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# Multiple successional pathways and precocity in forest development: can some forests be born complex?

Daniel C. Donato, John L. Campbell & Jerry F. Franklin

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**Donato, D.C.** (corresponding author, ddonato@wisc.edu): Ecosystem & Landscape Ecology Laboratory, Zoology Department, University of Wisconsin, Madison, WI, 53706, USA
**Campbell, J.L.** (john.campbell@oregonstate.edu): College of Forestry, Oregon State University, Corvallis, OR, 97331, USA
**Franklin, J.F.** (jff@u.washington.edu): College of Forest Resources, University of Washington, Seattle, WA, 98195, USA

DCD and JLC contributed equally to this work.

## Abstract

**Background:** In forests subject to stand-replacing disturbances, conventional models of succession typically overlook early-seral stages as a simple re-organization/establishment period. These models treat structural development in essentially 'relay floristic' terms, with structural complexity (three-dimensional heterogeneity) developing primarily in old-growth stages, only after a closed-canopy 'self-thinning' phase and subsequent canopy gap formation. However, is it possible that early-successional forests can sometimes exhibit spatial complexity similar to that in old-growth forests – i.e. akin to an 'initial floristic' model of structural development?

**Hypothesis:** Based on empirical observations, we present a hypothesis regarding an important alternative pathway in which protracted or sparse forest establishment and interspecific competition thin out tree densities early on – thereby precluding overstorey canopy closure or a traditionally defined self-thinning phase. Although historically viewed as an impediment to stand development, we suggest this process may actually advance certain forms of structural complexity. These young stands can exhibit qualities typically attributed only to old forests, including: (1) canopy gaps associated with clumped and widely spaced tree stems; (2) vertically heterogeneous canopies including under- and mid-stories, albeit lower stature; (3) co-existence of shade-tolerant and intolerant species; and (4) abundant dead wood. Moreover, some of these qualities may persist through succession, meaning that a significant portion of eventual old-growth spatial pattern may already be determined in this early stage.

**Implications:** The relative frequency of this open-canopy pathway, and the degree to which precocious complexity supports functional complexity analogous to that of old forests, are largely unknown due to the paucity of naturally regenerating forests in many regions. Nevertheless, recognition of this potential is important for the understanding and management of early-successional forests.

## Introduction

In the last two decades a great deal of attention has focused on the development of structurally complex forests (Spies & Franklin 1991; FEMAT (Forest Ecosystem Management Assessment Team) 1993; Lindenmayer et al. 2000; Keeton 2006; Wilson & Puettmann 2007; Bauhus et al. 2009; Strong 2009; Keeton et al. 2010; Wang et al. 2010; Zenner et al. 2011). Structural complexity – heterogeneity in canopy architecture, stem size and live and dead biomass – is linked to several major ecosystem functions (Spies & Franklin 1991) and is used as a surrogate indicator for biodiversity (McElhinny et al. 2006). In temperate regions subject to stand-replacement disturbances (e.g. severe fires, windstorms), forest structure is generally described as developing through a probabilistic succession, attaining spatial complexity only after tens or hundreds of years, after a period of competitive exclusion (self-thinning) and canopy gap formation (Bormann & Likens 1979; Oliver & Larson 1996; Franklin et al. 2002). Complex structure and function have therefore largely been attributed to late-successional forests. However, is it possible that the onset of heterogeneity exhibited by old forests can sometimes occur in the first few years following stand replacement? Is it


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useful to view the structural heterogeneity of some naturally regenerating forests as 'precocity' (i.e. advanced development) towards old-growth character, rather than simply delayed development as it is typically viewed?

A similar question has graced the vegetation science literature for decades, but mainly for community composition rather than structure (Clements 1916; Gleason 1917; Egler 1954; Connell & Slatyer 1977; Pickett et al. 2009). In the well-known models of 'relay' and 'initial' floristics, post-disturbance ecosystems either pass through a series of compositional stages, each facilitated by the preceding stage, or are initially composed of species present throughout succession but in varying proportions over time. Although this duality is now viewed as oversimplified (elements of both models occur within systems, Kayes et al. 2010), these and related frameworks have proven central to our understanding of vegetation ecology and remain important foundations for contemporary land management (Halpern & Franklin 1990; Bartha et al. 2003; Walker et al. 2007; Pickett et al. 2009). We suggest it is time to turn a similar eye to the development of structural characteristics during forest succession. While a great deal of attention has been paid to late-successional forest complexity (described so far in essentially 'relay' terms), early-successional complexity has been ignored in many regions, viewed instead as a simple re-organization phase or a problematic condition preceding desirable stand development (Swanson et al. 2011). This perception may arise, in part, from widely applied successional models that were constructed around managed disturbances such as clear-cut timber harvest or old-field succession, in which early-seral structure was often simplified. However, as post-disturbance management objectives broaden beyond the simple acceleration of tree growth, there is a need to better under-


**Fig. 1.** Key structural states exhibited by many temperate forests. These examples are all from mesic montane Douglas-fir communities of the Pacific Northwest, USA. Panel (**a**) shows the complex structure of a naturally regenerating forest 30 yr after stand-replacing disturbance, while panel (**b**) shows the homogenous closed canopy of an adjacent stand subject to intensive planting following the same disturbance event. Panel (**c**) shows a planted forest undergoing stem exclusion ca. 60 yr following clear-cut harvest. This closed-canopy stage is a major bottleneck in terms of structural complexity, with a single-layer overstorey, relatively homogenous stem sizes and minimal understorey structure. Panel (**d**) shows a structurally complex old-growth forest ca. 300 yr after stand replacement, with vertically distributed canopy foliage, a dense woody understorey and irregular stem spacing and sizes. Note the general parallels in spatial pattern and overstorey/understorey arrangement between the old-growth and natural young stands. We hypothesize that, when the open-canopy pathway is followed (skipping the dense stem-exclusion stages), these patterns can persist throughout succession.


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stand the ways in which early-successional forest can exhibit ecological complexity.

Here we explore the hypothesis of precocity in forest development, a potentially common but under-appreciated pathway in which sparse or protracted tree establishment and interspecific competition preclude overstorey canopy closure (Fig. 1). Forests developing along this open-canopy pathway may exhibit key structural features typically associated only with late succession, several decades earlier in stand development. These include: (1) clumped and widely-spaced trees; (2) vertically heterogeneous crowns and canopies; (3) co-existence of under-, mid-, and overstories; and (4) facilitation of shade-tolerant species. This early onset structural complexity likely has significant implications for the function of these systems as they mature. Components of this hypothesis have been suggested by others (e.g. Kint et al. 2004; Fujimori 2001; Franklin et al. 2002; Zenner 2005), but have not been integrated into a cohesive developmental model or explored regarding the timing of structural complexity.

We illustrate this hypothesis using the example of succession following stand-replacing disturbance in Douglas-fir forests of the Pacific Northwest, USA. However, the mechanisms we propose are general and may have relevance to several other forest types around the world, in systems where both early- and late-successional associates are prevalent during early stages (e.g. conifers and broadleaf shrubs), and where post-disturbance tree establishment can be sparse or delayed. Such ecosystems include the Sierra Nevada and coastal mountains of California (Bock et al. 1978; Harvey 2010), portions of the southeastern USA (Christensen 2000), mixed-wood boreal forests (Cumming et al. 2009; Strong 2009), eastern North American hardwood/conifer forests (Keeton 2006), some Eucalyptus forests of Australia (Attiwill 1994; Wood et al. 2010), mixed conifer–hardwood forests of Europe and Asia (e.g. Kint et al. 2004; Osawa 1992), and Mediterranean climate regions such as Spain and southern Africa (Lloret et al. 2005; Adie & Lawes 2009).

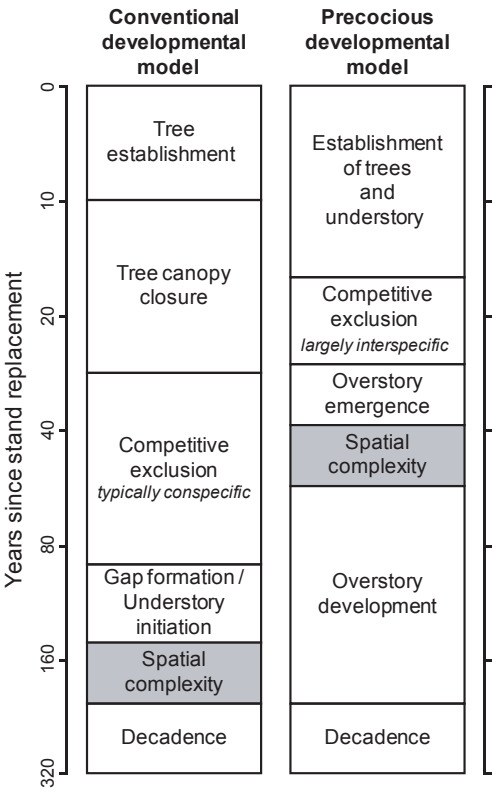


**Fig. 2.** Comparison of conventionally described and precocious forest succession, with approximate timing of each phase. Key differences in precocious succession include slower or lower-density tree regeneration, the immediate establishment of what will become the late-successional understorey, a shift in the competitive exclusion phase to very early in stand establishment (among regenerating trees and non-tree vegetation rather than among only trees in later decades), and that overstorey canopy closure may not occur during stand development. Early competition from non-tree vegetation results in differential mortality and/or stratification of tree saplings (the eventual overstorey), leading to lower tree densities, spatial heterogeneity in stem arrangement (gaps, clumps) and vertically complex foliage distribution. These elements of complexity therefore manifest much earlier than expected under the conventional model.

## Alternate forest developmental pathways

### Conventional successional model – closed canopy

Although the number of pathways by which forests develop is arguably infinite and influenced by chance events, the degree to which they fall into similar groupings has led to the construction of generalized succession models. The most broadly applied models of temperate forest development (e.g. Bormann & Likens 1979; Oliver 1981; Oliver & Larson 1996) generally involve four distinct stages: stand initiation, stem exclusion, gap formation/understorey re-initiation and old growth. This conventional model is widely applied and effectively describes stand development in many cases, particularly following silvicultural treatments such as clear-cutting and dense plantation establishment (Fig. 2).

According to this conventional model, severe disturbances are followed by establishment of a dense, largely even-aged cohort of pioneer tree species. Growth of this cohort leads to canopy closure, arguably the most dramatic developmental episode in the life of a stand (Smith 2000; Franklin et al. 2002). This even-aged tree cohort effectively dominates the site during subsequent decades, with a single-layer overstorey and minimal understorey (Fig. 1). Diversity of many organismal groups is lowest during this closed-canopy stage (Spies & Franklin 1991). Canopy closure is followed by a competitive exclusion


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phase (i.e. stem exclusion or self-thinning) in years ca. 30–100, during which keen competition for growing space and resources leads to density-dependent tree mortality. Only after this thinning and further mortality create canopy gaps (generally after 100–150 yr in many forests) do significant under- and mid-stories develop, leading to horizontal and vertical complexity (Figs 1–3). This late-successional complexity is often a management objective, with any attention given to young stands usually aimed at accelerating tree growth or reducing the homogeneity of a closed canopy (e.g. Hobbs et al. 1992; Wilson & Puettmann 2007). Early-successional stands have been perceived as structurally simple due in part to a focus on managed stands (post-timber harvest), which have historically been simplified due to removal of biological legacies such as dead wood, dense tree planting and active vegetation control (Bock et al. 1978; Swanson et al. 2011).

### Precocious successional model – open canopy

While developmental pathways involving canopy closure may be common, natural succession after disturbances such as wildfire is highly variable and often deviates from this sequence (Tappeiner et al. 1997; Franklin et al. 2002; Turner et al. 2009). Some stages may be skipped entirely and others prolonged. In many forest types, tree establishment can be a protracted process due to large patch sizes, distant seed sources, variable seed production years or unfavourable environmental conditions (Romme et al. 1998; Greene & Johnson 2000; Eugenio et al. 2006). This often results in substantially lower tree densities than described in conventional succession models, potentially by orders of magnitude. Further, early competition from other vegetation (e.g. woody shrubs) can slow tree growth and recruitment significantly. These limits to forest estab-

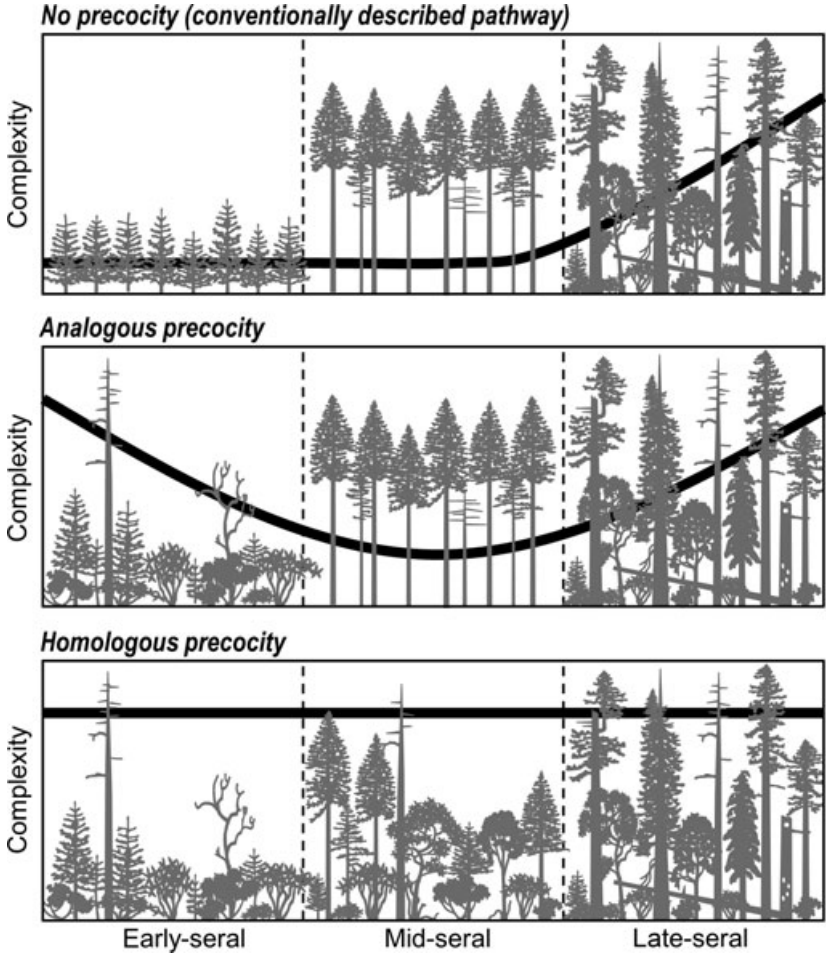


**Fig. 3.** Three alternate successional pathways for forest development, showing the relative levels of structural complexity exhibited in each seral stage. In the conventional successional model, both early- and mid-seral conditions are dominated by a relatively even-aged tree cohort, and structural complexity does not arise until the latest stage of development. In the case of analogous precocity, early-successional stands exhibit structural complexity in some ways similar to that in old stands, but canopy closure results in reduced complexity during mid-succession. In the case of homologous precocity, the lack of a tree canopy-closure phase results in a continuity of complexity throughout forest development.


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lishment can lead to open vegetation communities that may persist for decades, and have been viewed as impediments to stand development, prompting intensive management efforts to establish dense tree cover (e.g. Hobbs et al. 1992; Swanson et al. 2011).

However, we suggest that slow, sparse or suppressed tree establishment may actually accelerate the development of certain forms of spatial complexity that are typically associated only with late-successional forests (see Fig. 2). Low-density tree regeneration and competition with shrubs can function to thin out and stratify regenerating trees early on, replacing the conspecific exclusion phase, which is commonly expected to take ca. 100 yr after disturbance, with an interspecific exclusion phase that may transpire in the first ca. 30 yr. The resultant lower density of establishing trees – the eventual overstorey – may mean that overstorey canopy closure never occurs in such stands (see Fig. 1). Furthermore, because spatial features such as gaps, overstorey stem distribution and understorey presence are already established (rather than by new gap formation in >100-yr-old stands), a significant portion of eventual old-growth spatial pattern may already be determined in this early phase. This suggests that protracted overstorey establishment may not be a mere obstacle on the way to complex old-growth condition, as commonly viewed, but rather lead to important structural complexity much earlier.

## Example from western North America

The precocious model of forest development we describe above could theoretically apply to any system in which post-disturbance tree establishment can vary widely in initial density or rate, where both early- and late-successional associates are prevalent during early stages, and/or where long-lived pioneer species persist into the latest stages. An example with which we are most familiar is the montane Douglas-fir (*Pseudotsuga menziesii*) region of the Pacific Northwest, USA, in which forests are dominated by long-lived conifers that regenerate following stand-replacing fires, but also contain important components of broad-leaf hardwoods and shrubs. Many of these broad-leaf species respond to severe disturbance by sprouting vigorously from basal meristems or by rapid in-seeding (e.g. Hobbs et al. 1992).

Natural post-fire conifer regeneration in this region is often (although not always) highly irregular in both time and space, due to varying seed years and post-fire environmental conditions (e.g. Isaac & Dimock 1960; Tappeiner et al. 1997; Poage & Tappeiner 2002; Shatford et al. 2007; Donato et al. 2009a). Reconstructive studies in old stands (Tappeiner et al. 1997; Sensenig 2002) suggest that the number of post-fire seedlings recruited into emergent saplings is often very low to start, in the order of 100–120 stems $ha^{-1}$ – equating to nearly 10-m spacing on average – and that trees grew in relatively open conditions. Likely, these interspaces were occupied by broad-leaf hardwoods and shrubs (Tappeiner et al. 1997). Regenerating conifer seedlings are often rapidly overtopped by sprouting broad-leaf vegetation, resulting in localized mortality and a skewed size distribution of young conifers (Harrington et al. 1991; Tappeiner et al. 1997; Shatford et al. 2007). With this reduced density, conifer canopy closure and a decades-long period of conspecific stem exclusion are not likely to occur. Once conifers emerge above broad-leaf vegetation, these stands may develop along an open-canopy pathway that differs significantly from the conventional closed-canopy model.

## Parallels between precocious early-successional and old-growth forests

Studies conducted in old-growth forests have identified several structural characteristics (Table 1) attributed to

**Table 1.** Structural attributes contributing to forest complexity.

| Structural attribute | Old growth | Natural/precocious early-successional | Conventionally defined early successional |
|---|---|---|---|
| Vertical heterogeneity (continuous or multi-layered canopy) | Yes | Yes | No |
| Horizontal heterogeneity (irregular stem spacing, gaps) | Yes | Yes | No |
| Well-developed/dense understorey | Yes | Yes | No |
| Large standing snags | Yes | Yes | No |
| Abundant large-diameter woody debris | Yes | Yes | No |
| Co-existence of shade-tolerant and intolerant species | Yes | Yes | No |
| De-coupling of age and size (diverse growth rates) | Yes | Yes | No |
| Large branch systems and/or spreading crowns | Yes | Earlier | Later |
| Decadence (broken/multiple tops, bole rot, cavities) | Yes | Yes | No |
| Abundant/diverse epiphytes | Yes | No | No |
| Abundant large live trees | Yes | No | No |


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late-successional stages (e.g. Spies & Franklin 1991; Lindenmayer et al. 2000; McElhinny et al. 2006). These include vertical heterogeneity (e.g. emergent crowns, multi-layered or continuous canopy, vegetated ground layer), horizontal heterogeneity (e.g. tree diversity, canopy gaps, stem clumping), irregularity in physiognomic form or 'decadence' (e.g. broken or multi-apical forms, dead tops, bole rot, cavities), and large live and dead structures. We contend that, with the exception of abundant large live trees, naturally regenerating early-successional forests are at least capable of exhibiting all of these structural attributes.

The analogies we draw between complex structures in early- and late-successional (old-growth) forests arise largely from horizontal and vertical heterogeneity, and from biological legacies such as dead wood. The combined processes of seed dispersal, germination, early survival and competition lead to patchy and clumped rather than even or random tree distribution. Patchy stem distribution is often considered a key feature of old-growth stands, but natural stem distributions in young stands can be similarly heterogeneous. Further, gap-forming processes that operate late in succession can also occur early in stand development: toppling of snags from the fire-killed overstorey may contribute to patchy early mortality and heterogeneous biomass distribution (Lutz & Halpern 2006). Intermediate disturbances of varying severity, such as wind-throw and surface fires, can also create gaps and structural variation throughout succession (Attiwill 1994; Emborg et al. 2000; Zenner 2005; Turner et al. 2009).

Higher variance in tree heights in precocious young stands likely results in a more vertically heterogeneous, or multi-layered, distribution of foliage than is found in closed-canopy stands of the same age. This variance is due in part to variation among overstorey crowns but also between these crowns and those of other vegetation components. Notably, the same stand components that will likely form the late-successional under- and mid-stories (e.g. hardwoods in parts of the Douglas-fir region) can be established more or less immediately after disturbance; thus, diverse canopy layers are instigated during stand establishment rather than later on (Fig. 2).

Another feature that may arise early is irregular crown morphology and large branch systems. Under conventional succession models, the development of spreading crowns and large branches does not occur until advanced age, well after canopy closure and re-opening (Oliver & Larson 1996; Franklin et al. 2002). If canopy closure does not occur, many trees develop in relatively open light conditions after emerging over early competitors, resulting in more spreading crowns and retention of large lower branches (Sensenig 2002). Reduced competition for light among emergent trees may also lessen the crown uniformity typically associated with mid-seral trees. The multi-stemmed sprout forms of early-seral shrubs further contribute to canopy irregularity.

Structural complexity may also arise from the early expression of compositional diversity. In addition to the well-documented variety of herb, graminoid, shrub and tree forms in open stands (Halpern & Franklin 1990; Donato et al. 2009b; Swanson et al. 2011), shading by early-successional shrubs may also facilitate the co-establishment of shade-tolerant tree species, which could effectively accelerate compositional succession by 'as much as several hundred years' (Zavitkovski & Newton 1968).

Also like old-growth forests, young forests often contain large quantities of woody debris in the form of large snags and logs, a legacy of the previous stand (e.g. Lindenmayer et al. 2000). The primary structural characteristics of old growth for which there are no analogies in early-successional stands are those associated with abundant, large-diameter live trees.

## Homology vs analogy of complexity

In forests with stand-replacing disturbance regimes, conventional models of forest development do acknowledge structural complexity as an attribute of both the earliest and latest seral stages (Spies & Franklin 1991; Franklin et al. 2002). But in these models, the foundations of early- and late-successional complexity are typically viewed as being somewhat independent, with early-successional complexity resulting from stochastic re-colonization and biological legacies, whereas late-successional heterogeneity results from cumulative mortality processes following canopy closure (e.g. Lindenmayer et al. 2000). However, in cases where canopy closure and competitive exclusion do not occur, there is a potential for early-successional complexity to persist without interruption into the oldest age classes. In this scenario, the relationship between early- and late-successional complexity is one of actual homology rather than simply analogy (Fig. 3). This persistence of early heterogeneity suggests that structural succession can exhibit under-appreciated parallels with 'initial floristics' developmental models. But such continuity of complexity (Fig. 3) depends on a lack of overstorey canopy closure from which new, independent complexity is derived ('relay floristics' concept of structural development).

The most obvious example of such homologous complexity is the spacing of emergent trees. In systems with very long-lived pioneer species (e.g. Douglas-fir in the Pacific Northwest), an absence of a canopy closure stage may mean that the spatial distribution of large trees in old growth could result as much from patterns of initial tree establishment as long-term patterns of mortality. In addi-


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tion, variation in early growth rate of trees has been found to be a very strong predictor of tree size at 100–300 yr of age (Poage & Tappeiner 2002); in this way, early stratification (and size differentiation) of trees emerging from early interspecific competition may still be apparent in old-growth stands.

## Conclusion and management relevance

The perspective presented here is meant to explore the concept of multiple pathways of structural succession in forest ecosystems, and to challenge conventional notions as to when in development structural complexity can be exhibited. We use basic tenets of vegetation successional theory, drawing parallels with 'relay' vs 'initial' floristic frameworks to posit that, in naturally regenerating young forests, certain aspects of structural complexity may arise much sooner than expected under conventional forest succession models. Conventional models (e.g. Oliver 1981; Oliver & Larson 1996), although meant to apply to a broad range of disturbances, were fundamentally constructed around experiences with relatively simplified post-clear-cut and old-field succession, and therefore have not adequately characterized the complexity of structural succession following a full range of natural disturbances.

Ecosystem function in forests is often directly related to structural complexity (e.g. Franklin & Van Pelt 2004), but this relationship has been best described in old-growth forest. Proving positively that naturally regenerating young forests can exhibit functional complexity like their old-growth counterparts is a difficult task, due to both the variability of successional trajectories and the difficulties in identifying comparative metrics of complexity. Despite differences in stature, both early- and late-successional canopies may support equally complex functioning and biodiversity. Indeed, animals come in all sizes and spatial complexity is fractal. Small-stature forests therefore do not necessarily provide a smaller range of habitat than large-stature forests. While scientific and management focus has been on the structural complexity of large-stature forests and the habitat relationships of associated organisms, an emerging body of literature shows that a similar or even greater number of species such as songbirds and butterflies are closely associated with the structural and compositional features of small-stature pre-forest vegetation (Betts et al. 2010).

Various treatments have aimed to enhance the complexity of mid-seral forest stands, many of which are the legacy of past harvests, toward that of late-successional character (e.g. FEMAT (Forest Ecosystem Management Assessment Team) 1993; Keeton 2006; Wilson & Puettmann 2007; Bauhus et al. 2009). With the recent upsurge in wildfire activity in many parts of the world generating more young forest stands, this attention has become directed toward early post-wildfire ecosystems. To what degree should silvicultural activities historically employed to speed fibre production (e.g. tree planting, vegetation control) be used to accelerate the development of late-successional characteristics?

Silvicultural techniques can speed early tree establishment and growth (Hobbs et al. 1992), and some post-disturbance management encourages complexity (e.g. mixed-species planting, irregular spacing of seedlings, retention of coarse woody debris). However, many of these practices are implicitly geared toward acceleration of 'recovery' rather than incorporating the protracted establishment period, wherein precocious complexity is most likely to arise. For management objectives focused on timber production, actions that speed tree establishment and growth are well tested and clearly effective (i.e. the end justifies the means). When, however, management objectives are explicitly focused on ecological complexity, perhaps the journey is as important as the destination.

Fire exclusion and aggressive reforestation have left many landscapes mostly free of naturally regenerating forests for several decades. As a result, any functional distinctions between the open- vs closed-canopy pathways are largely unexplored. Similarly unknown is the relative frequency (or causes) of each pathway among the many regions with variable rates of natural post-disturbance tree establishment, and/or mixed assemblages of early- and late-successional associates (e.g. conifers and broad-leaves). There is a strong need for foundational studies aimed at the structural and functional qualities of natural early-successional forests. Only through such studies can the real capacity for precocious complexity be fully determined.

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