

Untangling the positive and negative effects of shrubs on herbaceous vegetation in drylands

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Abstract Woody vegetation, as an ecosystem engineer, can modulate the landscape such that the levels of resources in its vicinity undergo positive and negative changes as far as the herbaceous vegetation is concerned. To better understand how these processes play out in a semi-arid ecosystem, we examined resource modulation by woody vegetation, and the response of herbaceous vegetation to that modulation, at a fine spatial scale. Experimental manipulations were employed to separate the positive and negative effects of water, light and seed dispersal in determining herbaceous species density and biomass in three

patch types within and adjacent to the shrub (core, periphery and open). We synthesized our results into a multilayered landscape diversity (MLLD) model. Woody vegetation creates distinct multilayered resource patches at its core and periphery which do not correspond to the dichotomous structural pattern of shrub canopy versus intershrub background. The combined effect of these multilayered resource patches had higher herbaceous species density (8.2 vs. 4.0 species 400 cm^{-2}) and herbaceous biomass (5.4 vs. 1.0 g 400 cm^{-2}) in the periphery than in the core (3-yr averages). The periphery's net positive effects are due to enhancement of soil properties (water infiltration depth of 11.1 cm at periphery vs. 8.1 cm at core), while the core's net negative effects are due to modulation of seed (seed abundance per seed trap of 44.2 at periphery vs. 3.0 at core) and light availability (PAR transmittance of 41.9 % at periphery vs. 16.5 % at core) by the shrub canopy. Thus, when examined at this fine spatial resolution, woody vegetation has both net positive and net negative effects on herbaceous vegetation. Analysis of our results by means of the MLLD model emphasizes the importance of examining the landscape at the spatial scale of the modulated resources and of recognizing different patch types and their differing effects on herbaceous vegetation.

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