Floating neighborhoods reveal contribution of individual trees to high sub-stand scale heterogeneity

Eric K. Zenner*, JeriLynn E. Peck

Department of Ecosystem Science and Management, The Pennsylvania State University, 305 Forest Resources Building, University Park, PA 16802, USA

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ABSTRACT

Forest structure is typically characterized using approaches that fail to capture the sub-stand heterogeneity reflecting the processes shaping stand structure at neighborhood patch scales. We propose a focal-tree based approach that flexibly scales across natural tree neighborhoods and demonstrate it by quantifying small-scale structural heterogeneity using diameter distributions across multiple scales in an old-growth mixed conifer forest in western Oregon exhibiting a rotated sigmoid shape. Tree-centered delineation of neighborhoods *via* Delaunay triangulation (spatial tessellation) was used to connect natural tree neighbors. At the First-order neighborhood scale, each tree was connected to an average of 6 neighbors in 75 m^2 of convex hull area, which increased to 118 neighbors covering 2542 m^2 by the Fifth-order scale. Agglomerative clustering identified the ten most prevalent sub-stand diameter distribution types (DDTs). At the smallest scale, these ten DDTs were characterized by four different distribution shapes (negative exponential, concave, rotated sigmoid, and unimodal) and varied considerably in the abundance of trees in different size classes and species composition (Douglas-fir composing the larger trees and western hemlock and western redcedar the smaller). On average, each individual tree contributed to over 3 different DDTs at any given scale. Small-scale tree neighborhoods were tremendously heterogeneous, such that the stand-level diameter distribution represented an aggregation across extremely disparate sub-stand distributions. As expected, these distributions exhibited spatial smoothing (i.e., increasing homogeneity with increasing scale) as small, heterogeneous tree neighborhoods were expanded into larger neighborhoods with more similar average composition, which converged on a rotated-sigmoid shape by the Fifth-order scale. Structural complexity in the demonstration stand likely owes more to shade-tolerant ingrowth below residual trees than to gap processes. The diversity of structural contribution (e.g., the number of DDTs to which a tree contributes) may be a more informative measure of structural complexity than indices based on a fixed spatial perspective. The floating neighborhood delineation and scaling approach allows for the identification of natural neighborhoods, permits the assessment of multiple conditions for any given tree, and provides of a logical mechanism for exploring scale-dependent ecological phenomena.

1. Introduction

Forest structure, defined as the vertical and horizontal spatial arrangement of trees, species, sizes or age distributions in a three-dimensional space (Goff and Zedler, 1968), is a property that emerges after scaling-up individual tree attributes and life history traits to neighborhood, stand, and landscape scales (Enquist et al., 2009). In temperate forests, the process of structural development often involves disturbances (Barnes et al., 1998; Kimmins, 2004) and interactions among tree individuals or neighborhood dynamics (Weiner, 1984; Kenkel, 1988; Gratzer et al., 2004) that set in motion gap dynamics and the ecological processes of mortality, colonization, reproduction, recruitment, growth, competitive thinning, and senescence (Goff and

West, 1975; Runkle, 1982; Shugart, 1984; Harcombe, 1987; Coomes et al., 2003). Over time, the variation in species and age classes, the arrangement of species into different canopy layers, and the distribution of individuals among diameter classes increases (Smith, 1986), which is generally equated with greater structural complexity (cf. Zenner and Hibbs, 2000).

Small-scale disturbances, gap dynamics, neighborhood dynamics, and subsequent ecological processes occur concurrently in the later stages of forest development and profoundly influence horizontal structures, vertical structures, species composition, and demographic population dynamics (Parker and Sherwood, 1985; Runkle, 1982; Lorimer, 1989; Oliver and Larson, 1996; Gratzer et al., 2004). After centuries following stand replacement disturbances, structural

complexity culminates in old-growth forests that are typically characterized by multi-aged trees, multi-layered canopies, large variation in tree sizes, many large live old trees, standing dead trees, snags, large amounts of coarse woody debris, and heterogeneity in vertical canopy configuration and horizontal spatial patterns (Franklin et al., 1981, 2002; Franklin and Van Pelt, 2004). Structural heterogeneity, in turn, affects tree regeneration, growth, and mortality (Kubota, 1997; Boyden et al., 2005) and shapes patch diversity (Podlaski, 2010) and the space-time dynamics of forests (Harms et al., 2001; Nakashizuka, 2001).

Because tree size is the single most important structural element that affects resource use, growth and allometry, and survival and reproduction at the individual tree scale (West et al., 2009), aggregating individual tree sizes into size/diameter frequency distributions (DFDs) is a sensible scaling approach capable of capturing the basic structure of forests and the ecological processes that have generated it (Enquist et al., 2009). Ever since de Liocourt (1898) aggregated individual tree sizes into DFDs of population density and showed that multi-aged forests exhibit a regular inverse relationship between sizes and numbers of individuals, DFDs have become the preferred tool to characterize the vertical structural heterogeneity of temperate old-growth and managed uneven-aged forests in Europe (e.g., Jones, 1945; Leibundgut, 1959, 1993; Korpel, 1995; Podlaski, 2010), Asia (e.g., Kohyama, 1986; Wang et al., 2009), Oceania (e.g., Coomes et al., 2003; Coomes and Allen, 2007), and North America (e.g., Hough, 1932; Meyer and Stevenson, 1943; Schmelz and Lindsey, 1965; Goff and West, 1975).

Due to the linkage between tree age and diameter in old-growth forests (Lorimer, 1980), it is generally accepted that, despite often weak linkages for shade-tolerant species, DFDs broadly reflect age structures and past disturbances (Lorimer and Krug, 1983; Goodburn and Lorimer, 1999), as well as reasonably capture space-time dynamics (Coomes and Allen, 2007). As a rule, unimodal DFDs with varying degrees of skewness are often found in young single-layered even-aged stands, and more symmetric normal distributions in older even-aged stands (Baker, 1923; Meyer, 1930; Hough, 1932; Assmann, 1970). Widely varying DFDs that range from near normal to multi-modal and/or irregularly descending characterize multi-layered stands comprised of several age classes, where the specific DFD depends on the prominence and dispersion of age classes and the degree of shade-tolerance of the attending species (Hough, 1932; Leak, 1975; Oliver and Stephens, 1977; Lorimer, 1980). Steeply descending DFDs, with a more or less inverse relationship between the sizes and numbers of individuals, are often found in multi-layered mixed-species even-aged stands (Oliver, 1978; Lorimer and Krug, 1983; Hornbeck and Leak, 1992) and in multi-layered all-aged temperate old-growth forests of shade-tolerant species (de Liocourt, 1898; Hough, 1932; Meyer, 1952; Goff and West, 1975; Lorimer, 1980; Leibundgut, 1993; Korpel,1995; Peterken, 1996).

Old-growth forests that display an inverse relationship between the sizes and numbers of individuals are often thought to possess high levels of vertical heterogeneity with 'balanced,' 'sustainable (stable)' or 'equilibrium' population structures (Meyer, 1952; Schmelz and Lindsey, 1965; Goff and West, 1975; Lorimer and Frelich, 1984; Leak, 1996; Goodburn and Lorimer, 1999; Rubin et al., 2006). The shapes of the most important 'balanced' DFD types differ in subtle ways and include the (1) reverse-J/approximate negative exponential [NE], (2) increasing-q [IQ], and (3) the rotated sigmoid [RS], which resembles the reverse-J on an arithmetic axis but diverges in shape on a semi-log axis (Vrška et al., 2002; Schwartz et al., 2005; Westphal et al., 2006; Janowiak et al., 2008; Podlaski, 2010; Král et al., 2010; Kucbel et al., 2012). The NE type shows a constant reduction rate in the number of trees from one diameter class to the next larger one, and yields a monotonically declining straight line with a constant negative slope (i.e., the q-ratio) on a semi-logarithmic density scale (Hough, 1932; Meyer, 1952; Goff and West, 1975). The IQ type has a q-ratio that increases with tree sizes and exhibits a negative parabolic pattern on a semi-logarithmic scale (Leak, 1964, 1996; Schwartz et al., 2005; Janowiak et al., 2008). Because it reflects a low abundance or absence

of very large trees, the IQ type may indicate a transition toward the NE or RS types (Schwartz et al., 2005). The RS type is concave in the smaller—and convex in the larger—diameter classes and often yields a gently descending plateau in the mid-sized diameter range, or possibly a bimodal distribution (i.e., non-monotonic decline), on a semi-logarithmic scale (Goff and West, 1975; Goodburn and Lorimer, 1999; Podlaski, 2010). Ecologically, differences between the NE and RS types are generally linked to mortality rates that are presumed to be equal among the diameter classes for NE curves, and unequal (e.g., U-shaped) for RS curves (Goff and West, 1975; Leak, 1996; Lorimer et al., 2001). Competing conclusions have been reached, however, whether and why population structures in temperate multi-aged multi-layered old-growth forests are characterized by the NE (Hough, 1932; Muller, 1982; Leibundgut, 1993; Leak, 1996), the RS (Goff and West, 1975; Lorimer and Frelich, 1984; Westphal et al., 2006; Kucbel et al., 2012) or both the NE and RS types (Korpel, 1995; Goodburn and Lorimer, 1999; Westphal et al., 2006; Podlaski, 2010). This uncertainty raises three fundamental concerns about using DFD types to interpret forest structure and processes.

First, notwithstanding extensive use of different model-fitting techniques and functions (e.g., negative exponential, power, Weibull, Gamma) (Wang et al., 2009), for some time no widely agreed-upon framework with clear rules for objective and consistent assignment of DFDs into different types existed (Rubin et al., 2006). However, despite some challenges (Pond and Froese, 2015), the recent advent of such a framework, in which DFD types are designated using a polynomial regression-based classification (PRC) (Janowiak et al., 2008), has permitted more robust comparisons of DFD types among different old-growth stands (Gronewold et al., 2010; Alessandrini et al., 2011; Diaci et al., 2011).

Second, in light of the recognition of the importance of sample size/area (i.e., spatial extent) on the analysis of forest structure and the quantification of DFDs (de Liocourt, 1898; Meyer, 1952; Goff and West, 1975), comparing DFDs quantified at highly variable spatial scales and sampling intensities also poses concerns (Westphal et al., 2006; Pond and Froese, 2015). This may be particularly true for small sampling plots that are often subjectively placed into areas with higher volume (Holeksa et al., 2009), potentially biasing results (Innes, 1995). Nonetheless, the RS type in stands of shade tolerant species has been shown to be stable with increasing sample size (Janowiak et al., 2008) and is generally found at small scales in undisturbed areas of uniformly complex structure (Leak, 1964; Schmelz and Lindsey, 1965; Goff and West, 1975) as well as in old-growth areas of several hectares (Commarmot et al., 2005; Westphal et al., 2006; Alessandrini et al., 2011). In contrast, the NE type has mostly been found on fairly small and homogeneous old-growth tracts (Muller, 1982; Goodburn and Lorimer, 1999).

Third, the motivation to determine whether, and if so at what minimum scale, old-growth forests exhibit 'balanced' NE or RS types runs the risk of too readily discounting spatial variability. Disturbances are highly unpredictable and spatially patchy (Runkle, 1982, 1990; Pickett and White, 1985; Oliver and Larson, 1996), old-growth forests consist of a diverse assemblage of patches that form a space-time mosaic (Watt, 1947) of different development stages (Leibundgut, 1993; Korpel, 1995) with distinct DFD signatures (Král et al., 2010; Lorimer and Halpin, 2014), and ecological processes and neighborhood dynamics (Pacala et al., 1996; Gratzer et al., 2004) operate at different spatial and temporal scales (Bormann and Likens, 1979; Oliver and Larson, 1996). Highly variable spatial processes and interactions among tree individuals drive competition for resources (i.e., growth patterns) and shape the structures, DFDs, and the dynamics in deciduous and mixed temperate forests (Christensen et al., 2007). Stand-level summaries indubitably smooth over fine-scale spatial patterns of heterogeneity (Zenner et al., 2015) that reflect the endogenous ecological processes shaping natural stands (Smith and Urban, 1988). Stand-level DFDs, for instance, merge size hierarchies arising from differential