Extension Note



BiodiversityManagement Concepts
in Landscape Ecology

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Seral Stages across Forested Landscapes: Relationships to Biodiversity part 7 of 7¹

Introduction

Various plants and animals rely on different forest ecosystem "stages" to meet their habitat needs. Grizzly bears, for example, can range over hundreds of square kilometres in search of the food resources available in open and young forests before hibernating deep in mature forests. Some plant species can only develop on open, treeless, freshly disturbed sites, while certain canopy-dwelling insects spend their entire lifetime on the broad lichen- and moss-covered limbs of a single ancient spruce. During spring and summer, deer may sample tender herbs in clearcut areas, but, in severe winters, retreat several kilometres to protective old-growth

Landscapes and the ecosystems that compose them "age" through time. The process of forest aging called "succession" transforms the composition of forested ecosystems as biotic communities respond to and modify their environment. Succession is an important topic in landscape ecology because of its significant effects on landscape diversity and the subsequent biological diversity and viability of various plant and animal populations.

The Forest Practices Code acknowledges the importance of landscape

ecology concepts by enabling district managers to designate planning areas called landscape units, each with specific landscape unit objectives. The *Biodiversity Guidebook* (B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks 1995), a component of the Code, recommends procedures to maintain biodiversity at both the landscape and the stand level. This approach, which uses principles of ecosystem management tempered by social considerations, recognizes that the habitat needs of most forest and range organisms are met if a broad range of forest stand ages ("seral stages") are maintained across landscapes.

This extension note is the seventh in a series designed to raise awareness of landscape ecology concepts and to provide background for the ecologically based forest management approach recommended in the Biodiversity Guidebook. The focus here is on seral stages. We first define succession and seral stages. We then discuss the evolving views of ecosystem dynamics and succession theory, the role of disturbances in the current general model of forest development, and the influence of different seral stages on biodiversity. We conclude by suggesting how these concepts can be applied in landscape-level planning for biodiversity.

January 2000. Policy direction for biodiversity is now represented by the Landscape Unit Planning Guide. This Extension Note should be regarded as technical background only.



table 1 Classification of ecosystem characteristics according to their expected pattern of change during succession in Douglas-fir forests (from Spies and Franklin 1988).

Characteristics following a "U-shaped" curve (Curve 1)

Amount of coarse woody debris
Number of large snags
CWD as percentage of total
ecosystem biomass
Heterogeneity of understorey
Plant species diversity
Mammal diversity

Characteristics following an "S-shaped" curve (Curve 2)

Average tree size
Diversity of tree sizes
Incidence of broken tops
Forest floor depth
Surface area of boles and branches

Wood biomass

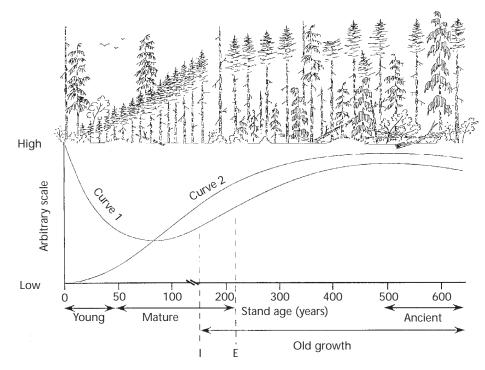


figure 1 Generalized curves of change in ecosystem attributes with long recovery periods after disturbance in old-growth Douglas-fir forests. These curves were developed for Douglas-fir forests; however, the patterns are expected to apply to other forest types in British Columbia, although the age scale will vary among forest types (adapted from Spies and Franklin 1988).

Seral Stages and Succession: Definition

In ecological terms, a "sere" is the series of biotic communities formed by the process of ecosystem development called succession. In forested landscapes, the various vegetation communities that occupy disturbed sites and make up a sere are called "seral stages." Seral-stage communities consist of vegetation types that are adapted to the site's particular set of physical and biotic conditions. In the unmanaged forested landscape, various natural disturbance agents (such as fire, windthrow, landslides, and insects) are responsible for creating forests containing a full range of stand ages.

For example, a forested landscape that has experienced a severe fire does not recover to its former state in one step. Instead, various types of vegetation will supplant each other over time on the burnt-over lands. In this process, some components of the

physical environment are altered, which influences the conditions for subsequent plant communities. Initially, species adapted to more exposed conditions will colonize the disturbed sites. These species create shade and influence the soil conditions by adding organic material as their leaves, stems, and roots decay. This produces favourable conditions for the next seral community of young coniferous trees and deciduous shrubs and trees, which displace the pioneers.

The process of succession is not restricted to plant communities. It also occurs at the ecosystem level within animal and microbial communities. These communities can experience sequential changes that are concurrent with vegetative seral stages. Seral stages can therefore be defined to include microclimate, soil, vegetation, animal, and microbial components (Kimmins 1987).

Although the word "stage" implies a simple linear sequence, contemporary ecological theory does not view succession as a predictable process where distinct assemblages of vegetation replace one another at each stage until an obvious end point is reached. Instead, succession can be viewed as a cyclical continuum where seral stages often overlap. For example, because the temporal distribution of species is highly variable, some plants are present throughout this cycle, while others appear only for short periods when specific conditions occur. However, the idea of "seral stages" continues to be a useful conceptual tool.

Seral Stages and Succession: Ecological Principles

Changing views of ecosystem dynamics

Like the landscapes and ecosystems they attempt to describe, theories of succession also evolve. Early in this century, F.E. Clements' theory of succession presumed that plant communities moved through an orderly, directional, and non-random process of change in species composition over time. This process was determined by regional climate and resulted in a stable, climax community where further changes were inconsequential (Spies 1996).

This theory supported the prevailing view that environments were essentially homogeneous and that natural systems such as forests were "closed" to outside influences. A state of ecological balance existed within forested communities. Genetic, species, and ecosystem diversity remained relatively stable, but changed gradually through natural succession. Therefore, environmental fluctuations were not important and natural disturbances played no role in plant succession. This steady-state equilibrium model mirrored the popular concept of the "balance of nature" (Parminter 1998).

Ecologists now recognize that ecosystems may not always exist in a state of equilibrium. Over the long term, the most frequent state for many ecosystems is that of non-equilibrium. Landscapes are routinely viewed as heterogeneous collections of diverse ecosystems recovering from the most recent disturbance. Environmental homogeneity is temporary at best. In fact, a great deal of the diversity we see in ecosystems is a function of variations in disturbance frequency and intensity.

Disturbances, scale, and succession

Current views of succession emphasize ongoing process rather than the climax community as the stable end point or product. Natural disturbance regimes are now accepted as a major influence on forested landscapes, significantly altering landscape structure and pattern through effects on stand development and, ultimately, species composition.2 Indeed, many forms of disturbance (e.g., fire) are critical for an ecosystem's regeneration and maintenance (Parminter 1998). However, disturbances alone do not determine community structure. The natural process of species recruitment in a heterogeneously disturbed, patchy environment will also influence the overall structure of a forest community.

The concepts of spatial and temporal scale are pivotal when discussing whether equilibrium or non-equilibrium conditions exist in the forested landscape (Rogers 1996). Non-equilibrium conditions likely result when the typical spatial scale of the disturbance approaches or exceeds that of the landscape units (Parminter 1998). Where large-scale fire, windstorms, disease, or insect infestations occur regularly, forests are unlikely to reach a steady state.

For example, forests in most boreal regions are characterized by relatively

² Part 2 of this Extension Note series (Disturbance Ecology) contains more information about natural disturbance regimes.

frequent, large-scale, stand-destroying disturbances that culminate in a coarse-grained mosaic with large patches of relatively young, even-aged stands. On the other hand, temperate rainforests experience large-scale disturbance infrequently, while small-scale disturbances are fairly common. This results in a finer-grained mosaic of older, often uneven-aged forest patches with a complex within-stand structure and a condition that approaches equilibrium (Lertzman et al. 1997).

A general model of forest succession

The individual forest stands comprising a landscape evolve in a complex and diverse manner. Their development is a function of the initial disturbance, existing environmental patterns and species mix, and intermediate disturbances. However, some general patterns of development appear across a wide range of forest types and locations. Following a disturbance, forest renewal typically takes place through a series of successional stages called:

- establishment (e.g., early/young seral);
- thinning, or stem exclusion (e.g., mid-seral);
- transition (e.g., mature seral); and
- shifting mosaic (e.g., old seral) (Spies 1996).

These idealized stages can encompass many spatial and temporal scales depending on the site's disturbance history and productivity. For instance, successional development can be initiated by disturbances at the gap, patch, stand, or landscape level (Rogers 1996). Multiple disturbances can leave patches of several different previous stands, which can create a mixture of phases occurring within a stand horizontally, vertically, or both. The type of propagules available at critical times during stand development will also govern the nature of forest regeneration (Spies 1996).

Establishment Also called stand initiation, this phase is characterized by an abundance of sites largely free from competition by established plants. These sites are colonized by plants from three general sources:

- pioneer herb or shrub species (both natives and exotics), which are well adapted to exposed conditions, and shade-intolerant tree species (both groups germinate from seed banks or disseminate from nearby seed sources);
- seedlings and saplings that survived the disturbance and are released with the removal of the overstorey; and
- 3. sprouting from belowground portions of plants injured by the disturbance.

The gaps, patches, or stands affected experience rapid changes in species dominance as a mix of old and new species develops. A mosaic evolves, which includes trees, shrubs, herbs, dead wood (both standing and downed), and bare ground, that reflects the existing microsite conditions, the previous stand's composition and structure, and the nature of the incipient disturbance.



figure 2 Establishment

Thinning This phase is characterized by the closing up or consolidation of the tree canopy, which provides more shade and tends to exclude shrubs, herbs, and tree species intolerant of shade. Typically, the number of species decreases during this phase as:

- understorey establishment and growth declines;
- understorey mortality increases; and
- shade-intolerant tree mortality increases.



figure 3 Thinning



figure 4 Transition and Shifting Mosaic

As the height of the forest increases, two relatively distinct layers emerge: an upper layer of canopy trees and a sparse lower layer of dying or surviving shrubs and herbs. Although more shade is available during this stage, the population of shadetolerant trees may not necessarily reestablish because of loss of seed sources, slow rates of dispersal, or excessive competition (Spies 1996). **Transition** Because of its extreme variability, this "maturation" phase of the forest development process is the least understood. It is consequently difficult to classify and, depending on the location, may be divided into several subphases.

Depending on forest type and disturbance history, this phase can last from less than 100 to more than 1000 years. The changes during this stage are of a diverse and gradual nature, with successive adjustments to population, stand structure, and vegetation processes (e.g., tree size, live biomass, and diversity of tree sizes and canopy layers peak; coarse woody debris declines to its lowest amount before increasing). The trees of the establishment stage slowly die out, while canopy gaps infill with new trees and understorey release increases (Spies 1996).

Shifting mosaic This final phase is marked by a shifting pattern of relatively small, patchy disturbances that create gaps of various shapes and sizes (e.g., individual or small groups of canopy trees die). This allows resources to be released for new trees in the understorey layer and for the increased height growth of trees in the lower and middle canopy layers. The resulting changes to forest composition and structure appear very small or even non-existent, and therefore this stage is often described as a stable, steady state or "climax." However, it is still vulnerable to larger disturbances and climate change.

It may typically take a severely disturbed site many hundreds to more



figure 5 Fire succession and seral stage development, showing the abundance of trees, shrubs, and herbs, respectively (from Stickney 1980)

than 1000 years to reach this phase. Consequently, forests at this stage of development are uncommon in currently logged landscapes or those that experience frequent natural disturbances.

Seral stages and biodiversity

The diversity of species and their total numbers vary greatly with successional stage (see Figure 5). Generally, the early herb/shrub (establishment) and mature to old-growth (transition to shifting mosaic) stages contain the greatest number of species. This pattern is common for many groups of organisms, including vascular plants, birds, fishes, and many classes of invertebrates. For example, mammal species richness in Douglas-fir forests is highest early in succession, drops to a much lower number of species after the forest canopy closes (i.e. during the thinning phase), and then increases to moderate levels in the mature and old-growth stages (Harris 1984).

The early-seral plant species of the establishment stage are relatively flexible in their habitat requirements and are capable of rapid site colonization. Species associated with the late seral stages of the shifting mosaic phase may have more specialized habitat needs and often require the large old trees and particular stand structures available in old-growth forests (e.g., large snags, wildlife trees, and coarse woody debris).

Old-growth forests represent the seral stage that is most reduced by intensive timber management. Consequently, these forests are of particular interest for landscape planning and biodiversity management because various species depend on this seral stage (Steventon 1994). For example, some plants (e.g., epiphytes such as arboreal lichens) and invertebrates are known to depend on biologically mature forests and the interior microclimate of old-growth stands (Steventon 1994). Therefore, it is

imperative that an adequate number and area of old forests are maintained over the landscape, not only because they represent one portion of the successional sequence, but also to support viable populations of the biologically diverse species that depend on this type of habitat (MacKinnon 1998). In regions where few old-growth forests are left, future management may focus on "growing" old stands, thus maintaining sufficient habitat for all species of a forest landscape, not just those associated with younger forests (Hunter 1990).

Applying the Principles: Achieving a Broad Range of Seral Stages

To successfully manage forested landscapes, the characteristics of the vegetation and the rates and patterns of succession in the area must be understood (Steventon 1994). The province's natural disturbance regimes have created landscapes with vastly differing patterns of forest stand age or seral stage distribution. For instance, landscapes that experience less frequent stand-initiating disturbances have a greater quantity of old seral forests, and consequently have more species adapted to older forests, than do landscapes with more frequent disturbances.

A coarse-filter approach to manage biodiversity at the landscape level should:

- protect old growth and other biologically important ecosystems; and
- maintain a range of seral stages (Steventon 1994).

Guidelines to sustain the diversity of naturally occurring seral stages are provided in the *Biodiversity Guidebook* by natural disturbance type. This ecosystem management approach assumes that deviations from the natural distribution of seral stages will increase the risk to biodiversity, whereas less change will decrease the risk.

The general goal is to have a variety

of patch sizes in various seral stages to meet the needs of a diverse range of species. Several management procedures can achieve this objective. For instance, the proportion of a landscape in various seral stages is determined by the overall rate of cut and the physical layout of the harvest units. This decision influences the potential distribution of seral stages, the demand for intensive silviculture. and the abundance of older forests. Using a variety of cutting patterns is recommended to avoid uniform landscapes; grouping cutblocks reduces the total amount of edge and maintains larger patches of older forest.

Developing the recommended seral stage distribution for the landscape unit should be implemented gradually and be adapted to local conditions. The length of time for second-growth stands to develop suitable structure varies by biogeoclimatic subzone, ecosystem, tree species composition, and silvicultural treatment (Steventon 1994). For instance, stand development and growth are slower in the colder, drier, higher-elevation Engelmann Spruce-Subalpine Fir zone, and faster in the warmer, wetter, lower-elevation Coastal Western Hemlock zone.

It may be difficult to achieve the recommended seral stage distribution in landscape units with an extensive harvesting history. For instance, because of the adverse climatic conditions and/or extreme disturbance regimes in some biogeoclimatic subzones, it might take a period of time equivalent to three harvest rotations to meet the old seral stage objectives. Including suitable forest that currently exists within parks and other protected areas (e.g., riparian areas) should help to meet old seral stage objectives across landscape units. Designating areas of younger forest as old-growth management areas may be required in these areas to meet old seral stage targets (B.C. Ministry of Forests and B.C. Ministry of Environment, Lands and Parks 1995).

Text by Susan Bannerman

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