a hierarchical split-plot design, where triplets were set as whole plots, while plots within a triplet represented split plots. Both triplets and plots within triplets were permuted freely, and the significance was tested by Monte-Carlo permutation tests. In the second group of analyses, the response variables were the mean values of traits of the grass community, so-called community-weighted means, calculated as values of species traits weighted by their relative abundance within each plot; the mean values for all traits were computed for each plot (Šmilauer and Lepš 2014). Covariates and the permutation scheme remained the same as in the first group of analyses. All multivariate analyses were performed in Canoco 5 software (Šmilauer and Lepš 2014).

## Results

*Herbivore load by habitat*

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Of the 67,100 records of herbivores (grazers and mixed-feeders) captured by camera traps over the study period, the majority were from perennial rivers (43,195 records; 64.4%), while seasonal rivers experienced an intermediate herbivore load (18, 961 records; 28.2%), and the fewest herbivores were recorded at crests (4,944 records; 7.4%). We recorded seven species of grazers (buffalo, hippo, tsessebe, waterbuck, white rhino, wildebeest, and zebra) and six mixed-feeders (common duiker, eland, elephant, impala, nyala, and sable antelope; Table 1). The most common herbivore was impala, accounting for more than half of all records (38,154 records; 54.1%), followed by elephant (11,644 records; 16.5%) and buffalo (4,616; 6.6%). The abundances of all herbivore species across habitats are shown in Fig 3. Species that occurred in the greatest number of plots were elephant (58 plots, i.e., 98.3% of the total of 60 monitored), impala (56 plots; 93.3%) and buffalo (52 plots; 86.7%). Species with only a few records (tsessebe = 8, sable antelope = 7, and eland = 2) were excluded from analyses (Table 1).

*Grass cover*

We recorded 99 grass species that, on average, reached the total cover, summed across all grass species in a plot, of 31.9%. There were significant differences in grass cover among habitats and bedrock type (Table 2). Grasses had a significantly higher cover at crests (p = 0.001, mean value of 41.5%) and at seasonal rivers (p = 0.001, 40.1%) than at perennial rivers (14.1%; Fig. 4A), and on basalts (p = 0.039, 39.2%) than on granites (24.5%; Fig. 4B). The grass cover was significantly negatively affected by herbivore abundance (Table 2), decreasing with increasing grazing load (p = 0.019, Fig. 5), while its interactions with habitat and bedrock were not significant. We found no significant effect of herbivore species richness on grass cover, either as a main effect or in interaction with bedrock or habitat (Table 2).

*Grass species richness*

Grass species richness did not differ significantly among habitats and bedrocks. Although the overall tests on the differences between habitats in models with herbivore abundance and species richness were significant and marginally significant, respectively (Table 2), no significant differences were detected between pairs of individual habitats (Fig. 6A and B). The highest grass species richness was recorded on granitic crests; however, the interaction of bedrock and habitat was not significant.

Herbivore abundance and species richness significantly interacted with bedrock (p = 0.034) but were not significant as main effects (Table 2). Grass species richness increased with herbivore abundance on basalts and decreased on granites (Fig. 7).

Grass species richness was significantly positively related to herbivore species richness at crests (p = 0.017) and negatively at seasonal rivers (p = 0.018); the relationship was non-significant at perennial rivers (p = 0.516, Fig. 8A). For the two bedrock types, the relationship between grass- and herbivore species richness was similar to that between grass species richness and herbivore abundance, i.e., significantly positive on basalt (p = 0.040) and negative on granite (p = 0.018, Fig. 8B).

*Grass community composition and grass traits*

The most common grass species were *Panicum maximum* , occurring in 54 plots (90% of the total number sampled), *Brachiaria deflexa*(52 plots; 86.7%) and *Tragus berteronianus* (49 plots, 81.7%; see Table 3). The most abundant in terms of the mean cover per plot was*Bothriochloa radicans* (14.1%, present in 20 plots),*Hyparrhenia hirta* (6.6% in 8 plots), and *Themeda triandra*(5.8% in 21 plots).

Using multivariate analyses with habitat, bedrock, and spatial arrangements as covariates, we did not find any significant effects of herbivore abundance and species richness on grass species' covers (F = 0.9, p = 0.66). Similarly, there was no effect of the abundance of particular herbivore species on grass species covers (p = 0.162); only when testing individual species by the forward selection, the effect of hippo (F = 2.9, p = 0.012) and scrub hare (F = 1.6, p = 0.092) had significant and marginally significant effects, respectively.

We did not find a significant effect of the herbivore abundance and species richness (F = 0.3, p = 0.932) nor by the abundances of individual herbivore species (F = 0.9, p = 0.592) on the mean grass traits.

## Discussion

*Grass cover*

The abundance of herbivores in our plots strongly depended on water availability/proximity to water; almost two-thirds of the individuals were recorded at perennial rivers, less than one-third by seasonal rivers, and only ~7% at crests. The concentration of herbivores at perennial rivers increases the impact on grasses, leading to a lower grass cover. This is in accordance with previous studies (Thrash et al. 1993, Thrash 1998b, Todd 2006, Smit and Grant 2009) that found the lowest cover of herbs and shrubs at artificial watering points and its increase with increasing distance from the water source. Olivier and Laurie (1974) report a similar pattern from the Mara River in Tanzania, where grass cover increased from 34% to 71% over one kilometer from the river, and grazing intensity declined from 86% at 20 m from the river to 35% at 880 m apart. Soil moisture could be higher near perennial and seasonal rivers, influencing the growth and abundance of deeper-rooting grasses. In general, grass biomass and cover increase with water availability (Zambatis 2003, Staver et al. 2019), and experiments show that grass abundance is higher in moist than in arid sites after herbivore exclusion (Staver and Bond 2014). This indicates that herbivore pressure, especially heavy grazing and other effects of animal presence typical of areas along perennial rivers (Olivier and Laurie 1974), likely outweighs the positive effect of enhanced water availability. This notion is supported by the intermediate grass cover and species richness we recorded at seasonal rivers, where herbivore abundances were also moderate. It needs to be noted, however, that the low grass cover by rivers, which is a proxy of actual biomass, does not necessarily mean low biomass production. Grazing can be compensated by increased growth of grasses (McNaughton 1979, Ritchie and Penner 2020), which is stimulated by increased nutrient input from dung and urine and by lower self-shading (Augustine et al. 2003, Zimmermann et al. 2010). Grazing lawns that often occur nearby rivers are an example of a highly productive grass ecosystem maintained by intensive grazing (McNaughton 1984, Archibald 2008, Hempson et al. 2015).

Finally, grass cover significantly differed between bedrock types, and this difference was most pronounced on crests where it was on average almost twice as high (53.4% cover) on clayey soils derived from basalts than on sandy soils on granites (29.4%). This corresponds with the results of Dye and Spear (1982), who found greater grass biomass on clayey soils in Zimbabwean savanna systems. In other habitats, such as seasonal and perennial rivers, the effect of bedrock was not as pronounced, probably over-ridden by grazing. Grasses on crests sometimes created a continuous cover, often dominated namely by *Bothriochloa radicans* and abundant *Themeda triandra* or *Cenchrus ciliaris* (Table 3).

*Grass species richness: mixed effects of grazing and habitat*

We found no relationship between herbivore abundance and grass species richness, which is in contrast with the results of McNaughton (1979) or Milchunas et al. (1988). However, when testing the effect of herbivore abundance or species richness without accounting for other predictors, we found a marginally significant unimodal relationship (p = 0.059 and p = 0.077 for herbivore abundance and species richness, respectively). Theoretically, the greatest grass species richness could be expected at intermediate grazing levels, when strong dominants are suppressed, and disturbances created by herbivores allow for early successional species also to occur (Thrash et al. 1993, Todd 2006). The positive effects of moderate herbivore pressure include the removal of biomass by grazing and other consequences of grazing animals' presence (trampling, urinating, wallowing, digging, etc.) that collectively result in a mosaic of microhabitats providing niches for more species than in a uniform grassland. These other animal activities are concentrated mainly at water sources because animals come to drink, cool down, and also rest in the shade of gallery trees (Olff and Ritchie 1998, Bakker et al. 2006). Such activities bring about different effects on plants than just grazing. For example, trampling often leads to a shift from tall palatable species like *Panicum maximum* or *Themeda triandra* to annual small-statured species, such as *Tragus berteronianus* or *Aristida* spp. that tolerate intensive soil disturbances and compaction, while intensive grazing itself promotes small-statured perennials like *Cynodon dactylon* or shrub-like statured grasses as *Bothriochloa radicans* or *Cenchrus ciliaris* . Further, the occurrence of some of the herbivores that we recorded in our plots is more or less restricted to the vicinity of water sources, such as hippo, buffalo, and waterbuck (Fig. 3). The patches with moderate grazing pressure can be inhabited by

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a range of grass species differing in their competitiveness, tolerance to disturbance or nutrient requirements.

While the gradient in herbivore abundances across all habitats largely followed the increase in water availability, with the lowest pressure on crests and highest at perennial rivers, the gradient in herbivore species richness is not primarily driven by habitat. With the exception of extremely poor and rich plots that are located at crests and perennial rivers, respectively, the herbivore species richness is more or less evenly spread across the gradient of water availability.

*Grass species richness: interaction of habitat and bedrock*

The effect of herbivore abundance on grass species richness interacted with that of bedrock: with increasing herbivore abundance, grass species richness increased on basalts but decreased on granites. The positive relationship on basalts may be explained by herbivores reducing the dominance of strong grass competitors, thus favouring the coexistence of more grass species (McNaughton 1979, Jacobs and Naiman 2008). On granites with lower grass cover and slightly higher (although non-significant) grass species richness, large herbivore pressure seems to lead to the loss of some species, hence a decrease in grass species richness.

The herbivore species richness interacted significantly with that of habitat and bedrock. In the case of bedrock, grass species richness increased with grazer species richness on basalts in a way similar to herbivore abundance; in fact, both these measures of the herbivore effect were positively correlated (r = 0.54, see Fig. S1). Similar trends could be partially attributed to greater herbivore pressure (as indicated by the above-mentioned mutual correlation). On nutrient-rich soils on basalts, there is a more intense competition among grass species, in particular at crests where the herbivore pressure is lower than by the rivers, leading to the dominance of fewer species, a pattern similar to what we observed in a previous study for all herbs (Hejda et al. 2022).

In terms of habitats, grass species richness increased with herbivore species richness at crests, probably because grazing there suppresses strong dominants, but decreased with herbivore species richness at seasonal rivers, which may be explained by a greater herbivore impact that over-rides the endurance of some species to grazing and trampling, leading to the decrease of grass species richness (McNaughton 1979, Milchunas et al. 1988). Besides the increase in absolute grass cover towards dry crests, it is also the relative cover of grasses that becomes increasingly important. Hejda et al. (2022) reported grasses to account for 83% of plant cover on the crest, with corresponding values of 68% at seasonal rivers and 50% at perennial rivers. Given that the relative cover of grasses on basalt exceeded that on granite (74% and 60%, respectively), basalt crests represent the environment where grasses gain the greatest advantage of all habitat/bedrock combinations we examined. The specific features of the clayey soils on basalt, with the quick water runoff and rapid desiccation, make it, at the same time, the most extreme environment for many forbs; this provides more niches for grass species, resulting in their greater species richness. Dye and Spear (1982) also found considerable interannual variation in grass biomass on clayey soils, probably in relation to precipitation variation, with large declines in biomass in dry years. Sandy soils were, in contrast, more stable in production of grass biomass, likely due to a carry-over effect of soil moisture stored in the subsoil from one year to another. Large moisture fluctuations in clayey soils may aggravate the establishment and survival of some species, leading to the persistence of fewer specialized species, such as *Panicum coloratum* or *Bothriochloa radicans,* that are typical of clayey soils, and, in turn, in lower species richness (Dye and Spear 1982).

*Grass species composition and traits*

We did not reveal any effect of herbivore abundance and richness on grass community composition and the traits of the species present. The only significant result was the effect of hippo and scrub hare abundance on grass species community composition. Our expectation was that the grass community composition would be shaped either by the overall grazing pressure, manifest by the total herbivore abundance or by the abundances of individual herbivore species. The total grazing pressure induces different levels of grazing, e.g., overgrazed dry grass communities with abundant annual species such as *Aristida adscensionis* and *Tragus berteronianus* , heavily utilized grazing lawns with adapted species such as *Cynodon dactylon* and*Bothriochloa radicans* , or moderately grazed veld dominated by tall competitive species such as *Themeda triandra* or*Panicum*

*maximum* (van Oudtshoorn 2018). Different abundances of herbivore species in particular plots may lead to the suppression or facilitation of certain species and traits via grazing selectivity (Bell 1971) or sward-height specialization (Farnsworth et al. 2002), which is reflected in traits of individual grass species (Díaz et al. 2007).

*Causality of the relationship between grasses and herbivores and methodological issues*

When interpreting our results, it needs to be borne in mind that the positive relation between herbivore species richness and grass species richness can act in both directions. First, herbivores may support grass richness by acting as a dominance control mechanism, suppressing potentially dominant species, and increasing microsite heterogeneity (e.g., Chaneton and Facelli 1991, Ritchie and Olff 1999, Jacobs and Naiman 2008, La Plante and Souza 2018). This is further supported by the positive effect of herbivore species richness manifest on basalts and crests, where the most intense competition among grass species can be assumed because this habitat/bedrock combination is where grasses reach the highest dominance; this also holds for their relative dominance with regards to other species (Hejda et al. 2022). Further, crests host fewer grazers than both seasonal and especially perennial rivers, and this may also contribute to their positive effect on grass species richness – presuming a unimodal relation between grazing intensity and grass richness (e.g. Frank 2005), the herbivores-grasses relationship can be expected to be positive under the conditions of relatively low herbivore abundances. Lastly, we believe that the presented causality of the relationships also applies to perennial and seasonal rivers due to abundant herbivores, such as elephants (MacFadyen 2019), that spend more time by the rivers, and their grazing selectivity is likely to decrease with grazing intensity (Cornelissen and Vulink 2015).

Alternatively, the richness of grasses can affect the richness of herbivores by providing a more diverse food supply, following the logic of the predator-prey relationship (e.g., Kallay and Cohen 2008, Malard et al. 2020). It is impossible to solve this dilemma using comparative data, and even exclosure experiments tend to give ambiguous results (Chikorowondo et al. 2017, Li et al. 2017, Fenetahun et al. 2021). Moreover, it is likely that both mechanisms with opposite directions are in play with differing importance depending on the specific environmental settings. It is probably more important in crests, where grazing selectivity is expected to be higher under low grazing intensities. In general, we suggest that the relationships between grasses and herbivores may work in both directions, but in environments with negative relationships, the effects of herbivores on vegetation prevail.

## Conclusions

In summary, herbivore impact on grass vegetation depends on water and nutrient availability. In our system, grass cover decreased with water availability towards perennial rivers, where most animals were recorded and was higher on more fertile soils on basaltic bedrock. Our main finding is that the relationship between grass species richness and herbivore species richness changes with water and nutrient availability. Grass species richness increases with herbivore species richness on basalts and on crests, where dominant grass species are suppressed by grazing but decreases on granites and by seasonal rivers. In plots where grasses were dominant, grazing and other animal activities further increase microsite heterogeneity, which provides more niches and supports grass species richness. This suggests that it is necessary to critically assess resource availability in protected areas that aim to support grass species richness. Depending on the context, the same herbivore abundance may lead to different outcomes and both overgrazing as well as low grazing pressure may lead to grasslands dominated by a few species. Grass species richness is important not only *per se* but because more grass species form a more heterogenous environment that supports the diversity of other species of animals and plants. Such a mosaic of species-rich grasslands offers a broad fodder supply and contain species of different successional stages, making them more resistant to different scenarios, such as fluctuation of grazing pressure, fire or drought.

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Table 1. Overview of herbivore (grazers and mixed-feeder) species recorded by camera traps in 60 plots in the Kruger National Park (see text for details). Mean biomass = mean of the male and female biomass; number of plots = number of plots in which the species occurred at least once; number of records = total number of records from all plots. Species are arranged by the number of records from camera traps. Data on animal body biomass were taken from Kingdon et al. (2013)[1], Kingdon & Hoffmann (2013a)[2] and Kingdon & Hoffmann (2013b)[3].

| Common name | Scientific name | Feeding strategy | Mean biomass (kg) | Number of plots | Numbe |
|---|---|---|---|---|---|
| impala | *Aepyceros melampus* | mixed | 58 | 55 | 38154 |
| elephant | *Loxodonta africana* | mixed | 4035 | 59 | 11644 |
| buffalo | *Syncerus caffer* subsp. *caffer* | grazer | 648 | 34 | 4616 |
| waterbuck | *Kobus ellipsiprymnus* | grazer | 209 | 26 | 3124 |
| common duiker | *Sylvicapra grimmia* | mixed | 19 | 40 | 2750 |
| zebra | *Equus quagga* | grazer | 242 | 44 | 2133 |
| hippo | *Hippopotamus amphibius* | grazer | 1400 | 22 | 1785 |
| wildebeest | *Connochaetes taurinus* | grazer | 275 | 18 | 1379 |
| nyala | *Tragelaphus angasii* | mixed | 87 | 12 | 1034 |
| white rhino | *Ceratotherium subsp. simum simum* | grazer | 2000 | 16 | 464 |
| tsessebe | *Damaliscus lunatus* | grazer | 129 | 3 | 8 |
| sable antelope | *Hippotragus niger* | mixed | 228 | 1 | 7 |
| eland | *Taurotragus oryx* | mixed | 561 | 1 | 2 |

Table 2. Results of LMM models for grass cover and grass species richness. List of predictors: herbivore abundance; herbivore species richness; habitat = location of plots at perennial, seasonal rivers or crests; bedrock = location of plots on granite or basalt. Significant results ($p < 0.05$) are marked in bold, marginally significant ($p = 0.1$–0.05) are underlined. Herbivore abundance was log-transformed in the model with grass species richness. The marginal coefficient of determination $R^2$ represents the variance explained by individual predictors and all fixed predictors by the full models without accounting for variation explained by the spatial arrangement of the plots.

| Predictors | Grass cover | Grass cover | | Grass species richness | Grass species richness | |
|---|---|---|---|---|---|---|
| | F | p | $R^2$ | F | p | $R^2$ |
| herbivore abundance (GA) | 6.16 | **0.019** | 0.077 | 0.01 | 0.944 | |
| habitat (H) | 6.74 | **0.004** | 0.145 | 4.19 | **0.024** | 0.08 |
| bedrock (B) | 5.03 | **0.038** | 0.072 | 2.96 | 0.102 | |
| GA×H | 0.03 | 0.968 | | 1.98 | 0.154 | |
| GA×B | 0.99 | 0.328 | | 4.94 | **0.034** | 0.01 |
| H×B | 0.80 | 0.456 | | 1.13 | 0.337 | |
| full model | | | **0.307** | | | **0.24** |
| herbivore species richness GSR | 2.46 | 0.127 | | 0.01 | 0.931 | |
| habitat (H) | 8.72 | **0.001** | 0.194 | 2.80 | *0.076* | 0.04 |
| bedrock (B) | 5.06 | **0.037** | 0.072 | 3.36 | *0.084* | 0.06 |
| GSR×H | 0.04 | 0.966 | | 4.95 | **0.013** | 0.11 |
| GSR×B | 0.01 | 0.930 | | 9.48 | **0.004** | 0.05 |
| H×B | 1.64 | 0.209 | | 1.74 | 0.191 | |
| full model | | | **0.314** | | | **0.30** |

Table 3. Ten most common grass species according to their frequency, expressed as their occurrence in plots. Number of plots (n = 60) in which the species was recorded and its mean cover within them (mean ± S.D.) are given. Life history data and grazing value were taken from van Oudtshoorn (2018), see text for details. Species were classified as annuals if they grow for one season, as weak perennials if they grow for two to five seasons, and as perennials if they persist for longer than five seasons.

| Species | Life history | Grazing value | Number of plots | Mean cover (%) |
|---|---|---|---|---|
| Ranked by frequency: | | | | |
| *Panicum maximum* | perennial | high | 54 | 5.0±11.5 |
| *Brachiaria deflexa* | annual | medium | 52 | 2.5±6.1 |
| *Tragus berteronianus* | annual | low | 49 | 0.9±2.3 |
| *Urochloa mosambicensis* | weak perennial | medium | 43 | 4.5±10.6 |
| *Aristida adscensionis* | annual | low | 41 | 0.7±2.4 |
| *Eragrostis superba* | weak perennial | medium | 36 | 2.6±7.3 |
| *Digitaria eriantha* | perennial | high | 35 | 1.3±3.5 |
| *Enneapogon cenchroides* | weak perennial | medium | 32 | 3.1±9.4 |
| *Cenchrus ciliaris* | perennial | high | 31 | 3.4±8.1 |
| *Heteropogon contortus* | perennial | medium | 30 | 0.3±0.8 |
| Ranked by cover: | | | | |
| *Bothriochloa radicans* | perennial | low | 20 | 14.1±20.2 |
| *Hyparrhenia hirta* | perennial | medium | 8 | 6.6±13.5 |
| *Themeda triandra* | perennial | high | 21 | 5.8±13.3 |
| *Panicum maximum* | perennial | high | 54 | 5.0±11.5 |
| *Panicum deustum* | perennial | medium | 10 | 4.5±11.6 |
| *Urochloa mosambicensis* | weak perennial | medium | 43 | 4.5±10.6 |
| *Bothriochloa insculpta* | annual | medium | 10 | 4±11.8 |
| *Cenchrus ciliaris* | perennial | high | 31 | 3.4±8.1 |
| *Setaria incrassata* | perennial | high | 12 | 3.4±10.8 |
| *Enneapogon cenchroides* | weak perennial | medium | 32 | 3.1±9.4 |
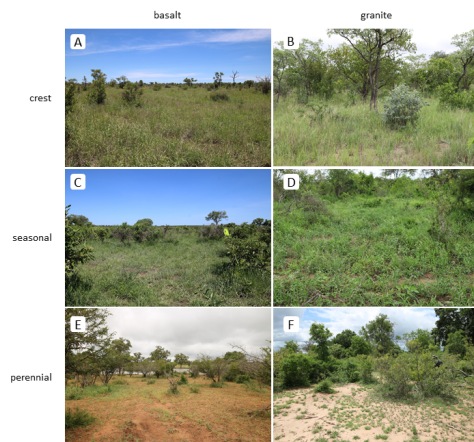
Fig. 1. Examples of six types of savanna grassland based on bedrock (basalt and granite) and habitat combinations (crests, seasonal rivers, perennial rivers). A) plot with a high grass cover at basaltic crest dominated by *Bothriochloa radicans* with *Cenchrus ciliaris* ; B) grass species-rich plot at granitic crest with *Urochloa mosambicensis* , *Eragrostis superba* , *Melinis repens* and *Trichoneura grandiglumis;* C) plot at seasonal river on basalt with abundant *Digitaria eriantha* , *Panicum coloratum* and *Panicum maximum;* D) plot at seasonal river on granite with *Urochloa mosambicensis* , *Panicum maximum* and *Eragrostis cilianensis;* E) plot at perennial river on basalt with a sparse vegetation with *Eragrostis rigidior* , *Urochloa mosambicensis* and *Tragus berteronianus* ; F) grass species-poor plot at perennial river on basalts with *Sporobolus nitens* and *Tragus berteronianus* .



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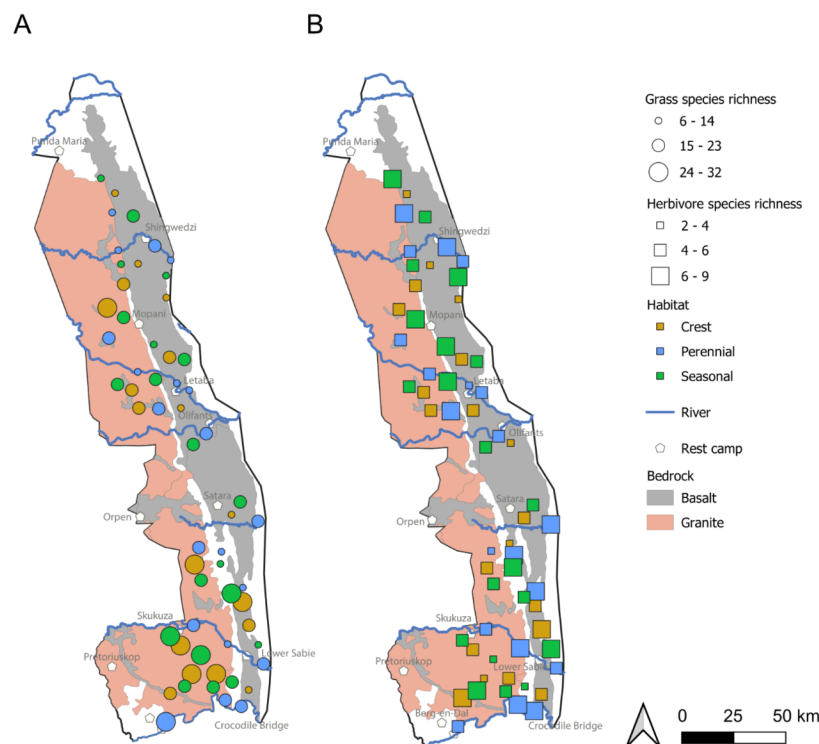
Fig. 2. Map showing grass (A) and herbivore species richness (B) in three different habitats on two bedrocks. Symbol size represents species richness within each group.
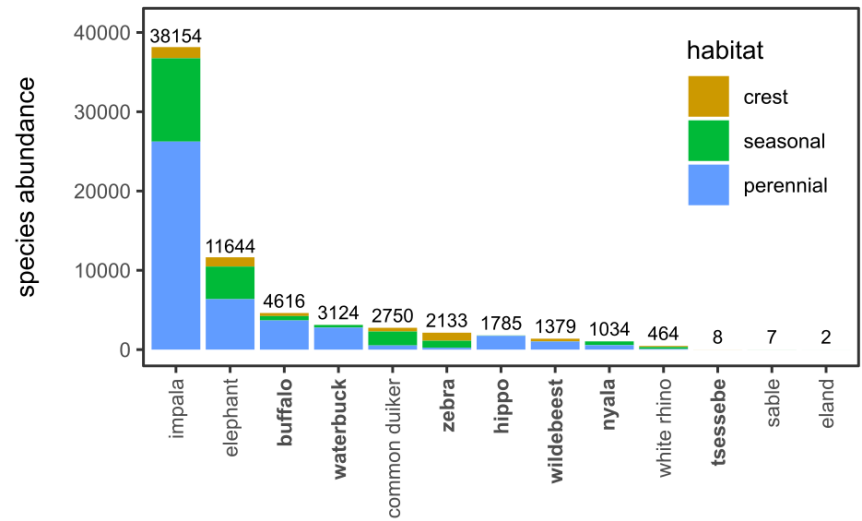


Fig. 3. The total number of records across all plots of herbivores (grazers in bold, mixed-feeders in plain font), with habitats (perennial rivers, seasonal rivers, crests) indicated by different colours. Altogether, we recorded 67,100 animals in 60 plots over 140 days (June 2018 to February 2019). Tsessebe, sable and eland were not included in further analyses because of the low number of records.
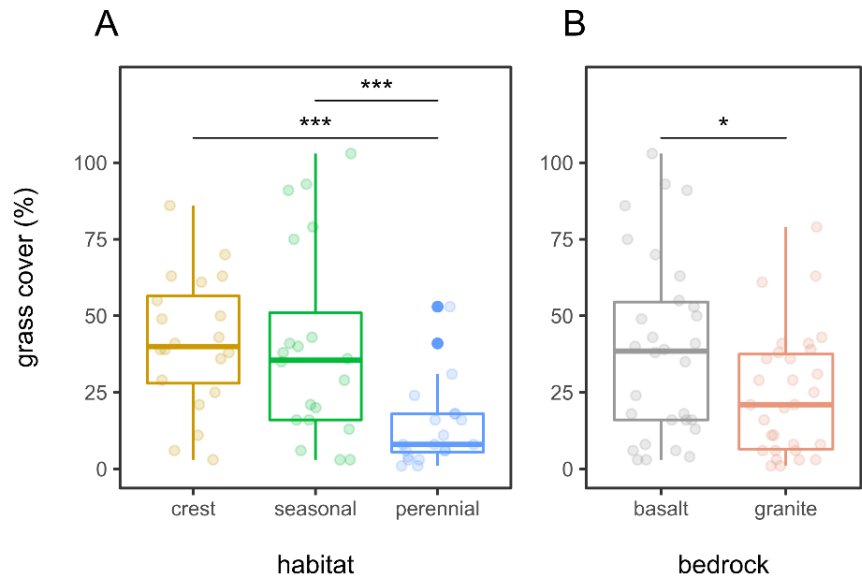


Fig. 4. Differences in total grass cover per plot, expressed as the sum of covers of all grass species recorded, between habitats (A) and bedrocks (B). Transparent points represent grass cover for each habitat (n=20)

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or bedrock (n=30), solid points (only for perennial rivers) represent outliers. Significance P: . (0.1–0.05), * (0.05–0.01), ** (0.01–0.001), *** (< 0.001), non-significant values are not shown.
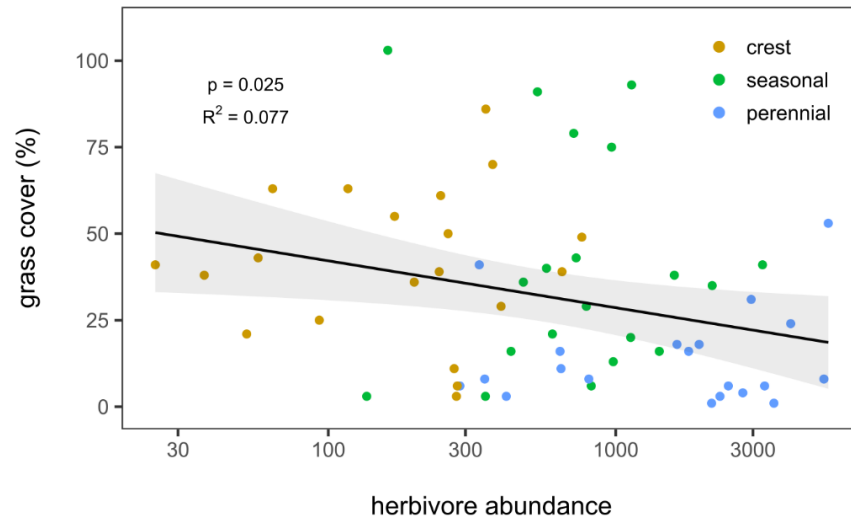


Fig. 5. Relationship between grass cover in a plot and herbivore abundance. Regression line shows fit of linear mixed-effect model; shaded area shows 95% confidence interval. Note that x-axis is on a logarithmic scale.
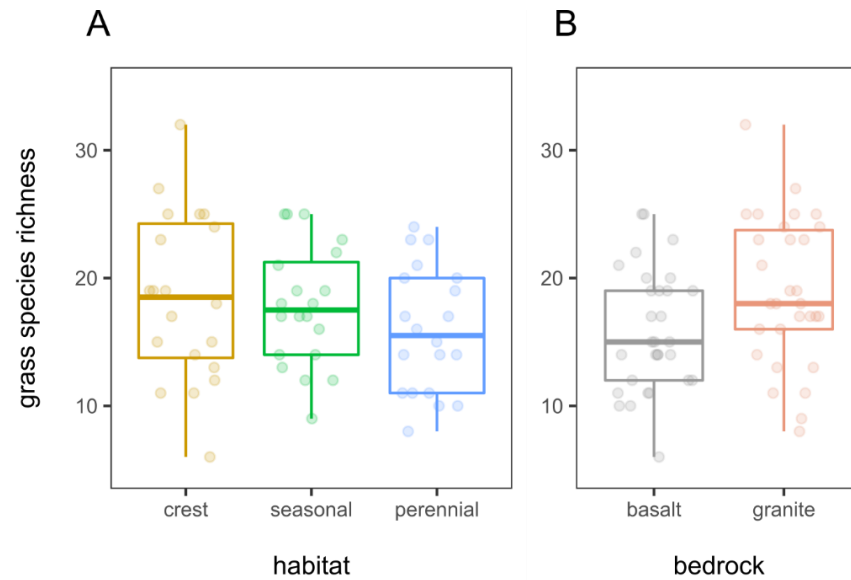


Fig. 6. Grass species richness per plot for different habitats and bedrocks. Transparent points represent grass cover for each habitat (n=20) and bedrock (n=30). No significant differences among habitats and bedrocks were found.
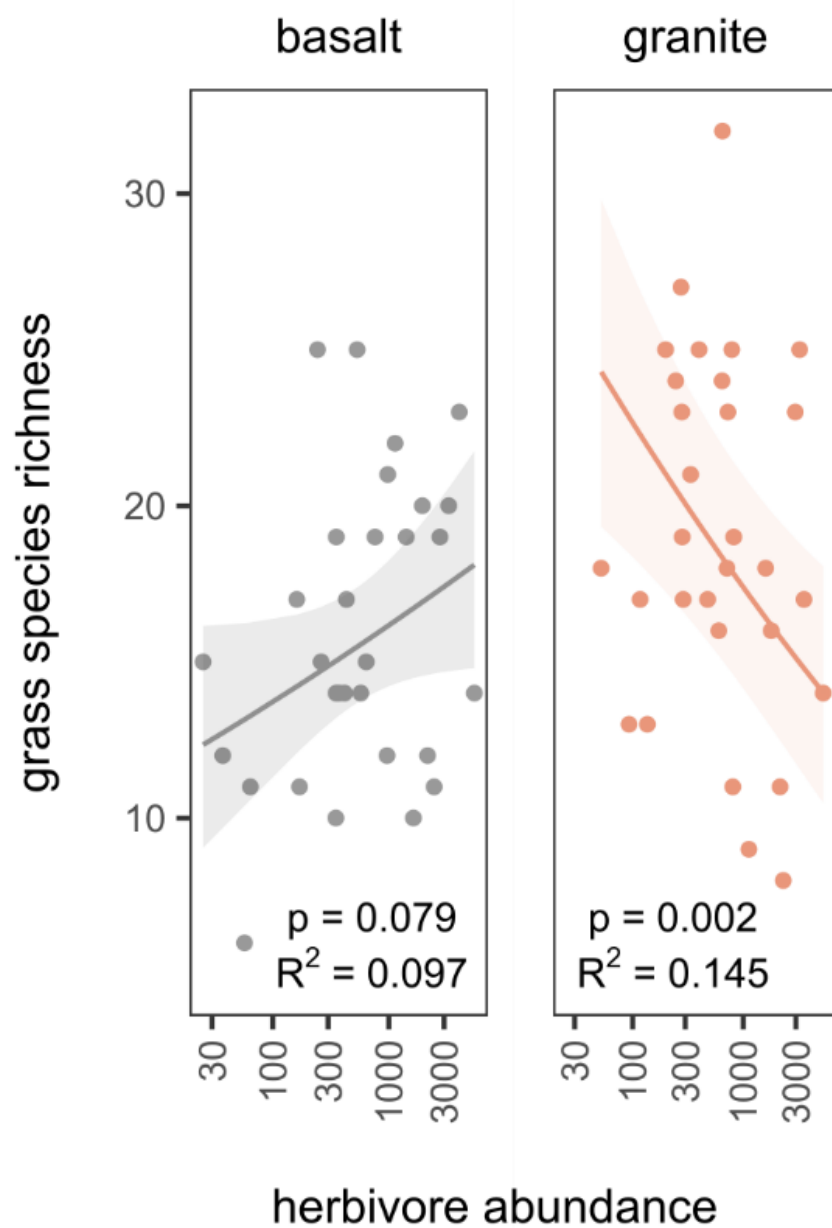
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Fig. 7. Relationship between grass species richness and herbivore abundance shown for different bedrocks. The regression lines show fit of linear mixed-effect models; herbivore abundance was log-transformed. Shaded areas show 95% confidence intervals. Note that x-axis has logarithmic scaling of the values.
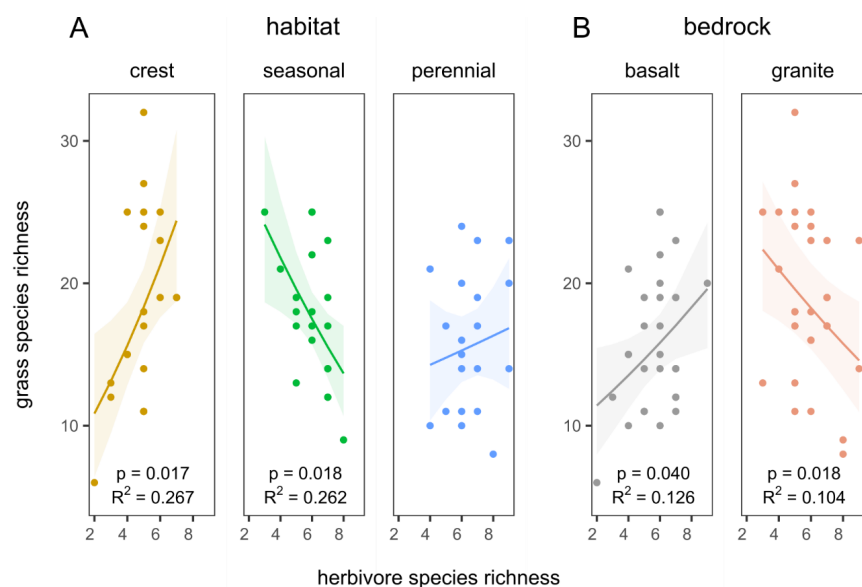
Fig. 8. Relationship between grass species richness and herbivore species richness shown for different habitats (A) and bedrocks (B). The regression lines show fit of linear mixed-effect models; herbivore abundance was log-transformed. Shaded areas show 95% confidence intervals. Relationships whose slope significantly differed from zero are indicated by p-values.