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Classification and dynamics of developmental stages in late-successional temperate forests

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ABSTRACT

Late-successional forests often have complex disturbance histories that can result in stands with widely varying structure, ranging from young pole stands to uneven-aged old growth. Arranging stands in chronosequences, however, is problematic because ‘stand age’ is not a meaningful concept for multi-aged stands and ‘time since last stand-replacing disturbance’ often cannot be determined from tree-ring evidence. In this paper, we describe a systematic approach for classifying developmental stages in late-successional forests using structural metrics known to be correlated with key ecological properties such as total biomass, carbon storage, stand production rates, and wildlife habitat. While conceptually based on the amount of aggregate crown area occupied by different size classes of trees, the computations in this study, for ease of use, are based entirely on absolute and relative basal area of four size classes (saplings, poles, mature, and large trees). Eight forest structural stages are recognized, including four stages of old growth (early-, mid-, late-transition, and steady state). The method was used to classify developmental stages of 70 primary northern hardwood stands (*Acer–Betula–Tsuga*) in large landscape reserves in upper Michigan, USA. The degree to which the developmental stages mimic underlying temporal trends in stand dynamics was investigated with the aid of 30-year permanent plot records in primary forests and multi-century simulations using the CANOPY forest dynamics model. Results indicated good correspondence between the postulated developmental sequence in the 70 field stands compared with CANOPY simulations of structural changes over time and changes observed on the permanent plots. Results support the Bormann–Likens hypothesis that the number of large trees reaches a maximum toward the end of the lifespan of an even-aged cohort and subsequently declines in the steady state. While most of the field plots were uneven-aged, both simulations and field data suggest that developmental pathways of even-aged and multi-aged stands after disturbance are very similar and are difficult to distinguish based on the form of the size distributions. In the study area landscapes, 78% of the stands were classified as old growth, with 39% in early or mid-transition and 39% in late transition or steady state. The method should be useful, with appropriate site-specific modifications, in evaluating the degree to which stands meet structural goals under ecological forestry methods, in monitoring responses to environmental change, and in examining biotic changes along a gradient of structural development following disturbance.

1. Introduction

Analysis of changes in plant species composition, structure, and animal populations over long periods of time in forests usually necessitates development of a chronosequence or ‘space-for-time substitution’ because of the slow rate at which forests develop. Permanent plots provide an alternative approach with fewer assumptions (Aldrich et al., 2005). But permanent plots spanning even a modest time period of 30–60 years are uncommon in most areas of the world and usually available only in certain forest types, habitats, and for a restricted range of age classes. If a sufficient number of temporary sample plots are taken and carefully stratified by habitat and age class, chronosequences can often yield valuable insights about certain long-term ecological trends (Walker et al., 2010). In cases where stand age can be determined accurately, trends in structural features or biotic populations can be plotted as a function of stand age or time since the last stand-replacing disturbance (Crowell and Freedman, 1994; DeWalt et al., 2003).

Late-successional forests of shade-tolerant species, however, present a number of special problems that often make it difficult

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to develop conventional chronosequences. Even when the oldest cohort can be aged accurately, it is often difficult or impossible to determine the time since last stand-replacing disturbance using conventional tree-ring analysis. The oldest cohort could represent either a remnant of a once-dominant even-aged overstory (Antos and Parish, 2002) or a more limited cohort that developed after minor or moderate disturbance in an uneven-aged stand (Parish and Antos, 2006).

Furthermore, the validity of chronosequences becomes increasingly doubtful as time since last major disturbance increases and the age structure diversifies. Forests of shade-tolerant species often have many major and minor age classes, reflecting a complex pattern of past disturbance (e.g., Splechtna et al., 2005; D'Amato and Orwig, 2008; Fraver et al., 2009). A chronosequence approach has sometimes been applied to such stands by using the age of the oldest cored tree as a proxy for stand age. But investigators have recognized that the oldest tree in a stand with many age classes and a variable disturbance history may not always bear a clear relationship with time since last major disturbance (Tyrrell and Crow, 1994; Lichstein et al., 2009; Keeton et al., 2011). Even relatively young stands a few decades after severe disturbance often contain 'legacy trees' more than 150 years old (Henry and Swan, 1974).

An alternative to a strict chronosequence in late successional forests is to arrange stands by developmental stages based on stand structure. Despite the often complex developmental pathways in late successional forests, structural variation among stands (evidenced, for example, by diameter distributions) appears to follow a more predictable trajectory over time that can be readily quantified (Assmann, 1970, p. 447; Mohler et al., 1978; Lorimer and Frelich, 1998; Podlaski, 2006). A systematic approach based on quantitative structural criteria would be useful in facilitating objective and repeatable methods of classifying stand stages. Developmental stages have significant ecological ramifications for matters as diverse as stand production rates, wildlife habitat, aesthetics, and carbon storage (Bormann and Likens, 1979; DeGraaf et al., 1998; Keeton et al., 2011). The density of large trees, for example, is highly correlated with aboveground tree biomass and potential carbon storage (Nunery and Keeton, 2010; Keeton et al., 2011; Carroll et al., 2012), and large trees provide important habitat for cavity-nesting birds and mammals (e.g., Johnson and Pelton, 1981). An understanding of long-term stand development under natural, 'baseline' conditions is an especially urgent task, as many rare old-growth remnants are potentially at risk of functional extirpation of dominant tree species by exotic insects and diseases (Ellison et al., 2005; Poland and McCullough, 2006; Dodds and Orwig, 2011).

Many studies have been conducted on the structure of old-growth forests (e.g., Antos and Parish, 2002; Svoboda and Pouska, 2008; Trotsiuk et al., 2012), but analysis of structural changes over time remains a difficult problem. Although it is possible to recognize old growth as a single stage (Oliver and Larson, 1996; DeWalt et al., 2003), there has been an increasing awareness that forests continue to change in structure and production rate after the old-growth threshold is reached. Based on simulations with the JABOWA model, Bormann and Likens (1979) predicted that old-growth northern hardwood forests would pass through three further stages of biomass accumulation: a late aggradation phase, a transition phase with peak biomass, and a steady state with reduced biomass and zero net growth. Spies and Franklin (1988) recognized various degrees of "old-growthness" in Pacific Northwest forests, and a number of investigators have provided evidence of continuous change in attributes as old-growth forests develop, such as coarse woody debris volumes, numbers of large trees, and soil carbon levels (Tyrrell and Crow, 1994; Luyssaert et al., 2008; Keeton et al., 2011). Yet interpretation of temporal changes in old-growth stands, especially in temperate deciduous forest, is often hampered by the rarity and small size of old-growth remnants. Often the small stands present at a given location only have one or two stages of development represented (e.g., Firm et al., 2009; Alessandrini et al., 2011).

A rare opportunity to study long-term forest development at a larger scale is provided by the existence of three sizable landscapes (23,000 ha) of late-successional northern hardwood forest with little past human disturbance in upper Michigan, USA. Previous work has suggested that these areas contain a mosaic of stands spanning all stages of development, from young pole stands originating after stand-replacing windstorms to all-aged, old-growth forests approaching a steady state (Lorimer and Frelich, 1998). Even old-growth stands differed widely in structure, with many having unimodal size distributions with variable mean diameters and a history of one or more moderate disturbances. In this study, we develop a systematic and quantitative classification of developmental stages for these forests of shade-tolerant species based on overstory and understory structure. These stages reflect progressive changes in the form of the diameter distribution from skewed unimodal to descending monotonic. The revised classification system recognizes eight stages of development, including four stages of old growth. An important objective of this study was also to evaluate the degree to which the stages reflect actual underlying temporal trends. This was done using a multi-faceted approach with long-term permanent plot records on sites with known stand histories, ecological inventories of stands spanning a wide range of stages on mesic sites, and computer simulation. The CANOPY model, which has been extensively tested across a wide range of stand stages (Hanson et al., 2011, 2012; Halpin, 2014), has opened up new possibilities for interpreting long-term temporal trends in data that otherwise could only be examined using the assumption of space-for-time substitution. While the classification system has been developed for northern hardwood forests in eastern North America, the general approach is probably applicable with modification to a number of other late-successional temperate forests (see Section 4.2).

A key point is that this method only identifies the probable position of each stand in a developmental series based on its structure. It does not identify either a specific stand age or time since the last stand-replacing disturbance, given that the latter approaches are not appropriate for multi-aged stands. As with traditional chronosequences, an underlying assumption of the method is that the stands being compared are of similar productivity, unless adjustments have been made for differences in growth rates and tree size among habitats. In mixed-species forests, it is also critical that the method be restricted to forests in which the component species have similar potential maximum diameters, maximum ages, and similar growth rates. Potential candidates are forests dominated by shade-tolerant and relatively slow growing genera such as *Fagus, Acer, Tsuga, Picea, Abies,* and *Thuja* (cf. Loehle, 1988). The method is not generally applicable as presented here in forests in which fast-growing species of low or moderate shade tolerance are mixed with slow-growing species of high shade tolerance. For example, forests of shade-tolerant species mixed with a substantial component of fast-growing species like *Pinus strobus* or *Liriodendron tulipifera* may not be suitable because large trees of the latter species may often be the same age or younger than smaller shade-tolerant canopy trees (Fajvan and Seymour, 1993; Oliver and Larson, 1996). The presence of large trees of fast-growing species would not necessarily signify that such stands are in a later stage of development than those with fewer large shade-tolerant trees.

2. Methods

2.1. Study areas

The three study landscapes in Michigan include the Porcupine Mountains Wilderness State Park, the Sylvania Wilderness on the