

## A HIERARCHICAL PERSPECTIVE OF PLANT DIVERSITY

Daniel A. Sarr

*Klamath Network-National Park Service, 1250 Siskiyou Boulevard*

*Ashland, Oregon 97520-5011 USA*

e-mail: dan\_sarr@nps.gov

David E. Hibbs

*Department of Forest Science, Oregon State University*

*Corvallis, Oregon 97331 USA*

e-mail: david.hibbs@oregonstate.edu

Michael A. Huston

*Department of Biology, Texas State University, 601 University Drive*

*San Marcos, Texas 78666 USA*

e-mail: mh54@txstate.edu

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**Abstract:** Predictive models of plant diversity have typically focused on either a landscape's capacity for richness (equilibrium models), or on the processes that regulate competitive exclusion, and thus allow species to coexist (nonequilibrium models). Here, we review the concepts and purposes of a hierarchical, multiscale model of the controls of plant diversity that incorporates the equilibrium model of climatic favorability at macroscales, nonequilibrium models of competition at microscales, and a mixed model emphasizing environmental heterogeneity at mesoscales.

We evaluate the conceptual model using published data from three spatially nested datasets: (1) a macroscale analysis of ecoregions in the continental and western U.S.; (2) a mesoscale study in California; and (3) a microscale study in the Siskiyou Mountains of Oregon and California. At the macroscale (areas from 3889 km<sup>2</sup> to 638,300 km<sup>2</sup>), climate (actual evaporation) was a strong predictor of tree diversity ( $R^2 = 0.80$ ), as predicted by the conceptual model, but area was a better predictor for vascular plant diversity overall ( $R^2 = 0.38$ ), which suggests different types of plants differ in their sensitivity to climatic controls. At mesoscales (areas from 1111 km<sup>2</sup> to 15,833 km<sup>2</sup>), climate was still an important predictor of richness ( $R^2 = 0.52$ ), but, as expected, topographic heterogeneity explained an important share of the variance ( $R^2 = 0.19$ ), showed positive correlations with diversity of trees, shrubs, and annual and perennial herbs, and was the primary predictor of shrub and annual plant species richness. At microscales (0.1 ha plots), spatial patterns of diversity showed a clear unimodal pattern along a climate-driven productivity gradient and a negative relationship with soil fertility. The strong decline in understory and total diversity at the most productive sites suggests that competitive controls, as predicted, can override climatic controls at this scale.

We conclude that this hierarchical, multiscale model provides a sound basis to understand and analyze plant species diversity. Specifically, future research should employ the principles in this paper to explore climatic controls on species richness of different life forms, better quantify environmental heterogeneity in landscapes, and analyze how these large-scale factors interact with local nonequilibrium dynamics to maintain plant diversity.