1. FINAL PUBLISHABLE SUMMARY REPORT

Based at the Centre for Ecological and Evolutionary Synthesis, Department of Biology of the University of Oslo, SPHERE explored the role of spatial heterogeneity of resources as a mediator of large herbivore population stability in African savannas. Recent studies show that the increased variability in rainfall that is predicted under local climate change scenarios and the resulting temporal variability in resource availability might lead to severe declines in African herbivore populations. However, new theory predicts that spatial heterogeneity of resources can act as a buffer against such temporal heterogeneity. Up to recently this theory awaited empirical testing. African savanna grasslands are an ideal system to test this theory, with characteristic grazing lawns as a clearly visible aspect of spatial resource heterogeneity. Grazing lawns represent clearly confined patches of specific grazing-tolerant grass species with high nutrient quality. As such grazing lawns are nutrient hotspots surrounded by grassland of relatively low food quality. Several mammalian grazer species concentrate foraging in these lawns but it is unclear how lawn abundance and spatial distribution affects grazer population dynamics on a larger scale. We used this system to investigate the hypothesized effect of resource heterogeneity on population stability in two protected savanna reserves in South Africa, Hluhluwe-iMfolozi Park (HiP) and Kruger National Park (KNP). We choose these two reserves because they lie at different ends of the heterogeneity continuum. Both parks host a complete and similar set of indigenous grazer species and have comparable variation in rainfall and general abiotics. However, there is a strong contrast between both parks in terms of size, herbivore density and resource heterogeneity (availability and distribution of lawns). HiP is a small reserve, 900 km^2, with high overall grazer densities (> 8000 kg/km^2) and KNP a large reserve, 20,000 km^2, with low grazer densities (~ 2000 kg/km^2). HiP is characterized by a very heterogeneous grazing system, where high habitat diversity is coupled with small-scale (~ 10-100 m) grassland patch diversity (grazing lawns). KNP, on the other hand, is much more homogeneous.

The first overall objective was to quantify resource heterogeneity in both reserves in terms of grazing lawn distribution and understand what drives these distribution patterns. We mapped grazing lawn distribution across Hluhluwe-iMfolozi Park on 24 line transects of ~8 kilometre long. In this way we repeated a mapping exercise in 2004. This allowed us to look at factors that drive the distribution and persistence of grazing lawns over time. Grazing lawns were more abundant in the parts of the reserve with relatively low rainfall and in areas with high density of features of white rhino presence (e.g., dung). This confirms previous work that grazing lawns are more likely to develop under relatively low rainfall conditions and that white rhino play a crucial role in creating lawns. Interestingly, our results also indicated that the persistence of grazing lawns was higher close to former boma sites. These boma sites are former cattle kraal sites that were abandoned when the last people were moved from the reserve in the 1960s. Hence, former human land use might be part of the explanation behind the high grassland heterogeneity in HiP. We also mapped grazing lawn distribution in the southern part of KNP. The first preliminary field surveys indicated that the type of grazing lawns, as known from HiP, are hard to find in KNP if present at all. Clear grassland nutrient hotspots, so-called sodic sites, are prevalent in KNP, but it is unclear to what extent they are functionally similar to the grazing lawns in HiP. Current studies suggest that they are more constrained in the landscape by abiotic factors than the lawns in HiP. As mentioned, the lawns in HiP seem to be for a large part created by white rhino. In contrast to HiP, white rhino went extinct in KNP towards the end of the 19th century and were only fairly recently re-introduced into KNP (1960s). This might explain why rhino-mediated grassland heterogeneity (especially grazing lawns) are not so obvious in KNP. Hence, before being able to compare population-level response of herbivores to variation in similar nutrient hotspots between both parks, it

was necessary to assess whether rhino-created grazing lawns similar to the ones in HiP are present in Kruger. Therefore, we walked transects in KNP in areas with high versus low rhino densities, and long versus recent colonization history and mapped structural heterogeneity in terms of variation in grass height, and presence of grazing lawns. Preliminary results suggest that there are still almost no rhino created grazing lawns in KNP but structural heterogeneity seems to be higher in grasslands with high rhino density and long colonization density. Final results should confirm this and will also give more insight in the recolonization patterns of KNP by white rhino and the factors that drive these patterns.

The second overall objective was linking lawn distribution and abundance, as a proxy for grassland resource heterogeneity, to herbivore population dynamics. Because of the differences in the type of heterogeneity between HiP and KNP we decided to limit this objective to the HiP system. We collected long-term population census data from the park of 12 large mammalian herbivores resulting in biannual data from 1986 up to and including 2010. We are now quantifying temporal variation in population dynamics for these 12 species to test if variation is reduced if proportion of grazing lawn in an area increases. According to our original hypothesis this relation should be especially strong for smaller, ruminant, grazers that are more limited by food quality. Although it is too early to present final results, very preliminary analyses indeed indicate that populations of small to medium-sized grazers, impala and wildebeest, are more stable (lower CV of census data) in areas with high % cover of grazing lawns, while populations of a large bulk grazer, African buffalo, are in fact less stable in these areas (higher CV). Results for non-grazing herbivores are mixed. Dynamics of Nyala, more a mixed-feeder, are also more stable in areas with high lawn abundance. Population dynamics of typical browsers, such as Giraffe, is not related to grazing lawn presence. We are currently checking to what extent these species indeed utilize grazing lawns as important resource areas. We installed camera traps on 10 grazing lawn plots and followed visitation by herbivores to these plots for a full year. First analyses show that lawns were especially visited by white rhino, but also impala and warthog. White rhino spent by far the largest amount of time grazing in the lawn plots. This latter result confirms that white rhino are important for creating and maintaining the lawns.

Concluding, the final results of SPHERE will contribute to our understanding of the importance of resource heterogeneity in savanna grasslands, and especially the role of grazing lawns. Our results create more insight in the factors that drive the creation and maintenance of resource hotspots in savanna grasslands. Moreover, they will highlight for what herbivore species they are especially important and how such resource hotspots affect population performance of those species. As such SPHERE importantly contributes to management of large herbivore populations in African savanna reserves, more specifically what drives their population numbers. The results are also of specific concern for both our study sites. Conservation management in HiP has increased concerns about the decline of grazing lawns in the park during recent years. Our results add to understanding what causes this decline. In KNP our results are important for the upcoming discussion on the potential impact of the increasing white rhino numbers in the park. We, therefore, expect SPHERE will continue to have important societal implications.

The project was very successful in it’s training and re-integration objectives of the fellow. The fellow significantly increased his skills in advanced statistics and writing for high-impact journals. The project already resulted in two peer-reviewed publications, 3 others are in review, and several in preparation. The fellow participated in several international conferences and workshops and hugely increased his scientific network. The successful re-integration of the fellow is exemplified by the fact that he has been offered an Assistant Professorship at the Swedish University of Agricultural Sciences in Umeå, Sweden.