

Variation in Local Density Results in a Positive Correlation between Plant Neighbor Sizes

Tomasz Wyszomirski^{1,*} and Jacob Weiner²

1. Institute of Botany, University of Warsaw, Al Ujazdowskie 4, PL-00-478 Warsaw, Poland; 2. National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101, and Department of Agriculture and Ecology, University of Copenhagen, Rolighedsvej 21, DK-1958, Copenhagen, Denmark

Submitted May 19, 2008; Accepted December 12, 2008; Electronically published March 20, 2009

Online enhancement: appendix.

ABSTRACT: A positive correlation between the sizes of plants and the sizes of their nearest neighbors has been observed in many plant populations and is most often attributed to variation in microsite quality. We demonstrate another potentially important cause, using a simple spatial simulation model in which a plant's size is determined by its available area plus stochastic variation. If the spatial arrangement of individuals is nonuniform and local crowding reduces individual size, a positive correlation between the size of a plant and the size of neighboring individuals is to be expected. If a plant is small because it is crowded, its nearest neighbors will also tend to be crowded and therefore small. Such positive correlations will be observed whenever any trait of an object is related to the area available to it. Looking at the performance of neighboring objects without explicitly considering distance can give a very misleading signal.

Keywords: available area, Moran's I , neighboring domains, spatial autocorrelation, symmetric competition, Voronoi tessellations.

Introduction

Within a population of plants, it is often observed that relatively large individuals tend to have relatively large neighbors, while smaller individuals have small neighbors (Liddle et al. 1982; Reed and Burkhardt 1985; Kenkel et al. 1989, 1997; Liu and Burkhardt 1994; Wilson and Gurevitch 1995; García 2006). Relationships between the sizes of individuals and the sizes of their nearest neighbors have been studied in plant ecology and forestry for decades (Pielou 1961). Since plant size reflects environmental conditions to a degree, such positive spatial autocorrelations have been most often interpreted as an indication of site heterogeneity. If some locations have better conditions or more resources than others, individuals growing in more favorable patches will be larger than those growing in less

favorable ones (Mitchell-Olds 1987; Fox et al. 2001; García 2006).

Other explanations have also been considered for positive spatial correlations in neighbor sizes. They may result from positive neighbor interactions, which appear to be more common than previously thought (Brooker et al. 2008). Genetic relatedness among neighbors and spatially correlated emergence times (Wilson and Gurevitch 1995; O. García, personal communication), as well as patterns of mortality during self-thinning (Kenkel et al. 1989), can also produce positive correlations.

Here we describe another potentially important cause of positive correlations in neighbor size, which has not been invoked explicitly so far. If competition among individuals is local and the spatial distribution of plants is not uniform, then a positive correlation between plant size and neighbors' sizes will occur due to local density dependence. The effect presented arises from geometric dependencies between neighboring domains and, as such, may appear in other systems as well.

We assume that plants compete for two-dimensional space, which can be considered a reflection of resources (e.g., light or soil resources). A large amount of space is potentially available to plant P if it has no or few close neighbors. In such a case, its nearest neighbors will also tend to have quite a bit of space because plant P—being one of their neighbors—is distant from them, which means that some space is available to them in the direction of plant P. Similarly, if a plant is very closely surrounded by neighbors and thus has very little space available to it, the area available to its neighbors will be restricted, at least in one direction. Therefore, the nearest neighbors of a crowded plant will also tend to be crowded, and a positive correlation between space available to neighboring individuals is to be expected. If the size of an individual is sufficiently dependent on the amount of space available to it, then a positive correlation between the sizes of neighboring individuals will result. Here we demonstrate this

* E-mail: wyszomir@uw.edu.pl.

point using a simple static model of local competition, in which the number and locations of neighbors influence plant size.

Methods

We generated 2,500 point locations within a square, at the average density of one individual per arbitrary unit. We used three spatial patterns, from highly hyperdispersed to fairly clumped, generated according to the method of Pielou (1960), slightly modified (see appendix in the online edition of the *American Naturalist* for details). A Thiessen/Voronoi polygon or tessellation, defined as the set of all points on the plane that are closer to a point than to any other point (Liddle et al. 1982; Mithen et al. 1984; Kenkel 1990; Berger et al. 2008), was determined for each point. We assume that individual plant size is a function of its Voronoi polygon area and random variation. Using arbitrary units, the size of individual i can be written as

$$w_i = C + A_i + R_i, \quad (1)$$

where A_i is polygon area, R_i is drawn from the normal distribution with 0 mean and standard deviation σ_R , and C is a positive constant ensuring that all sizes are positive. Since we are interested only in correlations between individual sizes, not their absolute values, the value of C does not affect the results of the analyses.

We looked at four values of σ_R (0, 0.3, 0.6, and 0.9). This parameter determines the amount of stochastic variation added to the polygon area. For $\sigma_R = 0$, individual size is completely determined by polygon area. The greater σ_R , the smaller the proportion of size variation determined by the “available area.”

To analyze simulated data, we considered two definitions of neighbors: (a) the nearest individual (each individual has only one nearest neighbor) and (b) all individuals sharing a border of Voronoi polygon with an individual (in this case, number of neighbors varies). We look at the simple correlation between the size of a plant and (i) the size of its nearest neighbor, (ii) total size of polygon neighbors, and (iii) mean size of polygon neighbors.

Second, we use Moran’s I statistic (Upton and Fingleton 1985; Bailey and Gatrell 1995), which has been used often in studies of spatial autocorrelation in plant populations. It is of the form

$$I = \frac{n \sum_{i=1}^n \sum_{j=1}^n u_{ij} (w_i - \bar{w})(w_j - \bar{w})}{[\sum_{i=1}^n (w_i - \bar{w})^2] (\sum_{i=1}^n \sum_{j=1}^n u_{ij})}, \quad (2)$$

where n is the number of plants, \bar{w} is mean size, and u_{ij} describes proximity between individuals i and j . Moran’s

I is a “generic” statistic: its precise form depends on the choice of proximity matrix. Here, we employ two specific definitions, corresponding to the definitions of neighbors given above: (a) $u_{ij} = 1$ if individual j is the nearest neighbor of individual i (otherwise, $u_{ij} = 0$), and (b) $u_{ij} = 1$ if individuals i and j share a boundary of Voronoi polygon (otherwise, $u_{ij} = 0$). For very large n , the expected value of I is close to zero when there is no spatial autocorrelation (Upton and Fingleton 1985; Bailey and Gatrell 1995).

For each pattern and for each value of σ_R , we performed 10 replicate runs. To avoid possible edge effects, we excluded from the analyses (1) individuals close to the square edge where a polygon was not completely defined by surrounding individuals, (2) individuals neighboring any individual in category 1, and (3) individuals neighboring any individual in category 2. As a result, nearly 1,900 individuals were used for the analysis in each run.

In a parallel analysis we applied a Box-Cox transformation (Wyszomirski 1992) to the data. This resulted in only very slight changes in the correlations, and these results are presented in the appendix in the online edition of the *American Naturalist*.

Results

The patterns used in simulations differed considerably in their degree of clumping and resultant distribution of polygon areas (table 1). When $\sigma_R = 0$, size is proportional to area, so size correlations are the same as area correlations (table A1 in the online edition of the *American Naturalist*). Values of Moran’s I are also positive, indicating the presence of positive spatial autocorrelation: neighbors’ sizes tend to be more similar than randomly selected pairs. With increasing amounts of added random variation, all size-area correlations become weaker and so do the correlations between individual size and sizes of neighbors (fig. 1; table 2). For highly nonuniform patterns, however, correlations are notable for all levels of added variation investigated (table 2; see appendix in the online edition of the *American Naturalist* for complete results).

Table 1: Summary statistics of the Voronoi mosaics for the spatial patterns investigated, based on approximately 20,000 points

	Hyperdispersed	Random	Clumped
Variance in counts (mean = 1)	.486	1.021	1.294
Mean polygon area	1.001	.997	.993
SD of polygon area	.262	.535	.746
Skewness of polygon area	.837	1.051	2.132

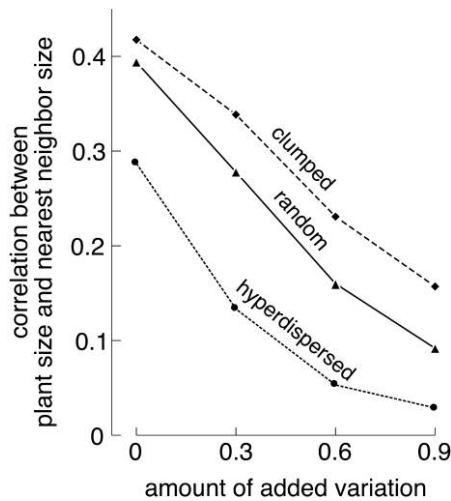


Figure 1: Correlation between plant size and nearest neighbor size versus the degree of added random normal variation (σ_R) for the three simulated spatial patterns investigated. Data points are means from 10 simulation runs.

Discussion

When points are not uniformly distributed in space, relatively large Voronoi polygons tend to abut other relatively large Voronoi polygons. If individual size is dependent on local crowding, large individuals tend to have large neighbors and small individuals tend to have small neighbors, simply due to local density dependence. This result is not dependent on the measure of local crowding used here; polygons are just an intuitive and tested method for simulation of spatial effects at the individual level. The nearest neighbors of plants that are crowded, and therefore small, will also tend to be crowded and therefore small. This effect may be responsible for patterns that have been attributed to site heterogeneity (e.g., Fox et al. 2001 and references therein; García 2006) or other factors. We conclude that looking at the performance of a plant and its

nearest neighbors without accounting explicitly for the distances to these neighbors can be very misleading.

Positive correlations between neighbor sizes that are due to this effect can be expected in nature when the dependence of size on the available space is sufficiently strong. The proportion of size variation explained by spatial effects ranges from nearly 0% to almost 90% (Hara and Wyszomirski 1994). Areas of Voronoi polygons are considered to be among the best spatial predictors of plant performance in even-aged monocultures (Kenkel 1990), often explaining more than one-third of the variation in individual plant size (Sletvold and Hestmark 1999; Jarzyna 2000). In our study, there were still marked positive correlations between neighbors' sizes when Voronoi polygon area explained only around 25% of size variation, suggesting that the effect may be common in the field. The effect is most pronounced for clumped spatial distributions. As the pattern approaches uniformity, variation due to differences in local density decreases, and other sources of variation dominate.

Of course, the phenomenon addressed here does not rule out other possible explanations for positive spatial correlations in plant size, such as patterns of mortality, spatial heterogeneity, genetic relatedness, or facilitation. When groups of small plants and groups of large plants are observed in the field, we suggest that researchers ask whether this could be a result of local density dependence.

We have focused on positive correlations in the sizes of neighbors, which are very common, but negative correlations between the sizes of neighbors have also been documented in forests (Zeide 1972; Fox et al. 2001), within crop rows (Yoda et al. 1957; Mead 1971), and in experimental populations (Franco and Harper 1988). The increase in spatial uniformity of surviving plants during the process of density-dependent mortality ("self-thinning"; Kenkel 1988) and the observation that it is the smaller plants that die during this process (Watkinson et al. 1983; Weiner and Thomas 1986; Kenkel et al. 1989) imply that negative correlations between plant size and sizes of neighbors occur

Table 2: Correlations of individual size and area available and sizes of neighbors, for the clumped spatial pattern

Correlation of individual size with	Amount of added normal variation			
	$\sigma_R = 0$	$\sigma_R = .3$	$\sigma_R = .6$	$\sigma_R = .9$
Polygon area	1.000 (.000)	.928 (.004)	.780 (.012)	.637 (.016)
Nearest neighbor size	.418 (.029)	.339 (.030)	.231 (.034)	.157 (.030)
Total size of all polygon neighbors	.876 (.007)	.794 (.007)	.636 (.017)	.479 (.017)
Mean size of all polygon neighbors	.689 (.017)	.618 (.019)	.483 (.018)	.349 (.017)
Moran's <i>I</i> :				
With nearest neighbor	.307 (.027)	.263 (.028)	.196 (.029)	.142 (.026)
With all polygon neighbors	.501 (.018)	.432 (.019)	.312 (.015)	.209 (.015)

Note: Standard deviations for 10 replicate runs are in parentheses. See the appendix in the online edition of the *American Naturalist* for results for the other spatial patterns and for Box-Cox transformed data.

before there is extensive density-dependent mortality. Since competition in a polygon model is size symmetric, our results suggest that size-asymmetric competition (Cannell et al. 1984; Weiner 1990) must be invoked to explain negative correlations in sizes of neighbors. Further investigation of the interactions between the effect described here and other effects influencing neighbor size correlations is needed.

While we address plant sizes and plant competition here, the phenomenon described may be more general. For any objects irregularly dispersed in space, if a trait of the object is correlated with the space available around the object, positive spatial autocorrelations in the trait can be expected.

Acknowledgments

We thank V. Grimm for encouragement and advice, O. García for helpful correspondence, and S. Bauer, I. Jarzyna, and two anonymous reviewers for helpful comments. The study was supported by a research fellowship from the Centre for Environmental Research, Leipzig-Halle, Germany (to T.W.); grant 3 P04F 030 24 from the Polish Ministry of Science and Higher Education (to T.W.); and a sabbatical fellowship from the U.S. National Center for Ecological Analysis and Synthesis, funded by National Science Foundation grant DEB-0553768, the University of California, Santa Barbara, and the State of California (to J.W.).

Literature Cited

- Bailey, T. C., and A. Gatrell. 1995. Interactive spatial data analysis. Longman, Edinburgh Gate.
- Berger, U., C. Piou, K. Schifffers, and V. Grimm. 2008. Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology, Evolution, and Systematics* 9:121–135.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Cannell, M. G. R., P. Rothery, and E. D. Ford. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. *Annals of Botany* 53:349–362.
- Fox, J. C., P. K. Ades, and H. Bi. 2001. Stochastic structure and individual-tree growth models. *Forest Ecology and Management* 154:261–276.
- Franco, M., and J. L. Harper. 1988. Competition and the formation of spatial pattern in spacing gradients: an example using *Kochia scoparia*. *Journal of Ecology* 76:959–974.
- García, O. 2006. Scale and spatial structure effects on tree size distributions: implications for growth and yield modelling. *Canadian Journal of Forest Research* 36:2983–2993.
- Hara, T., and T. Wyszomirski. 1994. Competitive asymmetry reduces spatial effects on size-structure dynamics in plant populations. *Annals of Botany* 73:285–297.
- Jarzyna, I. 2000. Asymmetry of competition between individuals and spatial effects in even-aged plant populations. PhD diss. University of Warsaw, Warsaw. [In Polish.]
- Kenkel, N. C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69:1017–1024.
- . 1990. Spatial competition models for plant populations. *Coenoses* 5:149–158.
- Kenkel, N. C., J. A. Hoskins, and W. D. Hoskins. 1989. Local competition in a naturally-established jack pine stand. *Canadian Journal of Botany* 67:2630–2635.
- Kenkel, N. C., M. L. Hendrie, and I. E. Bella. 1997. A long-term study of *Pinus banksiana* population dynamics. *Journal of Vegetation Science* 8:241–254.
- Liddle, M. J., C. J. Budd, and M. J. Hutchings. 1982. Population dynamics and neighbourhood effects in establishing swards of *Festuca rubra*. *Oikos* 38:52–59.
- Liu, J., and H. E. Burkhart. 1994. Spatial autocorrelation of diameter and height increment predictions from two stand simulators for loblolly pine. *Forest Science* 40:349–356.
- Mead, R. 1971. Models for interplant competition in irregularly distributed populations. *Statistical Ecology* 2:13–22.
- Mitchell-Olds, T. 1987. Analysis of local variation in plant size. *Ecology* 68:82–87.
- Mithen, R., J. L. Harper, and J. Weiner. 1984. Growth and mortality of individual plants as a function of “available area.” *Oecologia (Berlin)* 62:57–60.
- Pielou, E. C. 1960. A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology* 48:575–584.
- . 1961. Segregation and symmetry in two-species populations as studied by nearest-neighbour relationships. *Journal of Ecology* 49:255–269.
- Reed, D. D., and H. E. Burkhart. 1985. Spatial autocorrelation of individual tree characteristics in loblolly pine stands. *Forest Science* 31:575–585.
- Sletvold, N., and G. Hestmark. 1999. A comparative test of the predictive power of neighbourhood models in natural populations of *Lasalia pustulata*. *Canadian Journal of Botany* 77:1655–1661.
- Upton, G. J., and B. Fingleton. 1985. Spatial data analysis by example. Vol. 1. Point pattern and quantitative data. Wiley, Chichester.
- Watkinson, A. R., W. M. Lonsdale, and L. G. Firbank. 1983. A neighbourhood approach to self-thinning. *Oecologia (Berlin)* 56:381–384.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends in Ecology & Evolution* 5:360–364.
- Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. *Oikos* 47:211–222.
- Wilson, C., and J. Gurevitch. 1995. Plant size and spatial pattern in a natural population of *Myosotis micrantha*. *Journal of Vegetation Science* 6:847–852.
- Wyszomirski, T. 1992. Detecting and displaying size bimodality: kurtosis, skewness and bimodalizable distributions. *Journal of Theoretical Biology* 158:108–128.
- Yoda, K., T. Kira, and H. Hozumi. 1957. Intraspecific competition among higher plants. IX. Further analysis of the competitive interaction between adjacent individuals. *Journal of the Institute of Polytechnics, Osaka City University, Series D* 8:161–178.
- Zeide, B. B. 1972. Density waves in a forest stand. Pages 211–213 in A. L. Yanshin, ed. *Moskovskoe obschestvo ispytateli prirody*. Moscow University Press, Moscow.