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Author

Greve, Michelle

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commentary

Tree–grass ratios in savannas: challenging paradigms

One of the greatest challenges for plant ecologists is to ascertain which factors allow trees and grasses to co-exist in savannas (Moustakas et al. 2010; Figure 1). Two major hypotheses that address this issue have been proposed (Figure 2). The resource-based hypothesis states that grasses and trees have different root depths, and thus occupy different competitive niches (Scholes and Archer 1997). More recently, various versions of the disturbance hypothesis have been formulated, which postulate that disturbances such as fires and herbivory are major factors restricting the growth of trees (Higgins et al. 2000, Sankaran et al. 2005). In both hypotheses, rainfall is thought to benefit trees. Higher rainfall should cause deeper water infiltration, thereby benefitting the deeper-lying roots of trees and allowing them to grow faster and outcompete grasses by shading. Disturbances that reduce woody cover, such as fires, would explain lower woody cover in relatively high-rainfall areas.

Recently, these ideas have been the focus of a number of macroecological studies, which have found some support for the positive influence of rainfall, and the negative influence of disturbances, on woody cover. In their seminal pa-

per, Sankaran et al. (2005) showed that, for 854 sites across Africa, maximum woody cover increased with precipitation at sites with lower levels of precipitation (< 650 mm/year), but showed no relationship with precipitation at higher rainfall levels. They thus suggested that arid and semi-arid savannas are ‘stable’: here, even in the absence of disturbances, trees and grasses would continue to coexist. In contrast, in higher rainfall (mesic) savannas, tree–grass coexistence would be facilitated by disturbances such as fire and herbivory; in the absence of disturbances, high-rainfall savannas would be expected to become forests. Other continental studies have corroborated these findings (Bucini and Hanan 2007, Sankaran et al. 2008, Staver et al. 2011). These studies have contributed to the idea that, at continental scale, rainfall, with the mediating effect of disturbances, plays a pivotal role in the tree–grass ratio of savannas.

However, two studies that were recently published have challenged various aspects of these two hypotheses. February et al. (2013) set up experimental plots to assess the effect of rainfall manipulation on tree growth in a nutrient-poor mesic and a nutrient-rich semi-arid savanna



Figure 1. What determines tree–grass ratios in tropical savannas? (Photograph taken at Weenen Game Reserve, South Africa).

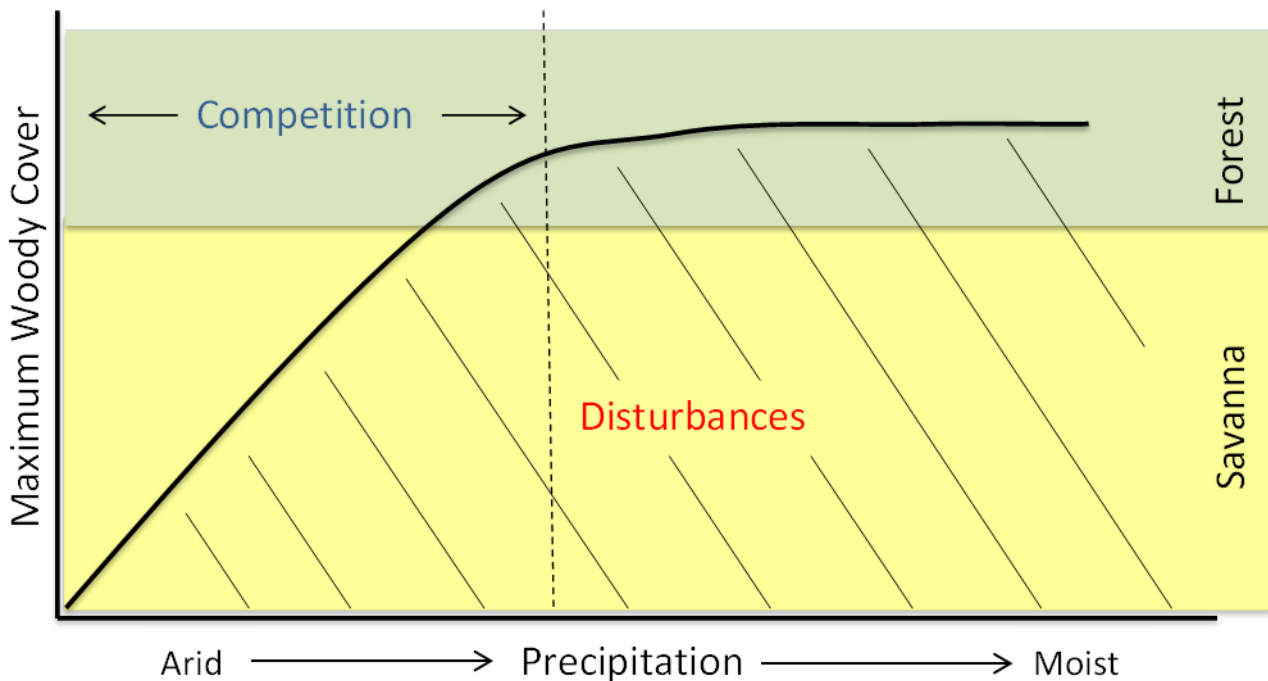


Figure 2. Illustration of resource-limitation and disturbance hypotheses. The trend line describes the maximum woody cover at increasing levels of precipitation. Resource-limitation hypothesis: trees and grasses inhabit different rooting zones. Grasses, with shallow roots, are better competitors in arid savannas than trees are. In moister areas, water percolates deeper into the soil and trees become more dominant. Disturbance hypothesis: disturbances such as fire and herbivory decrease woody cover at given precipitation levels (hatched area). According to the disturbance hypothesis, savannas at high precipitation levels (to the right of the stippled line) would become forests in the absence of disturbances.

from which large herbivores were excluded. In their experiment, some trees were given more water, less water or allowed to grow at natural rainfall. In addition, the effect of tree–grass competition on the growth of trees was measured by removing grass from some plots, and leaving the grass to grow on others. The growth of the trees and, in plots where grass had not been removed, the grasses was monitored over four years.

Surprisingly, rainfall manipulation had no effect on tree growth in either of the savannas, while it benefitted grass growth. This was contrary to what was expected from both the resource-based and disturbance hypothesis—that higher rainfall would increase water percolation into the soils and thus provide a competitive advantage for trees. Their finding that grass removal from plots increased the growth rate of trees furthermore challenged the idea that trees and grasses occupy different competitive rooting zones (though evidence for grass–tree competition had emerged previously, e.g. Riginos and Young 2007, February and Higgins 2010).

Bertram and Dewar (in press) approached the issue of savanna tree–grass ratios from a theoretical, rather than experimental, angle. Using maximum entropy techniques, they modelled tree–grass ratios in savannas based on assumptions about the evapotranspiratory requirements of the different components of savannas. Based on prior knowledge, maximum entropy techniques produce least-biased probability distributions of the modelled entity. In Bertram and Dewar’s (in press) model, in which evapotranspiratory requirements were assumed to decrease from trees to grasses to bare ground, the probability distribution of different tree–grass ratios measured across African, Australian and South American savannas was approximated by the stochastic processes of the models with surprising precision. Contrary to the disturbance hypothesis, they thus concluded that disturbances are not essential for tree–grass coexistence in mesic savannas: in high-rainfall areas, stochastic processes alone were sufficient to predict the existence of savannas.

It appears that the jury is still out as to what

precisely determines tree–grass coexistence in savannas. However, the question of what determines the savanna tree–grass ratio is increasingly becoming an exemplary field where ideas are being tested at a variety of spatial and organizational scales. Therefore, hypotheses that might have been widely accepted if only explored at one scale (e.g. disturbance hypothesis at a macro-scale), or using only one method (e.g. correlative studies), can be assessed more holistically. Therein lies a lesson for the field of macroecology and biogeography overall. Though the discipline was pioneered by ecologists with intimate field knowledge, raising questions about large-scale patterns in ecology, macroecology is increasingly being practised by scientists with relatively little understanding of field processes, but with large datasets and powerful techniques to test ideas. Therefore, just as macroecologists have contributed to the field of ecology by demonstrating that processes driving large-scale patterns might differ from local-scale drivers, it remains imperative that ecological hypotheses continue to be tested mechanistically and theoretically, to assess the extent to which mechanisms enjoying empirical support at coarser scales do act at the local level.

Michelle Greve

Department of Plant Science, University of Pretoria,
South Africa. michelle_greve@yahoo.com;
<http://web.up.ac.za/default.asp?ipkCategoryID=22067>

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