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EDGE EFFECTS IN THE USE OF AREA POLYGONS TO STUDY COMPETITION[1]

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The Dirichlet tessellation (also known as the Thiessen or Voronoi tessellation, or S-mosaic) is a subdivision of points in a plane such that each point has associated with it a polygonal area defining a region nearer to that point than to any other (Green and Sibson 1978). Brown (1965) and Mead (1966) independently suggested that these polygons can be used to measure the "area potentially available" to an individual plant in a population. Recent studies that have used this model in relating plant performance to various polygon parameters have based the tessellation on a coordinate map representing a "window" or section from a more extensive population (e.g., Liddle et al. 1982, Watkinson et al. 1983, Bülow-Olsen et al. 1984, Mithen et al. 1984, Matlack and Harper 1986, Firbank and Watkinson 1987). This note points out a problem in the treatment of edge effects in such studies, and outlines an easily implemented algorithm for excluding from consideration all polygons that are potentially influenced by individuals located outside the mapped study area.

The tessellation is obtained by first calculating the Delaunay triangulation (Upton and Fingleton 1985: 101), which determines the polygon neighbors of all points in the plane. Perpendicular bisectors are then drawn between neighbors to define the individual polygons (Fig. 1). Since the area so defined represents a

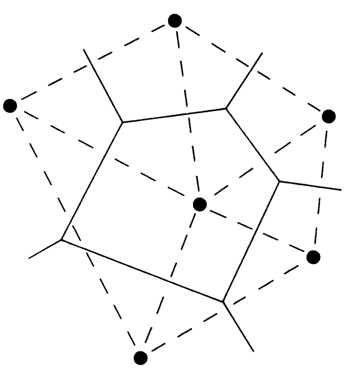

FIG. 1. Construction of a Dirichlet tessellation polygon. Solid circles (●) are points (plants) whose neighbors are joined by dashed lines (forming the Delaunay triangulation). The perpendicular bisectors (solid lines) define the polygons.

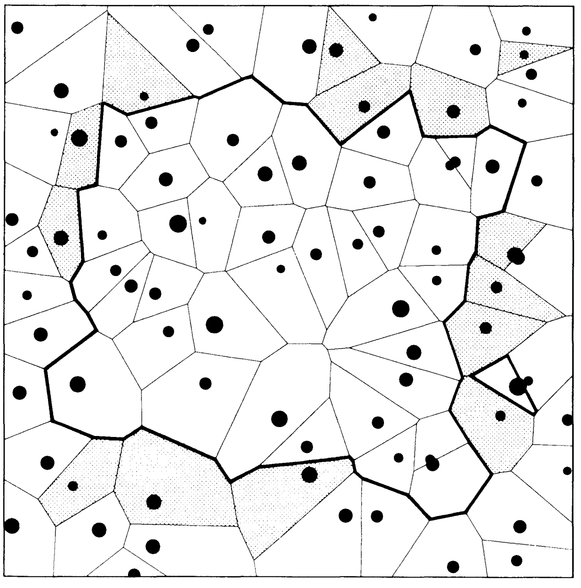

FIG. 2. Dirichlet tessellation of 83 jack pine trees in a 20 × 20 m stand. Circle (●) diameter is proportional to tree diameter at breast height (dbh). Polygons outside the solid line are those excluded by the edge effect algorithm described in the text. The 14 incompletely defined interior polygons are shaded.

region nearer to a given point than to any other, it can be thought of as representing the "territory" (Green and Sibson 1978) or "zone of influence" (Antonovics and Levin 1980) of that point (plant). Subsequent analyses generally relate some measure of plant performance (e.g., accumulated dry mass, growth rate, tiller production) to one or more polygon parameters: these include area, perimeter length, number of sides (neighbors), shape (eccircularity), and location of the plant within the polygon (abcentricity), as well as competition indices based on polygon parameters (Mead 1966, Matlack and Harper 1986, Firbank and Watkinson 1987).

A map representing the positions of 83 individuals of jack pine in a pure, 65-yr-old stand on a uniform sandy substrate is shown in Fig. 2 (the data are a subset of a larger study described in Kenkel 1988). Note that 31 of the polygons are partially bounded by an edge of the study area. Such polygons are incompletely defined by the data, and should therefore be excluded from any analysis relating plant performance to polygon area (or other parameter). Recent studies addressing the edge effect problem have in fact suggested that these "edge polygons," but only these, should be excluded from consideration (Bülow-Olsen et al. 1984, Hutchings and Discombe 1986, Matlack and Harper 1986, Firbank and Watkinson 1987). However, careful consideration of the edge effect problem reveals that a proportion of the "interior" polygons (those not abutting on an edge) may also be incompletely defined. Specifically, points occurring outside the mapped study area may be potential neighbors of some interior polygons (Fig. 2). Since nothing is known about the position of points outside the study area, polygons that potentially have one or more neighbors outside the mapped region must also be excluded.

The algorithm for determining which interior polygons should be excluded is straightforward. For a given point, center a circle at each vertex of its associated polygon (there will be n neighbors and vertices) such that it passes through the point: this circle will also pass through two adjacent neighbor points. A polygon should be omitted if any of these n circles intersects an edge of the study area, since points lying outside the study area but within the circle are polygon neighbors (Fig. 3).

The relationship between the proportion of points that must be excluded and the number of points in a study area was investigated using Monte Carlo simulation. For a given number of points, 20 sets of random coordinates were generated within a unit square using high-quality congruential random number generators (Arnason 1977), and the algorithm described above applied to each. The results (Fig. 4) indicate that the relationship, though monotonic, is nonlinear and approaches the theoretical asymptote (1.0) very slowly. Very few points are retained if <25 are mapped, while

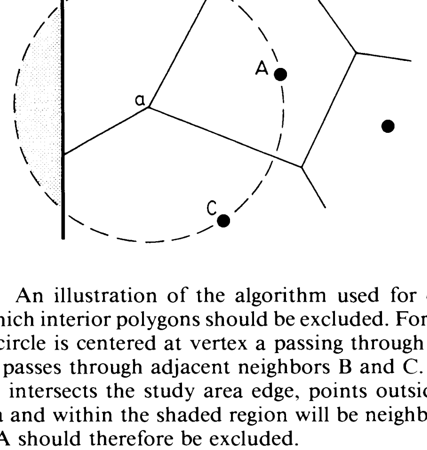

FIG. 3. An illustration of the algorithm used for determining which interior polygons should be excluded. For polygon A, a circle is centered at vertex a passing through point A: it also passes through adjacent neighbors B and C. Since this circle intersects the study area edge, points outside the study area and within the shaded region will be neighbors of A. Point A should therefore be excluded.

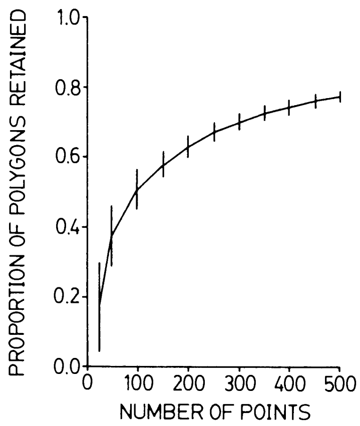

FIG. 4. The proportion of polygons retained as a function of the number of randomly sited points in a unit square. The curve passes through the mean value of 20 replicate sets for a given number of points. The vertical lines indicate the range obtained from the replicate sets.

only about half of 100 points are retained. Even with 500 points, only 77% are retained. Note that Hutchings and Discombe (1986) retained 84.6% of 500 points, since they excluded only those polygons partially bounded by a study area edge. That is, ≈9% of the polygons they retained should have been excluded from consideration.

In conclusion, studies relating individual plant performance to Dirichlet polygon parameters must exclude from consideration all polygons that could potentially be influenced by points lying outside the mapped area. This includes not only polygons partially bounded by a study area edge, but a proportion of interior polygons near the edges as well. This exclusion criterion, while conservative, is necessary given the lack of information regarding the spatial distribution of individuals outside the study area.

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