

Biodiversity and stability of grassland ecosystem functioning

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Pfisterer and Schmid (2002) report the results of an experiment which they claim provides evidence that plant species richness increases ecosystem productivity and reduces the resistance and resilience of plant biomass production to droughting. However, there are problems with both the design and interpretation of this study, and we believe that there are alternative plausible and simple explanations for their results which do not involve any causative role of plant species diversity.

The problem with the experimental design is that there were at least three factors that covaried with species richness across the experimental diversity gradient; this can be determined by tabulation of species compositional data of the plots used in this experiment and published elsewhere (Diemer et al. 1997) (Table 1). Firstly, the proportion of sown plots which contained nitrogen fixing legumes varied from 0% in the one-species treatment to 100% in the 32-species treatment. Secondly, the size of the total species pool used for the species richness treatments itself varied by over four-fold across the experimental plant species richness gradient. The species pool used for each diversity treatment consists of all the species used in the less diverse treatments, plus additional species. Thirdly, the relative

contribution of the three plant functional groups in the total species pool varied markedly across the different diversity treatments.

Each of these three confounding factors could conceivably contribute to the observed results of an experiment with this type of design. One likely mechanism involves the well known effects of fertilisation by nitrogen fixing legumes on ecosystem productivity whenever they appear in a mixture (Vandermeer 1990). The fact that legumes were present in a greater proportion of plots as plant species increased would in turn lead to a greater productivity on average in species-rich plots through alleviation of nitrogen limitation (Vandermeer 1990). These more productive communities should show higher net transpiration (Arkley 1963) and therefore more complete exhaustion of moisture from the soil. This would result in plants growing in these more productive plots being subjected to a greater soil moisture deficit (Huston 1997) and thus suffering greater loss of yield as a result of the experimental droughting (Arkley 1963, Huston 1997). This simple explanation for the results obtained by Pfisterer and Schmid does not involve any causative role of species richness.

Table 1. Factors that covaried with plant species richness in the experiment reported by Pfisterer and Schmid (2002).

Factors covarying with species richness	Species richness of treatment				
	1	2	4	8	32
Proportion of sown plots containing legumes	0.000*	0.285	0.500	0.600	1.000
Size of total species pool	8	10	16	21	48
Species ratio of grasses:legumes: forbs in total species pool	75:0:25	60:20:20	56:25:19	52:19:29	33:17:50

* Although four plots in this treatment were initially sown with legumes, the vegetation in these plots was all destroyed by fungal infection (Pfisterer and Schmid 2002).

Further, Pfisterer and Schmid do not interpret their results in the context of earlier studies which are very relevant to the issue of how plant species composition and diversity affect the stability (response to drought) of ecosystem functioning (Leps et al. 1982, MacGillivray et al. 1995, Grime et al. 2000, Wardle et al. 2000), even though one of those studies (Wardle et al. 2000) manipulated exactly the same two factors that this study manipulated. These earlier studies point to plant species composition and identity, and not species diversity, as being the primary drivers of ecosystem stability. Our alternative explanations for the results obtained by Pfisterer and Schmid is consistent with this conclusion.

The issue of how plant species diversity influences the stability of ecosystem properties and provides an insurance against external perturbations is an important one, and one that merits attention. We believe that to most effectively address this question requires experimental designs in which the effects of species and functional group identity can be separated from effects of species richness, and in which all component species are presented in replicated monoculture plots.

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