Distinguishing Microsite and Competition Processes in Tree Growth Dynamics: An A Priori Spatial Modeling Approach

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abstract: Spatially oriented studies have examined the role of competition on plant populations and communities but not the combined effects of microsite heterogeneity and competition. The aim of this study was threefold: first, to apply and test a common geostatistical tool (semivariograms) to disentangle competition and microsite effects; second, to assess the results of this methodology against a generalized early stand development model for tree populations; and third, to examine the role and timing of microsite and competition processes in early population stages. We mapped and measured annual relative growth rates of trees in three different-aged ponderosa pine stands in Patagonia, Chile. We tested the relative support of five a priori semivariogram-based hypotheses and showed that through stand development, many sites followed our expected sequence of semivariogram models. These translated to initial spatially random growth followed by microsite-dominated, mixed microsite and competition, and finally pure competition effects on growth. Our approach will have many and diverse applications wherever processes differ in the type of spatial pattern they exhibit as well as in spatial scale. We emphasize that this methodology works best when there is strong a priori support for the hypotheses being tested but the timing, strength, and occurrence of processes are not known.

Keywords: competitive interactions, microsite effects, Patagonia, ponderosa pine, forest stand development, semivariograms.

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Establishing general patterns that relate resource availability and competition intensity to growth is central to understanding plant population dynamics in ecology (Tilman 1988; Pacala 1997; Grime 2001; Gurevitch et al. 2002). In particular, one of the key challenges is determining the causes of size variation through time (Harper 1977; Weiner 1990; Pfister and Stevens 2003). Size variability in plants is a consequence of, first, a deterministic growth pattern that relates individual growth rate to current plant size and, second, stochastic growth patterns that represent variation in growth rates due to microsite heterogeneity, genetic variation, and neighborhood effects (Hara 1984; Bonan 1988). These effects are normally confounded in long-lived species (Adler 1996) because experiments to distinguish these would require decades and for many questions may be impossible (Gavrikov and Stoyan 1995; e.g., manipulation of tree competition at age 10 independent of tree competition status at age 5 is not possible). Furthermore, some processes, such as plant-plant competition, are difficult to measure directly (Korol et al. 1995; Gurevitch et al. 2002). However, the spatial pattern of plant growth can be measured (Dale 1999). In this article, we describe a methodological process that bridges the gap between a standard spatial analytical tool (semivariograms) and specific biological hypotheses in a way that allows for strong inference and that can separate apparently confounded effects. The overall approach we apply here can be used with any spatial analytical tool, such as wavelets (Keitt and Urban 2005) or principal coordinates of neighbor matrices (Borcard and Legendre 2002; Borcard et al. 2004), and is not defined by or limited to variography (Fortin and Dale 2005). We applied this approach to separating microsite and competition effects on tree growth in a forest stand system.

In the development of crowded populations, at least two processes can be important in accounting for the observed spatial structure in size through time: competition and microsite variability. Competition, by definition, involves a struggle to preempt limiting resources such as light, water, and nutrients that, together, determine rates of carbon