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Review

Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review

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ABSTRACT

Temperate forests have been fundamentally altered by land use and other stressors globally; these have reduced the abundance of primary and old-growth forests in particular. Despite many regional studies, the literature lacks a global synthesis of temperate old-growth structural characteristics. In this study we compare literature derived data on mature and old-growth moist temperate forests with the aim of: (i) exploring global commonalities; (ii) investigating sources of variability among systems; and (iii) highlighting data gaps and research needs. We compiled a dataset of 147 records from 93 papers, and analyzed a set of structural indicators: basal area, stem density, large living trees, live aboveground biomass, quadratic mean diameter, and coarse woody debris volume. These indicators were contrasted between mature and old-growth age classes at a global level and across continents and broad forest types, testing for significance through Monte-Carlo permutation procedure. We also related structural indicators to age, climatic and geographical descriptors. Our results suggest that all structural indicators vary across systems in relation to geographical, compositional, and climatic influences. However old-growth forests showed global commonalities in structure when compared to mature forests: significantly higher densities of large living trees, higher quadratic mean diameter, and higher amounts of live aboveground biomass and coarse woody debris. Furthermore we found inconsistency in the structural variables reported by different papers; lack of studies on temperate forests in Russia, and Western and Central Asia. The findings improve our understanding of old-growth structure and function, and will help inform sustainable forest management and conservation approaches world-wide.

Contents

Abbreviations: LLT, large living trees density; LAB, live aboveground biomass; QMD, quadratic mean diameter; CWD, coarse woody debris volume.

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1. Introduction

Temperate forests are generally more altered and reduced in extent globally than other forested biomes (Silander, 2001) due to their distribution at mid-latitudes with moderate climates, which are also some of the most heavily populated and developed regions of the world. About 35% of the world forests are considered primary (i.e. never cleared though subject to natural disturbances) but these mostly occur in tropical and boreal zones (FAO, 2010); according to one estimate less than 1% of the northern hemisphere's temperate broad-leaved forests remain in a primary condition (Silander, 2001).

Landscapes dominated by primary forests are comprised of complex patch mosaics and host a full range of stand development stages, from disturbance and cohort establishment to old-growth (Franklin et al., 2002). The latter is a late stage of stand development that typically does not occur or is rare in managed forest systems, and has been defined by many authors based on a combination of structural features, age, and sometimes human disturbance history (Wirth et al., 2009). The 'structural' approach, first developed through studies performed in the Pacific Northwest (Spies and Franklin, 1991), is useful because it can both be a good proxy of ecosystem function and is a readily measured surrogate for habitat of many taxa difficult to sample (Franklin et al., 2002; Burrascano et al., 2011).

Structural indicators, often combined with ecological and compositional information, have been proposed for temperate forests in North America (Franklin et al., 1981; Keddy and Drummond, 1996), Europe (Peterken, 1996; Nilsson et al., 2002), South America (Gutierrez et al., 2004) and China (Chen and Bradshaw, 1999). Nevertheless old-growth forests may display strong variation in their structure in different forest types (e.g. Jones, 1945; Burgman, 1996; Wells et al., 1998).

Such variation derives from the fact that the old-growth condition should be defined not only on the basis of a set of structures providing desired functions, such as habitat for late-successional biodiversity, but also of the developmental processes that produce those structures. However the lack of a global theoretical framework of temperate forest development has hindered broad application of a widely accepted process-based approach. Previous research on forest dynamics suggests considerable uncertainty in segmenting stand structural development, because many developmental processes operate continuously or episodically, often rendering discretely defined stages arbitrary (Franklin et al., 2002; Spies, 2004). Moreover, stand development may undergo several different pathways in relation to disturbance regimes and environmental controls (Donato et al., 2012). Furthermore, the age threshold to define developmental stages will differ by forest type and geographic region due to differences in stand development rates, tree longevity, disturbance regime and other factors related to these, such as climate and site conditions (Franklin et al., 1987; Motta et al., 2010). Recognizing these limitations, our review compares "mature" stands with stands classified as "old-growth". These largely age-based classes, commonly reported in the literature, are employed as surrogates for the developmental processes described in Franklin et al. (2002) and other models (e.g. Oliver and Larson, 1990). They generally correspond with the "maturation" (i.e. mature) and "vertical/horizontal diversification and pioneer cohort loss" (i.e. old-growth) stages proposed by Franklin et al. (2002).

We focus on late-successional stands since most temperate forests are either managed for wood production or reflect the long-term influence of human activities. As a consequence, old-growth forest structural features are underrepresented in most contemporary landscapes (Bauhus et al., 2009; Rhemtulla et al., 2009) and biodiversity provisioning and other functions associated with them are frequently impaired (Siitonen, 2001; Hatanaka et al., 2011). Though some extended rotation systems may approximate old-growth structural conditions (Keeton, 2006; Bauhus et al., 2009), most silvicultural regimes narrow the range of possible developmental processes as well as the type and spatial distribution of structures, since they do not allow the stands to develop past the maturation phase or they selectively remove certain structures, like large or dead trees (Hunter, 1999).

Our prediction was that moist temperate forests globally will share distinct differences when comparing mature to old-growth conditions, because stand structural heterogeneity (vertical and horizontal) is presumed to increase as late-successional stands develop. For example, coming out of the maturation phase a marked increase in coarse woody debris (CWD) volumes can occur (Harmon et al., 1986), and re-establishment of shade-tolerant trees in the understory initiates redevelopment of stand vertical complexity (Keeton and Franklin, 2005); while horizontal heterogeneity is primarily created by the shift from density-dependent to density-independent mortality (Franklin et al., 2002). These processes drive development of many structural characteristics associated with old-growth. Our review evaluates indirectly through a focus on structural indicators – whether these are universally operative or whether there is significant variation among systems.

Comparison between mature and old-growth forests allows identification of structures that could be promoted silviculturally in managed stands. There are a number of reasons why managers might be interested in this objective. For example, old-growth forests are known to host high plant (Aude and Lawesson, 1998; Burrascano et al., 2009), fungi (Odor et al., 2006; Persiani et al., 2010) and animal diversity (Mikusinski and Angelstam, 1998; McKenny et al., 2006; Winter and Moller, 2008). Recent studies have also shown the importance of old-growth forests in storing high quantities of carbon both as aboveground biomass (Keith et al., 2009; Keeton et al., 2010) and in soils (Zhou et al., 2006) and their ability, in some cases, to maintain positive Net Primary Productivity very late into stand development (Field and Kaduk, 2004; Luyssaert et al., 2008; Xu et al., 2012).

Based on the services they provide, old-growth forests represent an important reference point for evaluating human impacts on forest ecosystems, and for understanding forest development processes through observation of the temporal and spatial interactions between successional processes, disturbance events, and tree mortality (Peterken, 1996; Keeton, 2006; Rhemtulla et al., 2009; Hoover et al., 2012). Studying old-growth forests has long been considered the basis for developing natural disturbance-based (North and Keeton, 2008), 'close-to-nature' (Commarmot et al., 2005; Heiri et al., 2009) or 'natural dynamics' (von Oheimb et al., 2005) silvicultural systems able to emulate natural processes and fulfill socio-economic goals while maintaining a full range of