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

acquisition (Harper 1977; Grime 2001). Commonly, tree competition has been thought to be asymmetric: larger trees have a disproportionate competitive advantage (for their relative size) over smaller trees, suppressing the growth of the latter (Thomas and Weiner 1989; Weiner 1990; Schwinning and Weiner 1998). If two trees are growing next to each other, competition will tend, therefore, to create a negative spatial autocorrelation in size among neighboring trees (Yoda et al. 1957; Bachacou and Decourt 1976; Franco and Harper 1988; Magnussen 1994; Fox et al. 2001; Shi and Zhang 2003). Microsite effects describe heterogeneity in resource availability (i.e., as a whole: soil type, moisture levels, nutrient availability) across relatively small distances that can alter the competition status among trees (Yastrebov 1996; Wyszomirski et al. 1999; Bullock and Burkhart 2005). However, in the forestry literature, microsite resource variation in space has either been assumed to be homogeneous (e.g., Biging and Dobbertin 1995; Goreaud et al. 1999; but see Kleb and Wilson 1997; Peltzer and Wilson 2001, for ecological examples) or left as a stochastic process (Hara 1984; Weiner et al. 2001) when competition is analyzed. Microsite processes will tend to create a positive spatial autocorrelation in size among neighboring trees; similar-sized trees surround one another (Bachacou and Decourt 1976; Bullock and Burkhart 2005). The effect of microsite heterogeneity may last longer in the development of the stand, although it is often observed in young, pre–canopy closure stands and in older, senescent stands (Bachacou and Decourt 1976). It is believed, however, that with time, competition becomes more important at the population level, with trees suffering more from growing with large neighbors than they gain from being in a good patch (Stoll et al. 1994; Bullock and Burkhart 2005). To our knowledge, the interplay between these two factors is poorly understood.

Spatial patterns at many scales are ubiquitous in nature (Dale 1999; Jeltsch and Moloney 2002). It is a feature of much of landscape ecology that these spatial patterns have underlying mechanisms or processes (Turner 1989). For instance, competition between trees and microsite effects on growth will create spatial structures in the relative growth rate (RGR). These spatial patterns can be then described using spatial analytical tools, such as semivariograms or wavelets. As with any statistical technique, these spatial analyses provide powerful statistical tools to describe data. Traditionally, these patterns would then be related to hypothesized generating processes a posteriori (Legendre 1993). The traditional procedure of interpretation of spatial patterns as a consequence of underlying mechanisms a posteriori has the limitation that spurious relationships cannot be discounted (Anderson et al. 2001), and thus inference is limited to stating that correlations exist (as stressed by Borcard et al. 2004). Here, however,

we propose a priori that microsite processes create spatial patterns that differ in quality (shape of semivariogram) from competitive interactions (Bachacou and Decourt 1976), and these differences in quality can permit us to distinguish the two processes even if they act at the same scale. In light of Chalmers's "sophisticated falsification" (Chalmers 1999), we distinguish our two processes by making conjectures that are precise and thus minimize the chance of spurious model fits (Anderson et al. 2001). Our conjectures state that competition will create a spatial pattern best fitted by a wave semivariogram (neighboring trees differ greatly in size and performance [Bachacou and Decourt 1976; Reed and Burkhart 1985; Law et al. 2001]) with a range parameter at the same scale as neighboring tree-tree distances (1–4.5 m). The overall effect can be described by a density wave that damps down with distance, propagating in all directions from every tree (fig. 1). On the other hand, microsite effects will be best fitted by monotonically increasing semivariograms (exponential or spherical types). We leave detailed specifications on these conjectures to the "Inference" section below. Thus, we embrace the a priori multiple-hypotheses approach (Chamberlin 1965; Burnham and Anderson 2002) and expand it to spatial pattern analysis in a way that bridges mechanisms with observations where experimental manipulations and direct measurements are extremely difficult or not possible. In addition, by making predictions concerning the influence of specific processes such as competition and microsite, our approach can be testable in a way that former statistical methodologies have not been.

Approach

Inference

In our study, we departed from traditional descriptive or predictive semivariogram analysis, where the choice of semivariogram model is reported to not matter greatly as long as the model fits the data "reasonably" (Zimmerman and Harville 1991; ver Hoef and Cressie 2001). Instead, we tied specific biological mechanisms (competition and microsite effects) to the spatial patterns in an a priori way based on theoretical and empirical literature. To do this, we inferred two different processes (microsite and competition in addition to the null model) from five different theoretical semivariogram models fitted to RGR empirical semivariograms (fig. 1; see app. A in the online edition of the *American Naturalist* for the empirical semivariogram definition). Thus, we did not directly represent the processes of interest in our models (e.g., there were no parameters representing "competition") but rather analyzed the processes' predicted spatial patterns, which were depicted by the spatial structure of individual trees' RGRs.
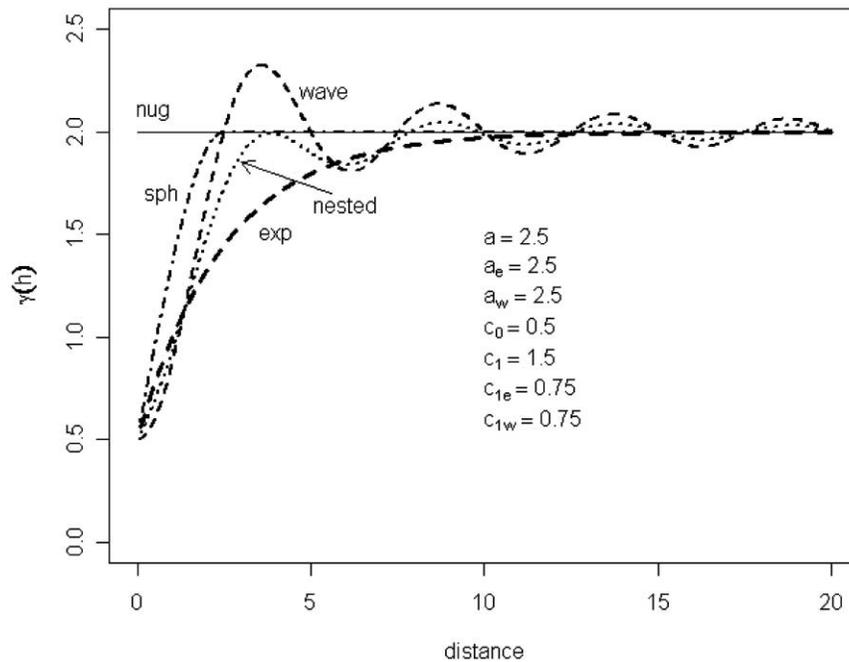
Figure 1: The five theoretical semivariograms used in this study, along with parameters used to define the models in this figure, where *nug* is for the nugget model, *sph* is for the spherical model, *exp* is for the exponential model, *wave* is for the wave model, *nested* is for the nested model, $\gamma(h)$ is the semivariance, *a* is the range, c_0 is the nugget, c_1 is the sill, and subscripts *e* and *w* indicate exponential and wave-specific parameters, respectively, in the nested model. Note that all range parameters are the same in this figure. For further details of parameters and what they mean in variograms, see appendix B in the online edition of the *American Naturalist*.

To describe competition among trees, we used the "wave" model, which depicts a very strong fine-scale difference that dampens with distance. Since competition also decays with distance (Bachacou and Decourt 1976; Stoll and Weiner 2000; Kint et al. 2003), the wave model captures the continued indirect effects of competition through many individuals (i.e., it detects a short-scale pattern in a global way). For the wave model to actually represent competition, however, it is necessary that the peak semivariance occur at a scale that represents neighboring trees within the direct influence. Hence, when fitting the wave variograms, we accepted only local optima for the range parameter that fall between 1 and 4.5 m, reflecting the intertree minimum range of distances. This parameter limitation is essential here for inference about competition because a wave model does not inherently represent competition; it represents a repeating and dampening spatial signal. In a forest, a repeating dampening signal occurring at a scale of 1–4.5 m most likely represents tree-tree competition (there are no other processes that we can conceive of that would show this strong, all-directional pattern in an apparently homogenous forest). In consequence, and in contrast to standard ecological model fitting, where only the model form determines the model, here both the

model form and a strict range of parameter values represent the biological process of interest.

To describe microsite effects, which acted as our catchall noncompetition effects, we used two alternate theoretical semivariogram models, exponential and spherical, that describe positive spatial autocorrelation continuity. We provided two different model forms to allow for our uncertainty about the processes associated with microsite effects. This type of autocorrelation is ubiquitous in ecosystems at multiple scales. In this study, we are interested only in those microsite effects that act at scales similar to those for competition; there will certainly be (micro)site effects acting at many other scales also, but these are not the focus of this study.

In many cases, we can also expect that both competition and microsite effects interact, forming a complex structural function. For this situation, where both processes are important, we built and tested a nested model that was a mixture between the wave and exponential models (see app. B in the online edition of the *American Naturalist* for all theoretical semivariogram formulas).

The fifth and final semivariogram model that we included was the "nugget" model (pure nugget effect), to test for a lack of spatial autocorrelation (stochastic vari-

ation). The nugget model represents no spatial pattern at the scales we measured, suggesting that neither biological process was important (the equivalent of a null hypothesis). A sequence of the prevalent processes expected in terms of stand development is shown in figure 2 (see "Stand Development Model").

Clearly, these five semivariogram models can represent other processes, such as highly structured and repetitive heterogeneity (also a wave function) or disease outbreaks (could be a monotonically increasing function). However, previous stand development models and data indicate that self-thinning mediated through tree-tree competition is the most important process affecting forests with interacting canopies (e.g., Bachacou and Decourt 1976; Oliver 1981; Reed and Burkhart 1985; Stoll and Weiner 2000). Likewise, microsite effects are ubiquitous at many scales (Borcard et al. 2004; Keitt and Urban 2005). While it is theoretically possible that a wave semivariogram pattern at the scale of 1–4.5 m can represent other phenomena and that a monotonically increasing function can represent other biological phenomena, such as disease, these are extremely unlikely (there were no apparent disease outbreaks or repetitive and strong spatial structures in our forest stands). Thus, parsimony and stand observations provide strong a priori evidence that we are detecting competition and microsite effects.

Stand Development Model

We propose an early stand development model within which the more traditional model (Oliver 1981; Pickett and White 1985)—initiation, self-thinning, understory reinitiation, old growth—is a special case without microsite effects (fig. 2). Our model proposes that planted seedlings initially show no spatial pattern in RGR (only stochastic variation) because it is too early for any spatial structure to be detectable in plant RGR from specific differences in resource availability and competition (root or crown overlapping among trees is not probable). As the young stand develops before canopy closure interactions, we expect that spatial differences in resource availability will appear because of relatively better microsites (Wilson and Gurevitch 1995) where neighboring trees share growth rates and similarities in size. Once crown overlapping begins, we expect the onset of asymmetrical competition leading to self-thinning. We note that root competition may also begin at some stage; however, this type of competition will likely be symmetrical (Schwinning and Weiner 1998; Raynaud and Leadley 2005) and will thus be detected as part of the microsite component of the analyses. After forest management thinning is practiced and if it is randomly applied, we expect the model to start over again: no spatial pattern, site effect, and then competition.
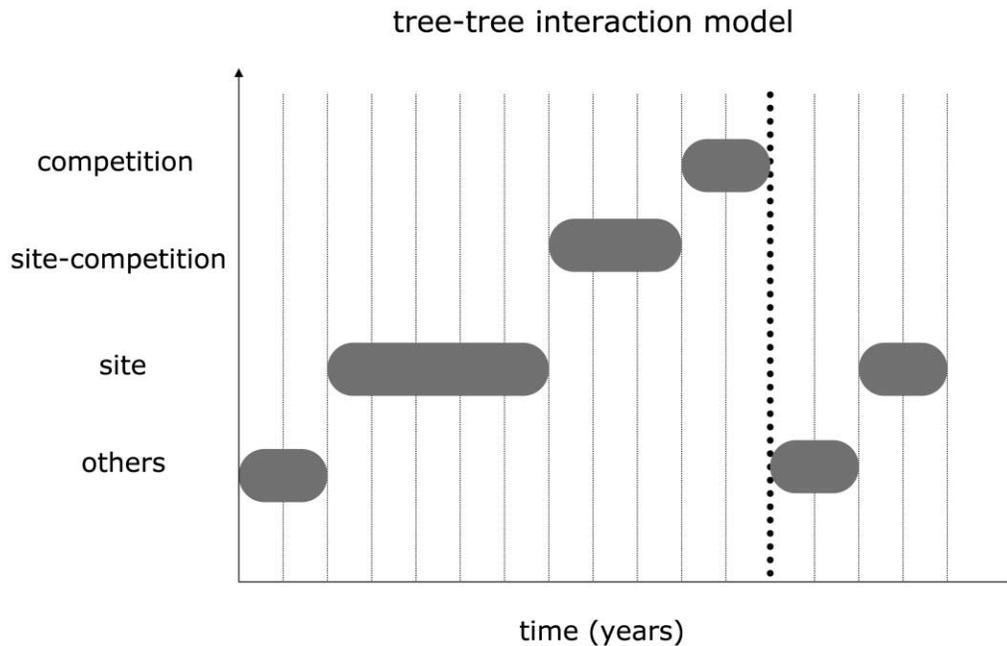

Figure 2: General stand development model proposed to depict tree-tree interaction processes through time and inferred from spatial patterns in even-aged monospecific plantations. Dotted line represents the eventual application of thinning.

Table 1: Stand descriptions by site for even-aged ponderosa pine plantations in Patagonia, Chile, in 2004

Site	Planting year	Thinning year(s)	BA[a] (m²/ha)	Mean height[b] (m)	Density (trees/ha)
Cóndor 1	1993		9.62	4.2 (.05)	1,382
Cóndor 2	1993		5.36	3.7 (.06)	1,139
Mirador 1	1987	1994, 2001	22.92	6.0 (.06)	906
Mirador 2	1987	1994, 2001	29.38	6.6 (.08)	933
Flamenco 1	1981	1998	8.57	4.9 (.08)	414
Flamenco 2	1981	1998	12.59	5.2 (.11)	532

[a] BA = basal area at breast height.
[b] Standard errors for height are in parentheses.

Objectives

We had two biological objectives and a methodological one: first, the application, evaluation, and testing of a common geostatistical tool with a priori conjectures to disentangle these previously confounded processes; second, to understand how the timing and relative strength of microsite effects versus competition compare in early even-aged stands; and third, to determine whether the proposed model of early stand development (i.e., initiation–no interaction, microsite effect, then competition) occurs and whether it occurs similarly in all sites. To evaluate the success of this methodology, we used four separate assessments. First, we used Ripley's K statistic to determine the presence and scale of microscale heterogeneity on the younger sites; then, we assessed, second, whether we had detected the traditional stand development trajectory (initiation, growth, self-thinning), third, whether we had avoided nonsensical results (such as high competition at time of planting or random growth at time of self-thinning), and fourth, whether we had accurately detected the artificial thinning that should remove competitive interactions. We tested these elements in three ponderosa pine plantation stands of different ages located in Patagonia, Chile.

Methods

Study Area and Sampling

The plantation stands are located in the surroundings of Coyhaique city (45°52′S, 72°00′W; 900 m above sea level), Coyhaique province (region XI), in the east Andean foothills of Patagonia, Chile. This zone belongs to the supratemperate belt, with humid climatic conditions (Amigo and Ramírez 1998). The annual precipitation falls mainly as snow and is approximately 1,100 mm in Coyhaique (Mirador and Cóndor stands) and 600 mm in Coyhaique Alto (Flamenco stand; CONAMA 1998). The soil is mainly derived from eolian volcanic ash deposits. Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) constitutes the most widely planted exotic species in the Patagonian Andes region of Chile and Argentina, where it grows vigorously and without any serious pest problems.

In January 2004, we randomly located two 0.17–0.35-ha plots within each of the three stands (Cóndor, Mirador, and Flamenco) where ponderosa pine was the only species planted. The initial density of these plantations was 1,666 trees/ha (2 × 3-m arrangement). The three stands differed in plantation age, site quality, and current density (more details in table 1). All the sites had slopes less than 5%. In each plot, we mapped and measured all trees. We estimated the coordinates of each tree stem center by using a handheld laser range finder (Forest Pro, Laser Technology) and a digital compass, which measure the distance and azimuth to the center of each tree to the nearest 1 mm. The field measurements were converted to coordinates using trigonometric functions. For each mapped tree stem, we measured diameter at breast height (DBH; breast height = 1.35 m). For trees whose DBH was greater than 10 cm, we extracted one core to the pith at approximately 20 cm of height, using an increment borer. When trees were larger than 20 cm DBH, we extracted two cores. All cores were taken perpendicular to the upslope side of the tree. Heights were measured with the laser range finder. We mapped, measured, and cored a total of 1,173 trees across the three stands. At the laboratory, we dried the tree cores, mounted them in grooved wooden boards, and sanded them with successively finer grades of sandpaper to reveal annual rings. For each tree core, we measured radial annual width, using a microscope mounted on a dendrochronometer with a Velmex slide. For cores that missed the pith of the tree, we followed procedures described by Duncan (1989) to estimate the number of missing rings. No correction was applied for time required to grow to coring height.

Relative Growth Rate (RGR)

Since absolute growth is clearly a function of the initial size of a plant (Ford 1984), growth rates are commonly

expressed in relative terms. We used RGR because it does not minimize spatial dependencies among the data in the analysis (Stoll et al. 1994; Wagner and Radosevich 1998) and because it is a measure of efficiency, with an increment of unit of size per unit time (Gurevitch et al. 2002). Furthermore, we used RGR to minimize the temporal autocorrelation within a given tree over time. The mean RGR over an interval of 1 year is defined as

$$\mathrm{RGR}_t = [\ln(\mathrm{BA}_{t+1}) - \ln(\mathrm{BA}_t)] \times 100,$$

where BA_{t+1} is the basal area (in cm^2 at core height) at the end of the time interval (1 year) and BA_t is the basal area at the start of the time interval (Hunt 1990). Correspondingly, basal areas were computed as

$$\mathrm{BA}_t = \pi r_t^2,$$

where r_t is the radius of the cross section at year t, based on the actual core length (from pith to annual ring). This simple BA computation is based on two assumptions relative to young pine tree plantations: first, the pith approximately represents the centroid of the cross section; and second, the stem cross section is approximately circular. In regularly spaced plantations located on relatively flat locations, these assumptions are expected to be valid under most conditions.

Semivariogram Models

Empirical semivariograms are estimates of the variance of the difference between random variables at two locations (Isaaks and Srivastava 1989; Fortin and Dale 2005; see app. A for a complete definition of the empirical semivariogram function). Theoretical variograms are models that can be fitted to these empirical semivariograms. We estimated empirical semivariograms for each year at each site and fitted them to each of the five theoretical models: nugget, exponential, spherical, wave, and nested wave-exponential (see app. B for the theoretical semivariogram formulas used). We examined the RGR data for outliers because of their potential dramatic effect on semivariograms (Basu et al. 1997) and found none. Thus, analyses were done on the raw RGR values.

We used weighted least squares to fit these models and selected among the best models using the small-sample adjustment to the Akaike Information Criterion (AIC_c; Burnham and Anderson 2002; see app. C in the online edition of the *American Naturalist* for the weighted least squares fit and a brief explanation of the AIC). Often, there was model selection uncertainty (i.e., more than one model was deemed equivalent, $\Delta\mathrm{AIC} \leq 2$; Burnham and Anderson 2002). Empirical variograms were estimated us-

ing the geoR package (Ribeiro and Diggle 2001) of the statistical software R (R Development Core Team 2004). Variogram model fitting was done in R as well.

Microsite Heterogeneity: Ripley's K

One of our tests of microsite effects was to use the bivariate version of Ripley's K function and its derived variable $L_{1,2}$ function (Ripley 1977; Lotwick and Silverman 1982), with the edge correction given by Diggle (1983). We assessed the $L_{1,2}$ statistic separately for the lowest and the highest 20% (quintile) of the annual RGR ("poor" and "good" RGRs). This $L_{1,2}$ spatial statistic estimates the spatial scale of clustering or repulsion, if any. We used only Cóndor sites because they had not been thinned; hence, we expected to have a better insight into the actual microsite distribution expressed on the tree performance. To test for significance of $L_{1,2}$, we compared $\hat{L}_{1,2}(d)$ against a 99% Monte Carlo randomization envelope (Goreaud and Pélissier 2003). The $\hat{L}_{1,2}(d)$ values above the envelope indicate spatial attraction, and values below it indicate spatial repulsion (i.e., spatial separation) between the two classes of trees (Lotwick and Silverman 1982). The spatial statistics program SPPA (Haase 2002) was used.

Results

General Stand Characteristics

We found that the basal area at breast height (BA) varied among sites from 5.36 to 29.38 m^2/ha (table 1). There was a striking difference in BA and mean height between the Mirador and Flamenco stands. This difference was accentuated by considering that the Flamenco stand was planted 6 years earlier than the Mirador stand. Although the Cóndor 1 and 2 sites have not experienced artificial thinning, their densities have decreased from the original 1,666 trees/ha (3×2 planting arrangement) by approximately 10% and 30% in Cóndor 1 and 2, respectively. The densities after thinning also varied in the other sites. Flamenco 1 and 2, for example, had decreased approximately 60% in density.

Semivariograms

Early in the temporal trajectory of most sites, the nugget model fitted best (figs. 3–5; see also app. D, for the summary of AIC selection models, Akaike differences, and Akaike weights, and app. E, for the weighted semivariogram range coefficients for the five models, in the online edition of the *American Naturalist*). Subsequently, the exponential and spherical models fitted at most sites, followed in time by the nested or wave model. Shortly after
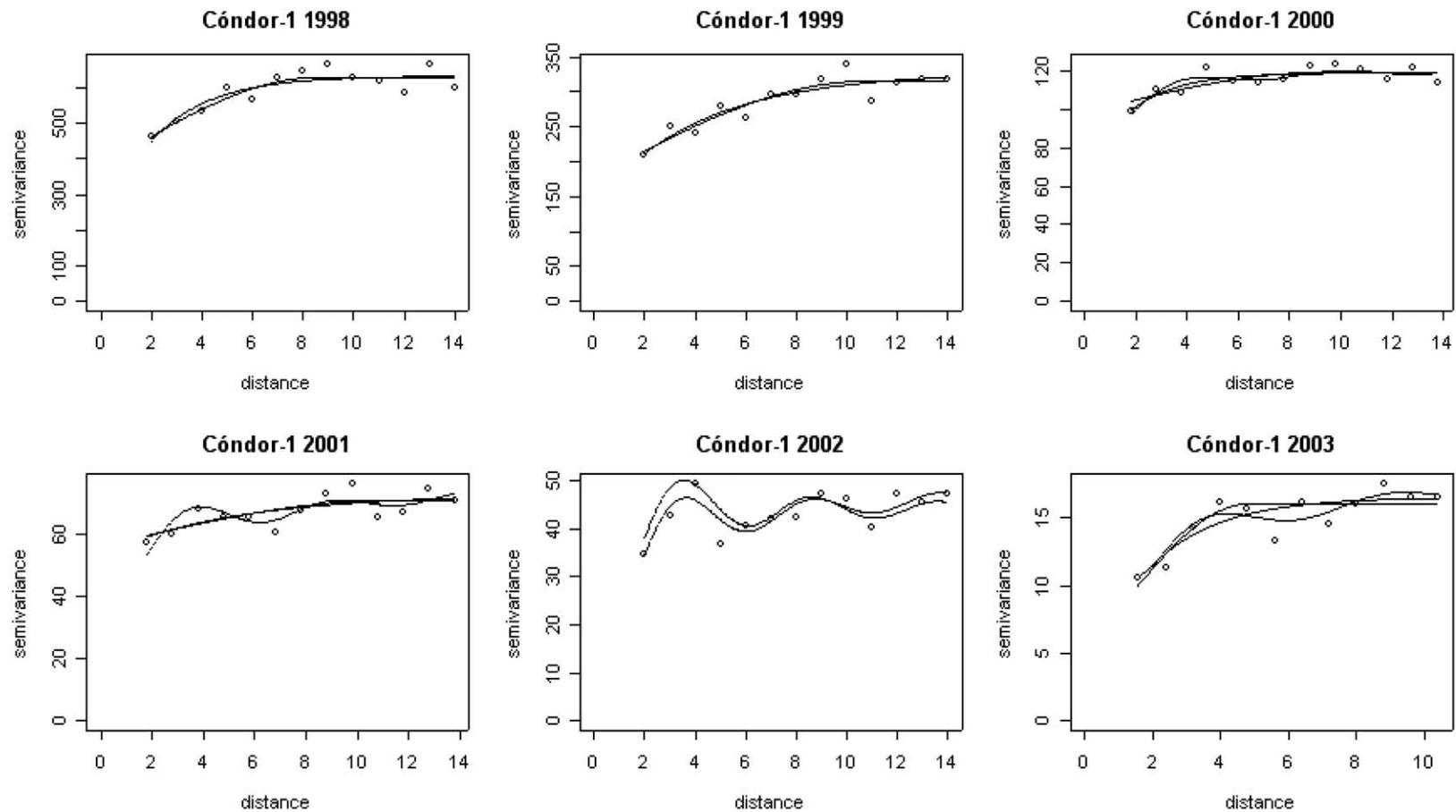
Figure 3: Empirical semivariograms and (only) best-fit (lowest Akaike Information Criterion for small samples) theoretical semivariogram model(s) for each of 6 years of relative growth rate (RGR) at site Cóndor 1 in even-aged ponderosa pine plantations in Patagonia, Chile. These plots can be cross-referenced to figure 5.
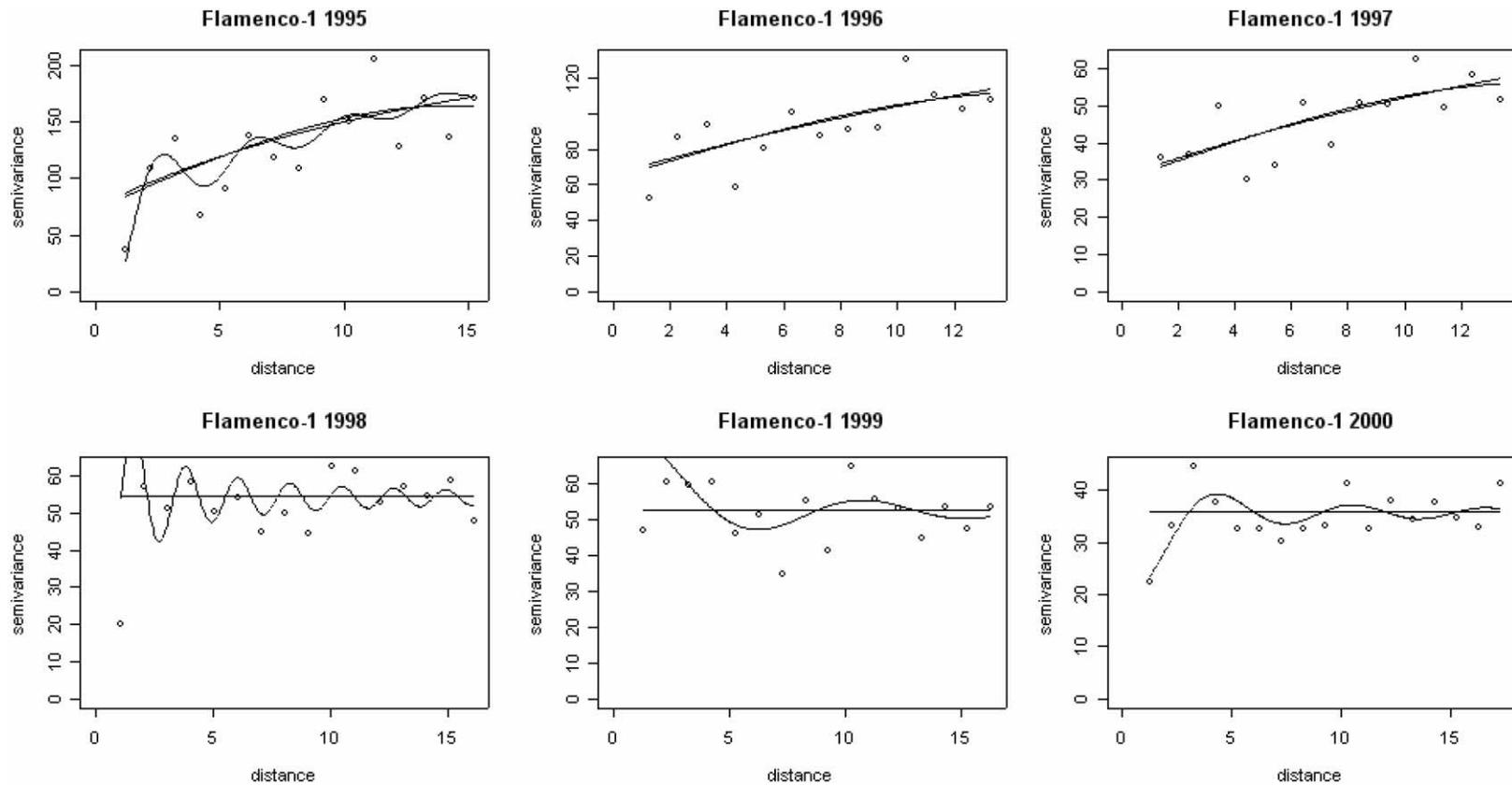
Figure 4: Empirical semivariograms and (only) best-fit (lowest Akaike Information Criterion for small samples) theoretical semivariogram model(s) for each of 6 years of relative growth rate (RGR) at site Flamenco 1 in even-aged ponderosa pine plantations in Patagonia, Chile. These plots can be cross-referenced to figure 5.
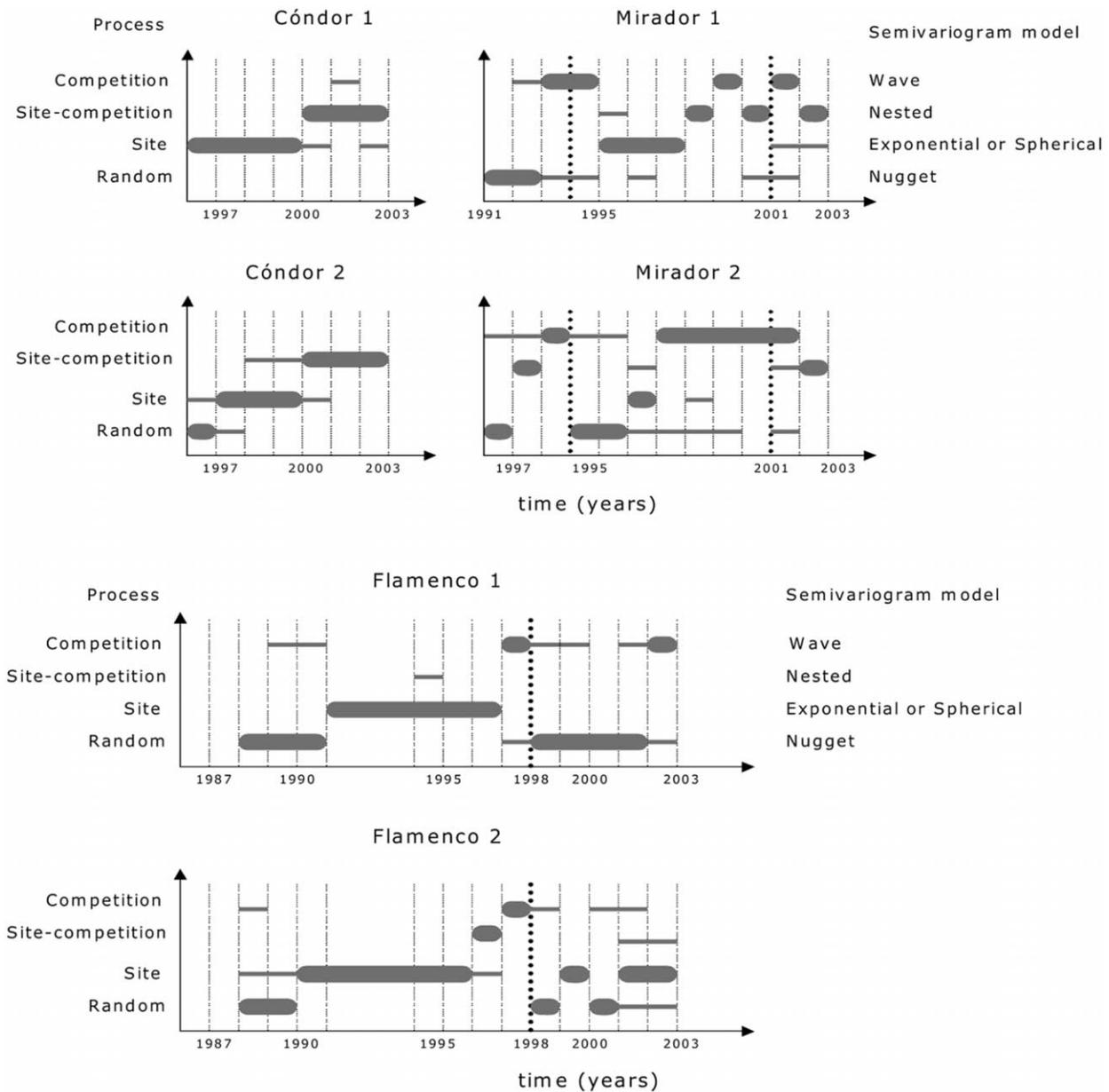
Figure 5: Tree-tree interaction models obtained from spatial patterns (using semivariograms) found in even-aged ponderosa pine plantations in Patagonia, Chile. Thick stripes represent the best model (lowest Akaike Information Criterion for small samples). Thinner stripes represent the second-best model within a range of two units. Dotted lines represent the times when thinning was applied.

artificial thinning, Flamenco 1 and 2 showed reduced support for the nested and wave models and had a reappearance of support for the nugget model. Mirador 2 showed a reappearance of support for the exponential/spherical models. Mirador 1 showed variable semivariogram model support before and after thinning.

Microsite Heterogeneity: Ripley's K

Individual trees belonging to the lower-RGR data set had a negative spatial association when compared to the upper-quintile annual RGR, particularly for later years in the two unthinned sites (table 2; fig. 6). For the Cóndor 1 site,

Table 2: Patterns of spatial association, between the lower and upper quintiles of annual RGR, for trees at sites Cóndor 1 and 2 of ponderosa pine plantations in Patagonia, Chile

Site, year	n_1/n_2[a]	Distance t (m)																P[b]
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Cóndor 1:																		
2003	58/58	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	.01
2002		−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	.01
2001				−	−	−	−	−	−	−	−	−	−	−	−	−	−	.01
2000																		.92
1999																		.92
1998					−	−	−	−										.42
1997		−	−	−	−	−	−	−	−	−								.05
Cóndor 2:																		
2003	38/38	−	−	−	−	−	−	−	−	−								.04
2002		−	−	−	−	−	−	−	−	−		−						.03
2001		−	−	−	−	−	−	−	−	−								.02
2000						−	−	−	−	−								.05
1999						−	−											.15
1998																		.71
1997																		.37

Note: Lower versus upper quintile of annual relative growth rate (RGR). A minus sign indicates significant negative association at distance t, based on the $L_{1,2}(t)$ function. Lack of a symbol indicates independence.

[a] n_1 = individuals in the plot belonging to the lower 20% annual RGR; n_2 = individuals in the upper 20% annual RGR. They are similar for all years.

[b] Significance was evaluated using a 99% Monte Carlo confidence interval (99 simulations) with a 1-m step. The Cramer–von Mises test was used to test for overall significance of patterns over the complete range of t, with P values reported here.

this spatial distinction between the two RGR classes is consistent throughout all scales. For the Cóndor 2 site, the scale of repulsion reached a maximum of 10 m.

Discussion

This study demonstrates that there is a relatively predictable sequence of best-fitting semivariogram models through early forest stand development. Because we proposed specific models in light of underlying mechanisms, we infer from this sequence of models a stand development that begins with a random growth pattern and develops into microsite-mediated growth leading to competition-mediated growth. While we found some noise in this sequence, this was not unexpected, as there should be both process variability (different growing seasons will adjust the balance between competitive and microsite factors) and sampling variability. We discuss this noise, as well as the success and limitations of our methodology, below.

Few other attempts have been conducted toward disentangling competition and microsite effects in mature trees. Bachacou and Decourt (1976) were pioneers in incorporating a geostatistics approach based on DBH semivariograms to tease potential processes apart. However, they did not use an objective criterion (e.g., AIC) to distinguish among multiple competing models, their development of combined models was incomplete, and they

were not testing for dynamic changes through time. Thus, this study provides a novel methodology and a new perspective on the dynamic interplay between microsite effects and competition through stand development.

Test of Methodology

One of the tests of our methodology was to examine whether microsites were detected using an established approach for finding microsites (Ripley's K). Our results indicated that there was spatial repulsion of the trees of the highest growth rate from those with the lowest growth rate. This clear spatial distinction between extreme-case performances corroborates the existence of microsite patches that differ in quality. This result did not provide a perfect test because the scale (10 m and greater) was larger than the scales detected through semivariograms. However, there can be many scales of microsite variability (e.g., Keitt and Urban 2005). While this did not contradict our semivariogram result, it did not fully corroborate it.

Second, we examined whether we reproduced the traditional known stand development model (initiation followed by self-thinning; Oliver 1981). In most sites, there was initial random growth followed by competition, supporting the known model and largely supporting our approach. We did, however, find noise in this pattern, reflecting either noise in the methodology or noise in the
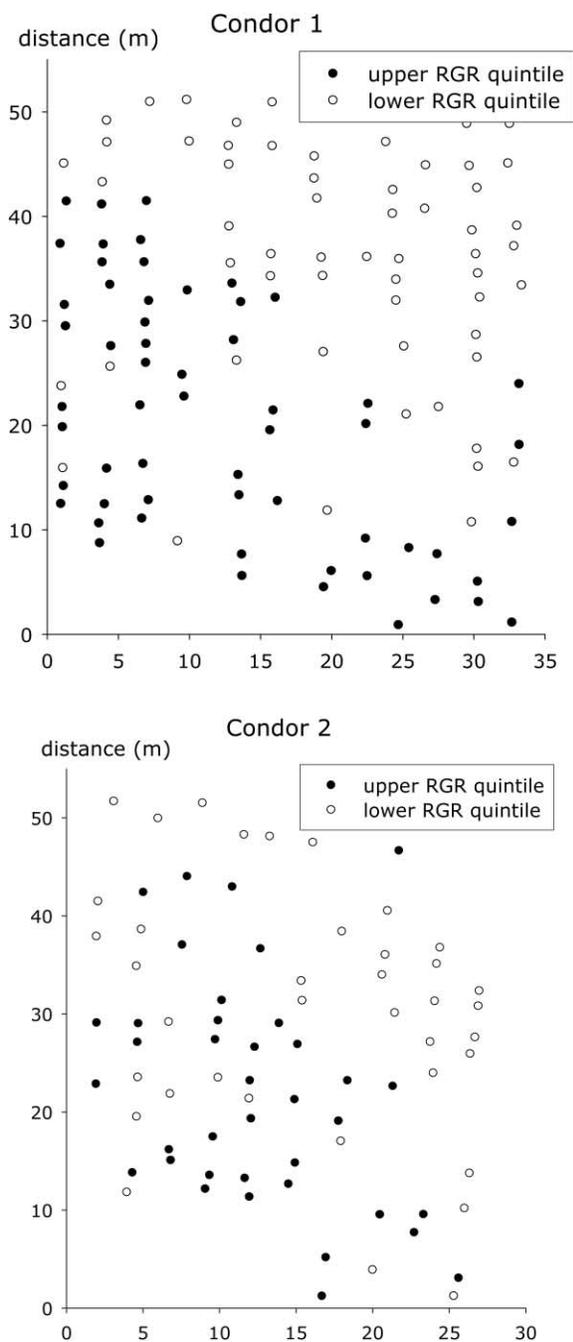
Figure 6: Stem maps showing the upper and lower relative growth rate (RGR) quintiles (20%) at the (*top*) Cóndor 1 and (*bottom*) Cóndor 2 sites in even-aged ponderosa pine plantations in Patagonia, Chile. Stems with middle RGR quintiles are not shown.

stand development model. For instance, Cóndor 1 did not show initial random growth.

Third, sites progressed through a reasonable sequence of patterns, with noise. No sites began with a competition

signal; similarly, strong nugget-model support (no spatial pattern) was observed only early or after artificial thinning. Finally, artificial thinning was applied at least once at four of our sites. The early thinning at Mirador and the Flamenco were both detected clearly, showing a loss of the competition signal. The later signal at Mirador did not show a clear loss of competition; however, we had only 2 years of data after thinning, so the signal was difficult to assess.

Stand Development Model

When only the spatial patterns of individual-tree RGRs were examined, these stands followed our proposed stand development model (fig. 2) for intraspecific interactions in the three tree populations (figs. 3–5), though not perfectly. As our model proposed, competition was detected to occur mostly after microsite resource effects had been accounted for as the prevalent process, except in the most productive site (Mirador), where we expected competition for resources to appear more rapidly (Stoll et al. 1994; Stoll and Weiner 2000).

Across all sites and for some years, we found model uncertainty because there was equivalent support for the best and the second-best models (fig. 5). This may suggest the existence of transitional periods when both models are supported, a situation that can exist where more than one underlying process may be operating simultaneously (Hilborn and Stearns 1982; Wyszomirski et al. 1999; Burnham and Anderson 2002). During these transitional periods, we can expect that trees belonging to different RGR classes will be at different stages in the competition process (Reynolds and Ford 2005), for example, microsite differences between "good" and "worse" patches (see first test in "Test of Methodology"; fig. 6 for Cóndor 1 and 2).

Potential Limitations

Our approach detected canopy competition before thinning and an abrupt loss of competition successfully at the Flamenco sites but only partially at the Mirador sites. This reflects either a lack of resolution in our approach (method error) or a possible thinning treatment that did not perform as intended to eliminate competition (thinning error). The latter could have been a thinning that was either too light (i.e., it did not reduce enough the stand density—consider Mirador densities relative to unthinned Cóndor densities, table 1), nonrandomly applied, or focused on a specific size class. In these cases, since the goal of most thinning strategies is to improve growth (Smith et al. 1997), the thinning performed here may not have maximized its goal because competition was still detected. To separate these possible causes (method error vs. thinning

error), we note that Mirador, where the competition signal was maintained, was the most productive site and had very high stand densities in 2004, suggesting that aboveground competition should be detectable. Likewise, the low-productivity site, Flamenco, saw a removal of competition with thinning and had very low tree densities, suggesting that aboveground competition may not be detectable for many years after thinning. Thus, if our methodology has accurately depicted growth dynamics, the apparent departures from the competition-thinning–no-competition model are consistent with site characteristics. The alternate view (methodology error), that all artificial thinning will always remove the competition signal, is certainly not universally valid, because the interest in the thinning may have been to improve growth but not necessarily to eliminate competition. Ultimately, we can determine which kind of error applies only with further study.

Alternative Approaches

A common approach to studying competition in forests is to use competition indices (Biging and Dobbertin 1995; Gratzer et al. 2004). Competition indices generally do not account for the spatial dependency of observations or use only trees that are spatially separated. In addition, Larocque (2002) argues that distance-dependent individual-tree models have performed relatively poorly since competition indices are inadequate to express the complexity of competition. The effects of genetic variation and microsite heterogeneity on individual tree growth are difficulties that have affected the development of individual-tree models with efficient predictive capacity (Firbank and Watkinson 1987; Barclay and Layton 1990). Some doubts have also arisen that the relatively simple mathematical expressions that have been derived can fully represent the complex processes involved in competition (Weiner 1984; Barclay and Layton 1990). We consider our approach to be an improvement relative to individual-tree models based on competition indices only, because it incorporates microsite heterogeneity as an important component explaining individual tree growth. A drawback of the current analysis technique is the added effort and expense that is required to obtain the spatially referenced data. However, this is a common feature of distance-dependent, individually based models and competition indices as well (Wimberly and Bare 1996; Courbaud et al. 2001).

Currently, there are several spatial statistical techniques that are being developed to identify spatial scale and spatial patterns in data sets, and they are proving to be very promising. For example, wavelet analysis (Bradshaw and Spies 1992; Keitt and Urban 2005) and principal coordinates of neighbor matrices (Borcard and Legendre 2002; Borcard et al. 2004) both propose techniques that identify all the significant spatial scales and patterns that exist in a data set. These show great promise for describing ecological systems in many instances, particularly where there are no specific mechanistic hypotheses being tested. When spatial patterns and scales are unknown and hypotheses need to be created for later testing, these techniques appear essential, as they do not bias scales and patterns onto the data. However, neither these techniques nor variography in themselves provide direct linkages between biological hypotheses and spatial patterns of interest. Thus, any of these spatial analytical tools can be used to infer mechanisms when the mechanisms are well described in the literature and they are presented with a priori predictions. Inference, of course, is strongest when predictions are very precise and are supported by the data analysis.

General Implications

Our study suggests that spatial patterns can be usefully decomposed into underlying processes, namely, competition and microsite effects, using strong a priori hypotheses linked to spatial pattern creation. The measurement of these processes' strength through time might be important for improving population development projections (Pfister and Stevens 2003). In fact, the development of size hierarchies in crowded populations has mostly been attributed to asymmetric competition (Schwinning and Weiner 1998; Stoll et al. 2002); however, at stand or plot level, they may also be the result of a patchy resource distribution (Pacala and Deutschmann 1995; Wilson and Gurevitch 1995), that is, small-scale environmental heterogeneity. Here, we quantify that both processes are acting on trees, but their importance changes through time. In general, the evidence for spatial interactions between neighbors depended strongly on the population development stage (Gurevitch et al. 2002), which accentuates the importance of having a dynamic overview of the interaction process rather than a static one (Damgaard et al. 2002). Before the current study, it was very difficult to separate the effects of these two dynamic processes (Turkington and Aarssen 1984; Weiner et al. 2001).

The approach we present here provides a potential analysis method whenever researchers cannot directly measure the process of interest (e.g., competition) and where they cannot experimentally manipulate factors of interest. As most ecological data are spatially dependent (Legendre 1993), ecologists can model the spatial variability that characterizes each set of data and attaches to specific processes. Even though there is a limited set of standard semivariogram models (e.g., linear, spherical, exponential, Gaussian), with further processing (the nested model) and constraints (in the range parameter), we can represent a

large number of ecological processes. The challenge is to accurately translate deductive predictions of processes—particularly known processes—into spatial patterns and to test the approach using experimental systems. We believe that with this spatial version of the hypothetico-deductive approach, we have explicitly incorporated the main components required for a better understanding of the observed plant performance variation (Damgaard et al. 2002; Gratzer et al. 2004; Reynolds and Ford 2005), including dynamic relationships between microsite variation and competition onset, under a spatial and temporal framework in a plant population.

Acknowledgments

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