Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes

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Abstract

Though the concept of grazing lawns has already been developed in the early 1970s the mechanisms and conditions that create these lawns are still poorly understood. There is a need for more experimental studies in natural environments. Past studies have suggested that an increased nutrient input induces lawn formation in combination with grazing by unselective herbivores. We argue that these ideas lack a spatial component. Using recent ideas that link self-organized patchiness to catastrophic shifts, we hypothesize that an increased nutrient input indeed promotes grazing lawn development but only after a disturbance above a certain threshold spatial resolution. We developed an experiment to test this hypothesis. In a diverse South African savanna we mowed short grass patches with different spatial resolution in formerly tall grassland and increased nutrient input of half of these plots. We stopped the treatments after two years, but continued monitoring the vegetation height and composition during the following two years. Grazing kept the vegetation short in the coarser, fertilized plots, while the grasses grew out toward their initial height in the finer grained and unfertilized plots. Moreover, stoloniferous lawn-forming grasses strongly increased in cover in the plots with an increased nutrient input but only above a certain threshold resolution. These insights provide a new spatial dimension to the concept of grazing lawn formation, and help to understand how vegetation heterogeneity in grassland ecosystems is created and maintained by herbivores.
Introduction

The grazing lawn concept was first formulated in the early 1970s (Bell 1971), after which McNaughton (1984) formally defined and further developed it as the co-evolution between herds of grazing animals and plant form. Central to this idea is the positive feedback between herbivore consumption and the availability of their food. Several studies suggested that herbivores can increase both the quality of their food by enhancing the nitrogen content of the grasses they graze (McNaughton 1979; Coppock et al. 1983a; Detling and Painter 1983; Ruess et al. 1983) and the availability of their food by accelerating primary production of the grazed vegetation (McNaughton 1976; Cargill and Jefferies 1984; Hik and Jefferies 1990; Ruess et al. 1997). Furthermore, grazers regularly influence plant community composition (Augustine and McNaughton 1998; Olff and Ritchie 1998), and induce changes in nutrient cycling (Holland and Detling 1990; McNaughton et al. 1997; Bakker et al. 2004), which both may affect plant productivity and quality.

The importance of grazing lawns in plant-herbivore interactions is widely recognized in systems ranging from tropical savannas to arctic tundra (Bell 1971; Coppock et al. 1983b; McNaughton 1984; Person et al. 2003). Studies in these systems generally focused on the role of lawns in the temporal dynamics of herbivore populations (Wilmshurst et al. 1999; Person et al. 2003). However, grazing lawns are also a critical component of small-scale spatial heterogeneity in grasslands, characterized by alternating patches of short and tall grass (Owen-Smith 2004). Next to the influence on the foraging behavior of large herbivores (Hester and Baillie 1998; Hester et al. 1999; Wallis de Vries et al. 1999) this small-scale heterogeneity might also mediate resource partitioning among large grazers (Ritchie and Olff 1999, Cromsigt and Olff in press) and hence contribute to their coexistence. Cromsigt and Olff (in press) indeed showed experimentally that differences in the size of short grass patches might promote spatial resource partitioning amongst large African grazers.

While the importance of grazing lawns in temporal and spatial dynamics of herbivore communities is increasingly recognized, we know much less about the mechanisms and conditions that create these lawns. Some work has suggested that grazing lawn distribution on a landscape scale is largely shaped by spatial differences in abiotic factors, like soil types, precipitation, altitude and fire (Bell 1971; McNaughton 1983a; East 1984; Archibald et al. 2005). An increased nutrient input has been argued to induce lawn formation on a more local scale (Ruess and McNaughton 1984; Day and Detling 1990). When nutrient availability is high lawn grasses show compensatory growth in response to grazing (McNaughton 1983b; Augustine and McNaughton 1998). Moreover, Huisman and Olff (1998) show that grazing by unselective herbivores may prevent bunch grasses from out shading the shorter lawn species. While unselective grazing of bunch grasses combined with an increased nutrient input might be essential processes that explain how lawn grasses replace bunch grasses, these mechanisms do not clearly link processes to spatial
scale making it difficult to explain observed small-scale spatial patterns of lawn and bunch grass patches.

Recent ideas that link self-organized patchiness to catastrophic shifts in vegetation patterns (HilleRisLambers et al. 2001; Rietkerk et al. 2004) provide a useful framework for thinking about how grazing can induce small-scale lawn-bunch mosaics. These studies suggest that the crucial positive feedback control between consumers and resources that underlies shifts between vegetation patterns is scale-dependent. In this study, we hypothesize that such a scale-dependent feedback plays an important role in grazing lawn formation and in the creation of lawn-bunch mosaics in savanna grasslands. We suggest that an increased nutrient input induces a positive feedback between grazing and grazing lawn formation, but only after a disturbance coarser than a certain threshold spatial resolution. Cromsigt and Olff (in press) showed that grazing intensity disproportionately increased if short grass patches were less fragmented (coarser resolution). Following this result we suggest that at resolutions finer than a threshold resolution grazing intensity is too low for a positive feedback to come into force, despite an increased nutrient input. Disturbances, ranging from local to landscape scale, typically structure savanna systems (Van Langevelde et al. 2003, Gillson 2004). On the local-scale of grassland mosaic formation we can identify fine-scale disturbances, such as small termite mounds, and more coarse scale disturbances, such as rhino middens and wallows (Fig. 1). These coarse-scale disturbances are typically caused by megaherbivores, like white and black rhino or hippo (Owen-Smith 1988, Cumming and Cumming 2003, Hobbs and Searl 2005). Both fine and

![Figure 1 - Examples of fine scale (small termite mounds on the left-hand side) and coarse scale (rhino midden) disturbances in savanna grassland systems. The disturbances are characterized by locally opening up the bunch grass vegetation and increasing nutrient input. Grazing intensity, however, is too low in the fine scale disturbance plots to keep bunch grass short, in contrast with the coarser scale disturbance, where bunch grass is kept short around the disturbance.](image)

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**Figure 1** - Examples of fine scale (small termite mounds on the left-hand side) and coarse scale (rhino midden) disturbances in savanna grassland systems. The disturbances are characterized by locally opening up the bunch grass vegetation and increasing nutrient input. Grazing intensity, however, is too low in the fine scale disturbance plots to keep bunch grass short, in contrast with the coarser scale disturbance, where bunch grass is kept short around the disturbance.
coarse scale disturbances open up the bunch grassland and for a prolonged period of time trample and graze down the bunch vegetation. Moreover, both disturbances are also characterized by an increased nutrient input, local nutrient concentration in case of termites (Jones 1990) and increased urine and dung input in case of megaherbivore middens and wallows. However, we hypothesize that only at the coarser scale resolution grazing pressure will be high enough to promote consumer-resource feedback that leads to grazing lawn development.

We tested this idea in Hluhluwe-iMfolozi Park, South Africa by creating disturbances with different spatial resolution by regularly mowing plots of different sizes in bush-encroached, tall grass vegetation and enhancing the nutrient input to half of these plots with artificial fertilizer. We followed the vegetation development over more than 3 years to see whether an increased nutrient input induced lawn formation and to what extent this process depended on the spatial scale of disturbed patches.

Methods

Study site
The study was performed in Hluhluwe-iMfolozi Park (HiP), a small (90,000 ha) but diverse protected area in Kwazulu-Natal, South Africa. This reserve is situated in the southern African savanna biome, with vegetation types ranging from open grasslands to closed Acacia and broad-leaved woodlands (Whateley and Porter 1983). The mean annual rainfall depends on altitude, ranging from 985 mm in the high altitude regions to 650 mm in the lower areas and mainly falls between October and March. Daily maximum temperatures range from 13 °C to 35 °C. The reserve is of strong conservation importance because it hosts a rich and complete set of indigenous large herbivores and carnivores.

The park is characterized by highly heterogeneous grasslands, in which tall bunch grass (tussock forming) communities of Sporobolus pyramidalis, Eragrostis curvula and Themeda triandra are interspersed with short lawn-forming (stoloniferous) communities of Digitaria longiflora, Urochloa mosambicensis, Dactyloctenium australe and Sporobolus nitens. These grazing lawns are important because they support high numbers and a high diversity of herbivore species.

Experimental design
In 2000 we created an experimental mosaic of short grass patches in open savanna woodland, dominated by the tall grasses Eragrostis curvula (Schrad.) Nees, Panicum maximum Jacq. and Sporobolus pyramidalis with bush encroachment of Dichrostachys cinerea (L.) Wight & Arn., Acacia spp and Gymnosporia senegalensis Loes.. Subsequently, we maintained the short patches with a lawn mower at a height of around 5 cm, in contrast with the surrounding tall grass matrix of around 25 cm. The experimental mosaic consisted of short grass patches of different size and with varying nutrient input. In a basic layout of adjacent 8x8 m treatment plots, short grass patches were created with a size of 1x1,
2x2, 4x4 and 8x8 meter (Fig. 2). We created 9 1x1 m, 4 2x2 m, 2 4x4 m and 1 8x8 m subplots per treatment plot to simulate disturbances at different scales. We applied slow-release NPK-fertilizer four times a year to half of the mown plots to create differences in nutrient input rate between patches. To patches of all sizes we applied 12 gram N, 3.9 gram P, 19.8 gram K, 22.1 gram Ca and 18.8 gram S per m² of short grass per year. Each combination of patch size and fertilization was replicated 4 times. This resulted in 32 8x8 m treatment plots (Fig. 2). Surrounding the 32 treatment plots we created 8 control plots of 1x1 meter. These control plots were covered by a cage of chicken mesh to exclude all mammalian herbivores. Half of these plots were fertilized. The control plots were mown and fertilized at the same time and in the same way as the 32 treatment plots. Because the control plots were protected from grazing we will refer to them as mown ungrazed plots, compared with the mown grazed (treatment) plots and the unmown but potentially grazed matrix vegetation. The mowing treatment was applied during one year. The fertilization treatment was applied for around two years. We measured vegetation characteristics to study how patch size and fertilization treatment affected the grazing – vegetation feedback after we stopped the initial mowing disturbance.

**Figure 2** - The experimental layout, existing of 8 x 8 meter treatment plots with a combination of two treatments (patch size and fertilizer application). Manipulated patches are shown in black and grey; the shaded background represents the untreated matrix of tall grass and shrubs. Half of the plots were fertilized (black) and the other half remained unfertilized (grey). Within each 8x 8 m plot, we created 4 different levels of spatial scale of short grass patches: 9 patches of 1 x 1m (G1), 4 patches of 2 x 2 m (G2), 2 patches of 4 x 4 meter patches (G4) and 1 patch of 8 x 8 meter (G8).
Vegetation characterization

Once a month we measured the height of the vegetation with a round disc of 46 cm width and a weight of approximately 460 grams. The disc, with a hole in the middle, was dropped along a pole with a height scale in cm. The height was measured to the nearest cm at 1 point in the middle of the 1x1 m (also in the control plots) and 2x2 m subplots. In the 4x4 m and 8x8 m subplots the vegetation height was measured in a grid of points 1 m apart and 1 m from the edge of the patch, resulting in 9 and 49 points for the two treatments respectively.

We determined the species composition of all the treatment plots January 2001 and July 2004 within 2 by 2 meter quadrates in the middle of each plot. We identified all grass species and estimated their percentage projected cover visually using the Londo scale (Londo 1976). For the 4x4 m and 2x2 m treatment plots, the quadrat was placed in the same subplot for both years. For the 1x1 m treatment plots, 4 subplots were selected (the same ones for both years) to get a total survey area of 2 by 2 meter. We identified species and estimated their cover for each of the 4 subplots and averaged the 4 cover estimates per species before further analysis.

Using the same method, we also measured the species composition in the control plots and in the matrix. For the matrix we measured the species composition in the 2x2 m matrix subplots in A4, C1, F3 and G2 (see Fig. 2), where the same subplots were measured in both years.

Animal visitation

We directly observed the visitation of different grazer species to the different treatments. The experimental site was situated on a hill slope. From the opposite hillside (about 450 meters from the experiment) there was an open view on the experimental site. From October 2000 up to November 2002, we observed for a total of 903 hours during separate 3 hour observation periods. For each observation every minute the position of the animal was recorded (according to the grid of 8x8 m cells shown in figure 2) together with the species and its behavior. Behavior was separated in two classes: grazing and other. For a full description of the methods see chapter 5.

Soil parameters

We took soil samples in the treatment plots as well as in the surrounding matrix in November 2004 to test if there were any long-term treatment effects on the soil. Per treatment plot 5 samples were taken randomly distributed over the mown subplots and 5 were taken randomly distributed in the surrounding matrix of each treatment plot. Samples were taken with a 5 cm diameter soil core from the upper 10 cm of the soil and dried at 105 °C. The 5 samples were pooled and 1 mixed sample was taken to the lab for the treatment plots and matrix separately, resulting in 64 samples. We ground the samples and analyzed them for total C and total N (using the Dumas dry combustion method), texture in three fractions (clay, silt and sand), electric conductivity (EC), pH (using a KCL solution) and extractable concentrations of Na, Ca, Mg and K. For a detailed description of the used methods see Manson and Roberts (2000).
Data analysis

Vegetation development

We first aggregated the vegetation height data as the average of the pseudo replicates per 8x8m treatment plot per measuring date. These averages were again aggregated as the average per treatment plot per season per year, dividing a year in 4 seasons; late wet (lw, January to March), early dry (ed, April to June), late dry (ld, July to September) and early wet (ew, October to December). These season classes were based on long-term rainfall data that are available for HiP. First of all, we wanted to know how the height in the ungrazed, control plots developed relative to the grazed plots. These ungrazed plots only had one size (1x1 m) and we, therefore, excluded patch size in this analysis. We tested for a difference between the ungrazed and grazed plots with a univariate analysis of variance with the factor grazing and fertilization. Time (season periods numbered chronologically) was included as a covariate in this model to account for the fact that height showed a long-term increase over the course of the experiment. Subsequently, we excluded the ungrazed plots to test how patch size and fertilization affected vegetation height in our grazed experimental plots with a univariate analysis of variance with fertilization and patch size as factors. Again we included season as a covariate in the model. After the identification we divided the grass species in two functional types; stoloniferous, lawn-forming species ('lawn grasses') and species with a caespitose growth form ('bunch grasses'). Three lawn-forming species were observed in the experiment; Digitaria longiflora, Dactyloctenium australe and Sporobolus nitens. For each treatment plot and for the matrix and control plots we summed the % cover of all lawn species into a percentage lawn cover for each plot. Using a univariate analysis of variance, we tested the effect of year, fertilization and size (as fixed factors) on the total cover of lawn grasses. In this analysis we included the matrix and control plots as a level in the fixed factor patch size.

Total grazing pressure

Before further analysis we aggregated the total number of observed grazing minutes as the sum of observed grazing minutes over all herbivore species per 8x8m treatment plot. A detailed analysis per species is presented in chapter 5. We calculated grazing pressure per square meter by dividing the aggregated sum of grazing minutes per plot by the total area of short grass in a plot (9, 16, 32 or 64 m²). Finally we calculated an average observed grazing pressure per week by dividing the minutes per square meter per plot by the total of 903 observation hours and multiplying these values with 168 hours in a week. We tested whether a possible generic effect of patch size (1, 4, 16 or 64 m²) on grazing pressure depended on fertilization using a univariate analysis of variance with the logarithm of patch size as a covariate and fertilization as a fixed factor. The log of patch size was used to make the distance between patch sizes equal and allow a linear regression between grazing pressure and log (size).
Soil parameters

We tested for an effect of treatments on all soil parameters using a univariate analysis of variance with the fixed factors, patch size and fertilization. To test whether soil parameter values differed between matrix and experimental plots we divided the data in three groups; matrix, unfertilized mown plots, fertilized mown plots. Using a one-way analysis of variance followed by Student-Newman-Keuls \textit{a posteriori} contrasts we tested for differences between these groups.

Results

Vegetation development

The temporal dynamics in vegetation height depended on the presence of grazers. Vegetation height increased more in the ungrazed plots than in the grazed plots (Fig. 3, interaction grazing x time, $F_{1,554} = 65.795$, $P < 0.01$). Vegetation height increased faster in the unfertilized plots than in the fertilized plots (interaction fertilization x time, $F_{1,435} = 14.155$, $P < 0.01$). Furthermore height increased more in the 1x1 m patches than in the larger patch sizes (interaction size x time, $F_{3,435} = 3.837$, $P = 0.01$). The effect of patch size also depended on fertilization (interaction fertilization x size, $F_{3,435} = 8.329$, $P < 0.01$, Fig. 4 shows Student-Newman-Keuls \textit{a posteriori} results). We included log (patch size) as a covariate in the analysis of variance model, with fertilization as a fixed factor, to test the generic effect of patch size that can be seen in figure 4. Vegetation height decreased with increasing patch size in the fertilized plots, while the height was constant for the different sizes in the unfertilized plots (interaction fertilization x log (size), $F_{2,445} = 12.856$, $P < 0.01$).

Figure 3 - Mean vegetation height (- 1 s.e.) over time for fertilized (A) and unfertilized (B) plots and different levels of size of short grass patches, including control plots that were protected from grazing. Height data is aggregated as the average per treatment per season per year, according to the seasons that are explained in the methods section. The experiment was burnt just after it was created, half a year before we started height measurements and once again at the end of the experiment before our final height measurement.
The effect of patch size on cover of lawn grasses depended on the year (Fig. 5, interaction size × year, $F_{5, 66} = 7.354$, $P < 0.01$). In 2001 there was no difference in the cover of lawn grass between the different patch sizes (including the matrix and control) and the cover was close to 0 for all these treatments (Fig. 5A). In 2004 the cover of lawn grasses had increased in the 8x8 m plots with respect to the other patch sizes (including the matrix and control) (Fig. 5B). The effect of patch size on cover of lawn grass also seemed to depend on fertilization, but this interaction was not significant (interaction fertilization × size, $F_{4, 66} = 2.197$, $P = 0.079$, also see Fig. 5B). For the 2004 data we therefore included log (patch size) as a covariate in the analysis of variance model to test if the generic effect of patch size depended on

Figure 4 - Mean vegetation height (+ 1 s.e.) for different levels of size of short grass patches (see fig. 2) and fertilizer application. Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance).

Figure 5 - Mean percentage cover (+ 1 s.e.) of lawn grass species in the control plots, the matrix vegetation and the different levels of size of short grass patches and fertilizer application. In the matrix vegetation we did not have fertilized plots. The results are shown for 2001 (A) and 2004 (B). Different letters indicate a significant difference between treatments ($P < 0.05$, Student-Newman-Keuls test after two-way analysis of variance).
fertilization. In 2004 the increase in lawn cover was indeed larger in the fertilized plots than in the unfertilized plots (interaction fertilization × log (size), $F_{2, 29} = 6.898, P = 0.004$).

Total grazing pressure

The following herbivore species were observed grazing in the short subplots (within brackets the number of grazing minutes for the species as a % of total observed grazing minutes): warthog (*Phacochoerus aethiopicus*, 50%), impala (*Aepyceros melampus*, 33%), zebra (*Equus burchelli*, 12.3%), white Rhino (*Ceratotherium simum*, 1.9%), nyala (*Tragelaphus angasi*, 1.9%), wildebeest (*Connochaetes taurinus*, 0.4%), buffalo (*Syncerus caffer*, 0.3%) and waterbuck (*Kobus ellipsiprymnus*, 0.2%). Total grazing pressure of all species together increased with patch size in the fertilized plots in contrast with the unfertilized plots where it remained constant (Fig. 6, interaction fertilization × log (size); $F_{2, 29} = 18.665, P < 0.01$, log (size) as covariate).

Soil parameters

The fertilized plots had a higher electrical conductivity (EC) than the unfertilized plots ($F_{1, 24} = 8.395, P = 0.008$), as well as higher concentration of extractable Ca ($F_{1, 24} = 8.585, P < 0.01$), Mg ($F_{1, 24} = 5.463, P = 0.028$) and K ($F_{1, 24} = 25.542, P < 0.01$). The pH was significantly lower in the fertilized plots than in the unfertilized plots ($F_{1, 24} = 5.177, P = 0.032$). The soil of the matrix vegetation did not differ from the mown unfertilized plots ($P > 0.05$), except for the potassium concentration. The soil concentration of K was higher in the matrix than in the unfertilized mown plots, but lower than in the fertilized mown plots ($F_{2, 61} = 12.377, P < 0.01$). Total C and N content of the soil, soil texture and soil sodium concentration were not significantly different between any of the size and fertilization treatments ($P > 0.05$).
Discussion

The results showed that in our study site enhanced nutrient availability induced the formation of grazing lawns, but only above a certain threshold disturbance resolution. After we stopped mowing the vegetation height started increasing, but the strength of this increase depended on whether the plots were grazed and on the resolution and nutrient status of the plots. The height increased faster in the unfertilized plots with finer resolution. Grazing seemed to keep grass short at grazing lawn level in the coarser, fertilized plots (4x4 and 8x8 m). Two and a half years after we had stopped mowing a shift in grass community composition had taken place in the least-fragmented fertilized plots, showing a strong increase in the cover of lawn species. Overall grazing pressure was also significantly higher in those plots. In conclusion, as hypothesized, our results suggest that the positive feedback between grazing and grazing lawn formation depends on nutrient status as well as the resolution of the initial disturbance.

We showed that colonization of stoloniferous lawn grass species was most clear in the fertilized 8x8 m plots (Fig. 5B), where grazing pressure increased most strongly (Fig. 6). This result supports the idea that lawn grasses can colonize under circumstances of high nutrient availability in combination with a high grazing pressure because these grasses show compensatory growth in response to grazing in contrast with the grazing sensitive bunch species (McNaughton 1983b; Augustine and McNaughton 1998). The evolution of grazing tolerance in grass species is still under debate. It has been attributed to convergent selection processes to cope with drought, which results in traits that also make plants more tolerant to grazing, e.g. basal meristems and short growth-form (Milchunas et al. 1988; Augustine and McNaughton 1998). In this respect it is interesting to note that many lawn-forming grasses in Africa are halophytes (i.e., adapted to physiological drought due to high salinity) and occur in semi-dry to dry areas.

Our results suggest the existence of two types of lawns; patches of potentially tall bunch grass that are temporarily kept short (temporal lawns) and patches of short, stoloniferous grazing tolerant lawn grass species (long-term lawns). Field examples of temporal lawns are patches of Themeda triandra that are grazed and kept short for some time period by buffalo and white rhino in Hluhluwe-imfolozi Game Reserve (Owen-Smith 1988 and personal observation). Our results show that bunch grass patches that are grazed short can remain in a temporal lawn state for a considerable period (Fig. 3A, 3 years) before a community shift takes place to a compositional lawn. Archibald and Bond (2003) argued that a grazed patch needs to stay short for >4 years to be colonized by stoloniferous lawn grasses. Our results indicate that this process can be somewhat faster, because lawns had formed within 4 years after we created the short grass patches. Moreover, this community shift seems to depend on scale of the disturbance and only occurs in the coarser grain patches whereas in the finer grained 4x4 and 2x2 patches the vegetation remains in a structural lawn state. We hypothesize that the
temporal lawns are less stable than the long-term lawns, because the bunch growth form will directly grow back to a tall state again if grazing pressure decreases or e.g. rainfall increases while stoloniferous species will remain short for a considerable period even when grazing pressure decreases. The latter is in fact observed in exclosure experiments (H. Olff and W.J. Bond, personal observations). In this respect, Archibald and Bond (2003) developed an interesting theory on the effect of fire frequency on the persistence of grazed patches and the community shift to long-term grazing lawns. They hypothesize that frequent fires create a more homogenous grazing pressure; hereby decreasing the pressure on grazed patches and preventing formation of long-term grazing lawns (see also Archibald et al. 2005).

The main driver behind lawn formation in our study was grazing in interaction with increased soil fertility. In the east African savanna systems short grasslands support dense herds of medium-sized grazers such as wildebeest, zebra and gazelles (McNaughton 1984). Owen-Smith (1988), however, suggested that only the megagrazers, white rhino and hippo, can create real permanent grazing lawns. He acknowledges that dense herds of e.g. wildebeest in the Serengeti transform tall grasslands into short grass but argues that their intense grazing is too temporal to induce changes in grassland composition. In our study warthog were responsible for 50% of the grazing pressure (number of observed grazing minutes) and impala 33%. In the fertilized 8x8 plots, where grazing lawns developed, warthog were responsible for 65% of the observed time grazed and impala for 26%, while white rhino only contributed 1.5%. I.e. in our study warthog and impala seemed to be mainly responsible for maintaining structural lawns and promoting the colonization of stoloniferous lawn grasses. So the fact that white rhino is considered to be the main driver behind creating grazing lawns in Southern Africa savannas (Owen-Smith 1988), might very well underestimate the role of the smaller grazers, like warthog. Rather, we propose that a diverse community of large and small herbivores promotes lawn formation, where megaherbivores are responsible for the first disturbance but smaller species (help) keep the grass short and promote colonization of stoloniferous grazing lawn species.

We choose two contrasting disturbance types to illustrate our hypothesis (Fig. 1). In reality there are many more disturbance types that could possibly replace or complement our examples. Large termite mounds, for example, could play the same role as middens or wallows. In fact, studies indicated the role of these large mounds as grazing hotspots (Holdo and McDowell 2004, Mobæk et al. 2005). More studies are needed that quantify these small-scale disturbances in savanna grasslands to get better insight in the processes that drive grazing lawn formation. Our results suggest that the spatial resolution of the disturbance is an important characteristic that should be measured.

In conclusion, our results suggest that scale-dependent foraging decisions influence formation of local lawn-bunch mosaics. On other spatial scales other factors can determine lawn grass distribution. Therefore it is important to see our
results as part of a nested design of mechanisms that create lawn-bunch patterns, where our study gives insight in within-grassland pattern formation. On landscape scales the catena position, distance to water and variation in soil type have been argued to influence lawn formation (Bell 1971; Swemmer 1998). On an even higher regional scale potential occurrence of grazing lawns is probably determined by parent material, rainfall, herbivore geographic distributions, and possibly fire regimes (East 1984; Archibald et al. 2005).

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