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Abstract

Six chronosequences were established on southern Vancouver Island, British Columbia, to address the concerns regarding the potential loss of species diversity and increased risk to rare or old-growth–dependent species due to large-scale harvesting of old-growth forests. Each chronosequence comprised three post-harvest seral stages, representing regeneration, immature and mature, and an old-growth forest. Composition and cover of trees, shrubs, herbs, and cryptogams were sampled in each stage. On forested plots, cryptogams (i.e., bryophytes and lichens) made up about half of the species, of which most occurred on coarse woody debris and rock substrates. Sites dominated by Douglas-fir on eastern Vancouver Island exhibited substantial differences among successional stages in the numbers of herbs, shrubs, and cryptogams, but the overall number of species did not change dramatically between stages. On western Vancouver Island, where western hemlock was the dominant species, the regeneration stage supported far more species than later stages did. Mature and old-growth forests do not necessarily maintain larger numbers of species than younger successional stages do, but they may support species that are uncommon or absent in immature forests and regeneration sites. Those species found to be restricted to older forests differed between eastern and western Vancouver Island, suggesting that care must be taken in applying information about species distributions, patterns, and tolerances from one ecosystem type to another. The implications of our findings to forest management are discussed.

Key words: chronosequence, Douglas-fir, species diversity, succession, western hemlock

Résumé

Six chronoséquences ont été établies pour le sud de l'île de Vancouver, en Colombie-Britannique, afin de traiter les questions liées à la perte potentielle de biodiversité et à l'accroissement du danger pour les espèces rares ou anciennes dépendantes de cette biodiversité, en raison des coupes de forêts anciennes réalisées à grande échelle. Chaque chronoséquence comprenait quatre stades biotiques se rapportant respectivement aux peuplements de régénération, aux jeunes peuplements, aux peuplements mûrs et aux forêts anciennes. Pour chaque stade, des prélèvements ont été effectués sur le couvert forestier, les arbustes, les herbes et les cryptogames. Sur les parcelles boisées, les cryptogames (bryophytes et lichens) représentaient environ la moitié des espèces identifiées, dont la plupart ont été prélevées sur des débris ligneux grossiers et des substrats rocheux. Dans l'est de l'île de Vancouver, les sites dominés par les douglas de Menzies affichaient d'importantes différences d'un stade évolutif à l'autre au regard du nombre d'herbes, d'arbustes et de cryptogames identifiés. Toutefois, le nombre total d'espèces n'était pas radicalement différent selon les stades évolutifs. Dans l'ouest de l'île de Vancouver, où la pruche de l'Ouest constituait l'espèce dominante, les peuplements de régénération abritaient un nombre d'espèces bien plus important que les stades évolutifs plus avancés. Si les peuplements mûrs et les forêts anciennes n'abritent pas nécessairement un nombre plus important d'espèces que les zones plus jeunes, il n'est pas rare qu'ils abritent des espèces peu communes, voire absentes des forêts plus jeunes ou des sites de régénération. Ces espèces consignées aux forêts plus anciennes étaient différentes selon que les zones échantillonnées se trouvaient dans l'est ou dans l'ouest de l'île de Vancouver. Il convient donc de faire preuve d'une grande circonspection avant d'interpréter pour un type d'écosystème les données provenant d'un autre type d'écosystème en ce qui concerne la répartition, les tendances et les tolérances relatives aux espèces. Le document traite des conséquences de nos conclusions pour l'aménagement forestier.

Mots clés : chronoséquence, douglas de Menzies, biodiversité, succession, pruche de l'Ouest

1. Introduction

An increasing concern regarding species management and conservation in coastal forests of British Columbia, Canada, is how conversion of old-growth forests to managed forests affects the structure, function, and species diversity of ecosystems, and whether converted forests will eventually recover to a state that mimics many of the characteristic traits of old-growth stands.

Research addressing these concerns has been largely restricted to the Pacific Northwest of the USA and has focused primarily on wildlife species (Orians 1992; Carey and Johnson 1995; Hansen et al. 1995), although some studies have investigated vegetation (Mueller-Dombois 1965; Long 1977; Halpern 1988; Schoonmaker and McKee 1988; Halpern and Spies 1995; Qian et al. 1997). However, vegetation succession from a newly disturbed to an old-growth stand is still poorly understood in this region and information is particularly scant regarding nonvascular species (bryophytes and lichens) and their contribution to species diversity.

The conversion of old-growth forests into a mosaic of forest stands of different ages due to logging and fires in coastal British Columbia provides an opportunity to investigate the impacts of large-scale disturbances on changes in the composition, diversity, and structure of the forests. When managed and natural stands are arranged according to age (the time since disturbance), they form a successional gradient, termed a chronosequence. Arranging forest stands into a chronosequence is perhaps the most widely used approach in studying vegetation succession (Glenn-Lewin and van der Maarel 1992; Foster and Tilman 2000). Its importance lies in the fact that it provides useful information for inferring the intensity of disturbances, characteristics of initial stands, and habitat conditions, and it provides a reasonable tool for investigating and predicting the dynamics in the structure, function and species diversity of forest stands.

Changes in species diversity along a successional gradient in a chronosequence are important not only for understanding the forest dynamics and the underlying processes but also for providing management implications (Long 1977; Halpern and Spies 1995). However, interpretation and predictability of species diversity depend on many factors, including how it is measured (e.g., number of species, coverage, biomass), community types (e.g., forested or grassland), environmental conditions (e.g., wet or dry site), and characteristics of disturbances (e.g., fire or clearcutting). Unlike direct observations on permanent plots, in which changes can mainly be attributed to time, successional observations from chronosequences are influenced by numerous factors, because the constituent stands often differ in environmental conditions and histories. Although the confounding effects of these factors on chronosequences are inevitable, they can be minimized by carefully selecting and replicating sites of similar habitat conditions.

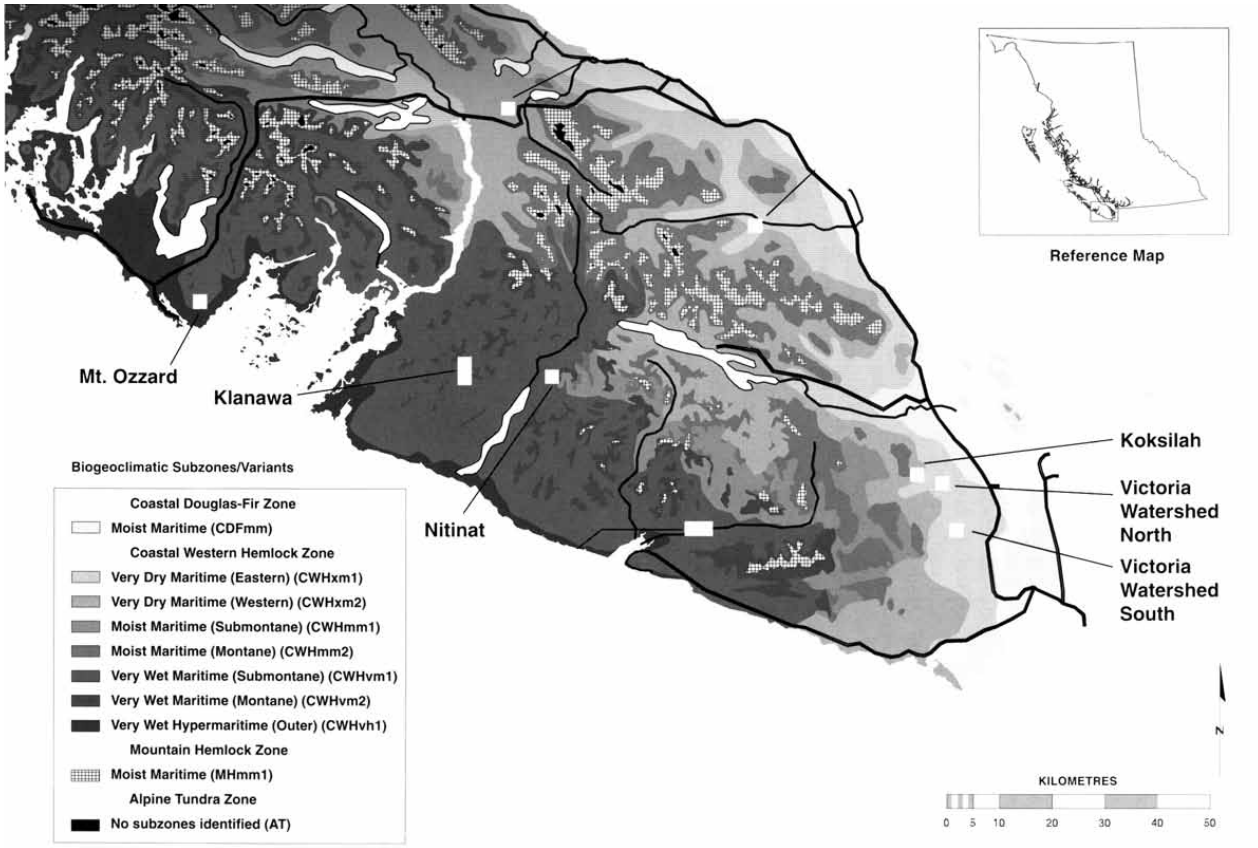
In this study, our interest is to investigate successional changes in vascular and nonvascular plant species diversity in the fragmented forest landscapes on southern Vancouver Island, British Columbia, using the chronosequence approach. We were particularly interested in understanding how the conversion of old-growth forests into secondary-growth forests would affect the plant-species diversity and what implications these results would have in terms of management in this region.

2. Materials and methods

2.1 Study sites

Six chronosequences were established by the Canadian Forest Service on southern Vancouver Island (Fig. 1; Trofymow et al. 1997). Each chronosequence comprised four plots representing four successional stages: 3–8 years (regeneration), 25–45 years (immature), 65–85 years (mature) and > 200 years (old growth). Criteria used for site selection required that the plots belonging to each chronosequence be located within a 5 km × 5 km area and occur on the same soil type and slopes with similar aspects and elevations (difference < 200 m). Three chronosequences were located on the east side of Vancouver Island (Victoria Watershed South, Victoria Watershed North, and Koksilah) and three were located on the west side (Nitinat, Klanawa, and Mt. Ozzard; see Figure 1 for a map of the sites). Most second-growth stands had regenerated after harvesting, except for three mature stands that had regenerated from wildfire (Koksilah and Klanawa) or slope failure (Mt. Ozzard).

Figure 1. Locations of the 10 coastal forest chronosequences on southern Vancouver Island, British Columbia, Canada. Four sites (Loon Lake, Nanaimo River, Red/Granite Creek and Renfrew) were excluded in this study. The map (from Trofymow et al. 1997) was prepared from 1:250,000 biogeoclimatic ecosystem classification maps of the British Columbia Ministry of Forests.



According to the Biogeoclimatic Classification System of British Columbia (Klinka et al. 1991), the east-side chronosequences occurred in the very dry maritime Coastal Western Hemlock (CWHxm) subzone, which has a mean annual temperature 9.3° C and a mean annual rainfall of 1505 mm (Pojar et al. 1991). The Watershed South site was in the very dry maritime (eastern) CWH variant (CWHxm1), the Koksilah site was in the slightly wetter very dry maritime (western) variant (CWHxm2), and the Watershed North site occurred in a transitional area between the CWHxm1 and CWHxm2 variants. Chronosequences located on the western side of Vancouver Island (Nitinat, Klanawa and Mt. Ozzard) occurred in the very wet maritime Coastal Western Hemlock submontane variant (CWHvm1). This variant differs from the eastern variants in that it has a lower mean annual temperature of 8.2° C and a higher mean annual rainfall of 2787 mm (Pojar et al. 1991). Most plots were assigned to the zonal mesic site series within their respective variants, but several were assigned to other near-mesic site series (Trofymow et al. 1997).

2.2 Data collection

Four 60 m × 60 m plots, representing regeneration, immature, mature, and old-growth forests, were established in each of the six chronosequences. Each plot was divided into four 30 m × 30 m quadrats. Within each quadrat, all plants (excluding epiphytes) were identified to species. Following the methods outlined in "Describing Ecosystems in the Field" (Luttmerding et al. 1990), visual cover estimates were made for each species encountered in the following vegetation layers: dominant trees, main canopy trees, sub-canopy trees, shrubs (including trees < 10 m tall), herbs, and cryptogams (bryophytes and lichens). Separate cover estimates were also made for each cryptogamic species according to the type of substrate on which it occurred: humus, coarse woody debris, rock (including bedrock), and mineral soil. Subsequently, all cover estimates were averaged across the four quadrats comprising each plot.

2.3 Data analysis

The 24 plots were ordinated using detrended correspondence analysis (DCA) to investigate indirect gradient patterns. The working matrix comprised the cover values of all 337 species present in the 24 plots. The PC-ORD program was used for the analysis (McCune and Mefford 1995).

Jaccard's similarity index is defined as $SI = \frac{a}{a + b + c}$, where a is the number of species jointly occurring in two plots, b and c are the number of distinct species occurring in each of the two plots, respectively. The complement of Jaccard's similarity (1-SI) was used to calculate species turnover. These values were used to compare differences in species composition between successional stages and between plots located on eastern and western Vancouver Island

3. Results

3.1 DCA ordination

Four groups of plots were apparent in the ordination plane of the first two axes of the detrended correspondence analysis (Fig. 2). The first axis separated eastern Vancouver Island plots, dominated by Douglas-fir *(Pseudotsuga menziesii)*, from western Vancouver Island plots, dominated by western hemlock *(Tsuga heterophylla)*. Along the second axis, regeneration plots were well separated from forested plots (I, M and O), although western regeneration plots appeared to be as dissimilar to one another as they are to forested plots. This may reflect differences in the degree of soil disturbance during harvesting and the intensity of post-harvest prescribed-burning among western regeneration plots; all eastern regeneration plots and the Klanawa site on western Vancouver Island were heavily burned, whereas the Nitinat site was lightly burned and the Mt. Ozzard site was not burned.

Meaningful patterns among the forested plots were much less evident, although the eastern plots seem to be ordinated based more on plot location than on successional stage, whereas western plots showed the opposite pattern.

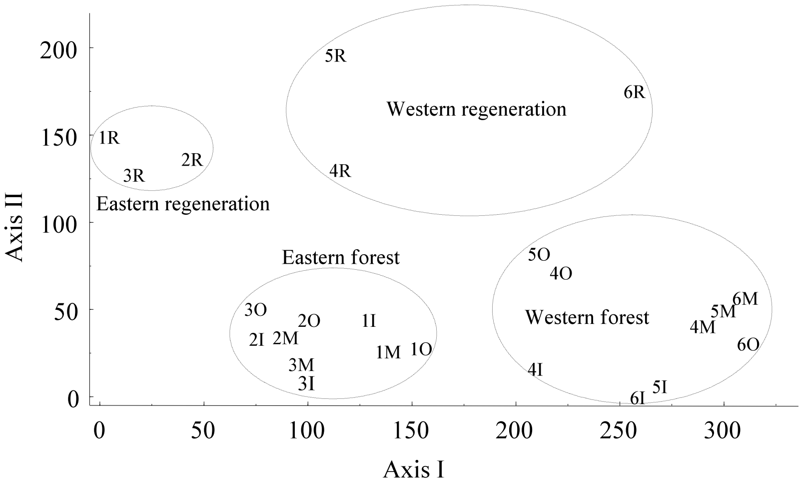
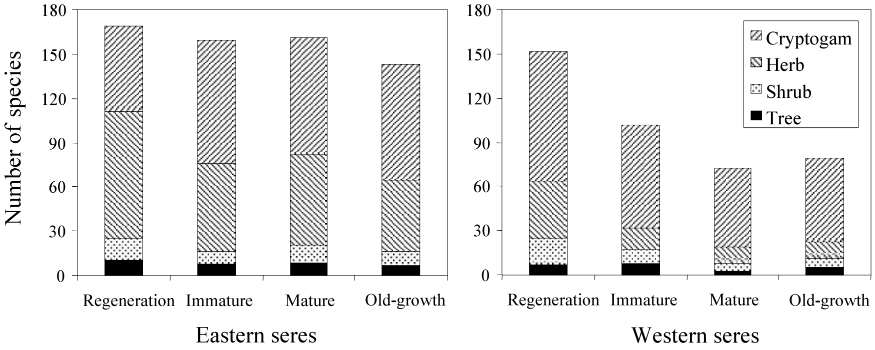


Fig. 2. Detrended correspondence analysis of the 24 sample plots of the six chronosequences on southern Vancouver Island. 1–3: eastern plots representing Victoria Watershed South, North and Koksilah, respectively; 4–6: western plots representing Nitinat, Klanawa and Mt. Ozzard. R, I, M and O represent regeneration, immature, mature and old-growth stages, respectively.

3.2 Species richness

A total of 337 species comprising 14 trees, 32 shrubs, 130 herbs and 161 cryptogams were recorded for all sites. All successional stages of eastern plots had a larger number of species than their western counterparts had, particularly among forested plots where eastern plots had about twice the number of species that were found to the west (Fig. 3). Differences among several stages were much greater among western plots than among eastern plots. Western regeneration plots had the largest number of species (152), followed by a sharp decline on forested plots. Much of the decline arose from a reduction in the number of herbs and, to a lesser extent, shrubs. This may be attributed to the large number of invasive shade-intolerant species that colonize regeneration sites but are subsequently eliminated once canopy closure occurs in immature forests. Although there was a similar decline in shrub and herb species in eastern plots, the number of cryptogamic species increased on forested plots, thus maintaining a large total number of species.

Fig. 3. Total number of species for each of the four vegetation layers. Each stacked column is the sum of distinct species on three plots.



3.3 *Species turnover rate*

Species turnover rates among eastern and western successional stages varied from 0.440 to 0.713 (Table 1). The smallest turnover rate (the highest similarity) occurred between mature and old-growth stages, whereas the largest rate (the least similarity) occurred between regeneration and mature stages. Species turnover rates were higher when successional stages were compared between eastern and western plots and varied from 0.754 to 0.925 (Table 2).

Table 1. Species turnover rates among successional stages for eastern and western Vancouver Island. The values are the average species turnover rates of three plots from regeneration (R), immature (I), mature stage (M) and old-growth (O) seres. Standard errors are given in parentheses.

	Eastern successional stage			Western successional stage		
	I	M	O	I	M	O
R	0.678 (0.079)	0.713 (0.095)	0.687 (0.078)	0.701 (0.067)	0.706 (0.052)	0.700 (0.072)
I		0.615 (0.075)	0.592 (0.061)		0.525 (0.111)	0.578 (0.092)
M			0.568 (0.099)			0.440 (0.099)

Table 2. Species turnover rates between eastern and western successional stages on Vancouver Island. The values are the average species turnover rates of three plots among regeneration (R), immature (I), mature (M) and old-growth (O) seres. Standard errors are given in parentheses.

		Western successional stages			
		R	I	M	O
Eastern successional stages	R	0.825 (0.035)	0.868 (0.055)	0.925 (0.012)	0.923 (0.018)
	I	0.795 (0.052)	0.754 (0.070)	0.817 (0.046)	0.822 (0.045)
	M	0.796 (0.048)	0.760 (0.052)	0.806 (0.037)	0.806 (0.041)
	O	0.814 (0.058)	0.777 (0.062)	0.820 (0.042)	0.818 (0.038)

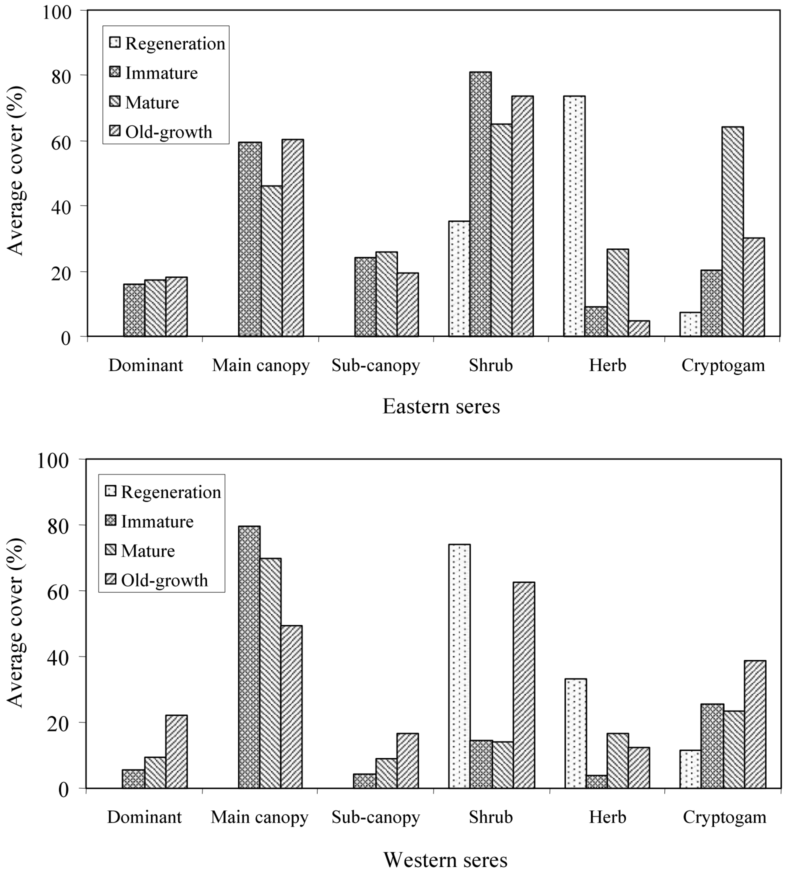
3.4 Cover values

The average cover values of the vegetation layers varied among successional stages and between eastern and western sites (Figure 4). The tree layer cover of eastern plots did not vary substantially between successional stages; the main canopy ranged between 45% and 60% and the dominant and sub-canopy layers varied between 15% and 25%. Alternatively, the main canopy cover on western plots approached 80% on immature plots, followed by a decline on mature and old-growth plots, whereas the dominant and sub-canopy layers exhibited an increase in cover. The high cover of the main canopy on western immature and mature plots was reflected in the depauperate understorey-vegetation layers that, in general, had lower cover values than their eastern counterparts had.

Shrubs differed between eastern and western plots in that the cover in forested plots of eastern sites was substantially higher than that of the regeneration plots (Figure 4), whereas regeneration and old-growth plots in the western sites had higher values than immature and mature plots had. In eastern and western sites, herb cover was highest in regeneration plots, followed by a sharp decline in immature plots. It then increased in mature plots, followed by a decline in old-growth plots.

Cryptogams were dissimilar to other vegetation layers in that cover values generally increased with time: initial cover was low in regeneration plots where logging, prescribed burning, and high light levels drastically limited the cover but, once canopy closure had occurred in immature plots, the shaded understorey became suitable to the establishment and growth of many species of mosses and liverworts. There was a decline in cryptogam cover in eastern old-growth plots, whereas it continued to increase in western old-growth plots.

Fig. 4. Average cover for trees, shrubs, herbs and cryptogams for each eastern and western successional stage.



3.5 Cryptogams and Substrate

Cover by cryptogams varied between substrate types and successional stages (Figure 5). On eastern plots, humus supported the largest cover by cryptogams and generally increased over time, except on old-growth plots. Coarse woody debris (wood) and rock substrates supported lower covers, but followed a similar trend to that observed on humus. Overall, mineral soil supported the lowest cover of cryptogams.

In general, western plots exhibited similar results, except that coarse woody debris closely approached humus in terms of cover, and both exhibited a general increase in cryptogam cover with stand age (Figure 5).

When the number of cryptogamic species recorded for different substrates is compared to cover values, it is evident that, despite supporting a low cover of cryptogams, coarse woody debris and rock supported greater numbers of species than that found on humus (Figure 6). Even mineral soil, despite contributing little to cryptogam cover, supported almost as many species as were found on humus. Much of the humus of eastern and western plots was dominated by a few large pleurocarpous mosses; it may be that many of the smaller species found on coarse woody debris and rock substrates cannot compete with these larger, faster-growing species. In addition, it is likely that small species cannot become established on humus without being smothered by litter and are largely restricted to elevated microsites such as those provided by coarse woody debris and rocks.

Fig. 5. Average cryptogam cover on four substrates: humus, wood (coarse woody debris), rock, and mineral soil for each eastern and western successional stage.

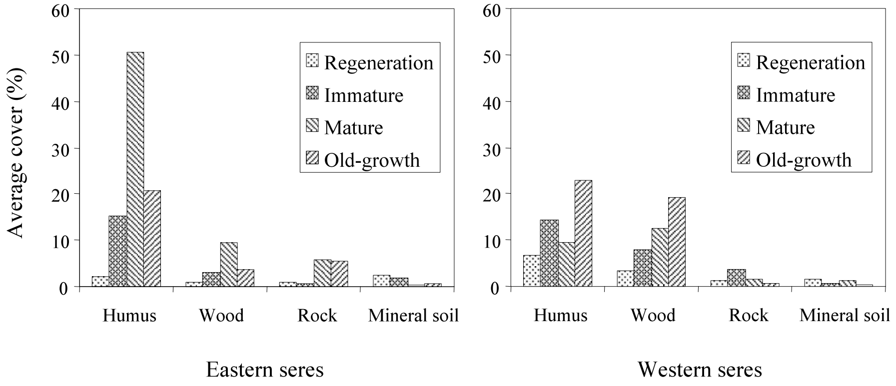
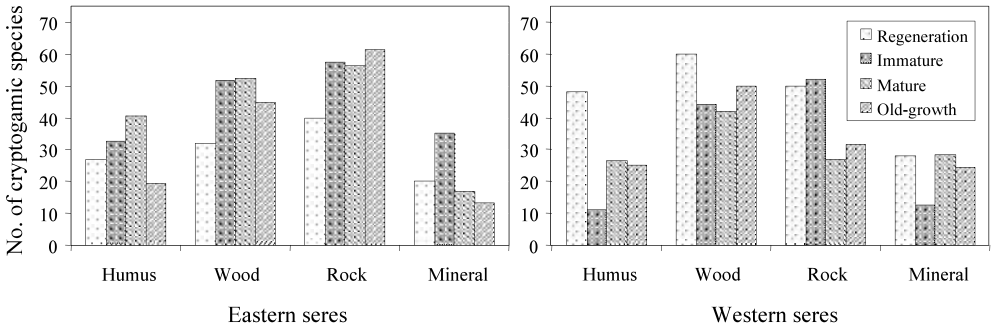


Fig. 6. Total number of cryptogam species on four substrates: humus, wood (coarse woody debris), rock, and mineral soil for each eastern and western successional stage. Each column is the sum of distinct species on three plots.



3.6 Restricted species

There were distinct differences in the number of species that were restricted to one or two successional stages (tables 3 and 4). Regeneration plots had the largest number of restricted species, with 35 and 63 species in eastern and western plots, respectively. These high numbers resulted from the colonization of regeneration plots by a large number of invasive herbs (26 species each). Fourteen of the 35 species restricted to the eastern regeneration plots were introduced species, whereas only five of the 63 species in western regeneration plots were introduced species. Furthermore, western plots had 27 cryptogamic species, of which many are typical of recently disturbed habitats.

Both eastern and western plots exhibited a decreasing number of restricted species with increasing stand age; i.e., immature plots had more restricted species than were found on mature and/or old-growth forest plots. The lowest numbers of restricted species occurred in old-growth (7) and mature (4) plots for eastern and western Vancouver Island, respectively.

Table 3. Species restricted to a successional stage or the regeneration and immature sites or the mature and old-growth sites on eastern Vancouver Island. Species followed by an asterisk (*) are introduced species. Species are listed in alphabetical order, beginning with vascular plants, followed by cryptogams.

Eastern Vancouver Island

Regeneration			
Agrostis exarata	*Allium cernuum*	*Anthoxanthum odoratum**	*Aquilegia formosa*
Arbutus menziesii	*Carex lenticularis*	*Carex pachystachya*	*Cirsium arvense**
*Cirsium vulgare**	*Crepis capillaris**	*Cytisus scoparius**	*Digitalis purpurea**
Epilobium minutum	*Epilobium brachycarpum*	*Gnaphalium microcephalum*	*Gnaphalium purpureum**
*Holcus lanatus**	*Juncus effusus*	*Lathyrus nevadensis*	*Lilium columbianum*
Mimulus moschatus	*Prunus emarginata*	*Prunella vulgaris**	*Ranunculus repens**
*Rubus laciniatus**	*Rubus leucodermis*	*Rumex acetosella**	*Salix sitchensis*
*Sonchus asper**	*Stellaria calycantha*	*Veronica officinalis**	*Vicia americana*
Barbula sp.	*Cephaloziella* sp.	*Cladonia* sp.	
Immature			
Athyrium filix-femina	*Carex* sp.	*Equisetum arvense*	*Festuca subuliflora*
Huperzia miyoshiana	*Orobanche* sp.	*Pterospora andromedea*	*Trisetum cernuum var. cernuum*
Anthoceros punctatus	*Brachythecium frigidum*	*Cladonia squamosa*	*Cladonia gracilis*
Cladonia pyxidata	*Dichodontium pellucidum*	*Didymodon vinealis*	*Diplophyllum albicans*
Lophozia ventricosa	*Marsupella emarginata*	*Philonotis fontana*	*Scapania umbrosa*
Scleropodium obtusifolium	*Tortula ruralis*		
Regeneration and Immature			
*Aira caryophyllea**	*Arctostaphylos columbiana*	*Cerastium fontanum*	*Danthonia spicata*
Deschampsia elongata	*Epilobium ciliatum*	*Leucanthemum vulgare**	*Lonicera ciliosa*
Madia exigua	*Pinus contorta*	*Ribes lobbii*	*Trisetum cernuum var. canescens*
Viola adunca	*Funaria hygrometrica*		
Mature			
Blechnum spicant	*Epipactis helleborine**	*Ilex aquifolium**	*Paxistima myrsinites*
Symphoricarpos albus	*Trillium ovatum*	*Cladonia verruculosa*	*Homalothecium fulgescens*
Peltigera pacifica	*Porotrichum bigelovii*		
Old Growth			
Collinsia parviflora	*Listera caurina*	*Barbilophozia* sp.	*Encalypta affinis*
Heterocladium macounii	*Metaneckera menziesii*	*Porella cordaeana*	
Mature and Old Growth			
Allotropa virgata	*Calypsobulbosa*	*Hemitomes congestum*	*Hypopitys monotropa*
Madiasativa	*Monotropa uniflora*	*Taxus brevifolia*	*Frullania tamarisci*
Isotheciumm cristatum	*Lophozia incisa*	*Neckera douglasii*	*Plagiochila asplenioides*
Plagiomnium venustum	*Psoroma hypnorum*	*Timmia austriaca*	

Almost all species restricted to one or two successional stages were cryptogams or herbs. In particular, with the exception of the orchid, *Goodyera oblongifolia,* all of the species restricted to western mature and/or old-growth plots were bryophytes, of which most were leafy liverworts that are generally less desiccation-tolerant than mosses and require moist and shaded habitats. Of the seven vascular species restricted to eastern mature and old-growth plots, four were unexpectedly achlorophyllous species belonging to the family *Monotropaceae,* which is represented by five species in British Columbia.

Table 4. Species restricted to a successional stage or the regeneration and immature sites or the mature and old-growth sites on western Vancouver Island. Species followed by an asterisk (*) are introduced species. Species are listed in alphabetical order, beginning with vascular plants, followed by cryptogams.

Western Vancouver Island

Regeneration			
Acer glabrum	*Anaphalis margaritacea*	*Boschniakia hookeri*	*Bromus* species
Bromus vulgaris	*Carex laeviculmis*	*Carex obnupta*	*Carex echinata*
Carex sp. B	*Coptis asplenifolia*	*Crepis capillaris**	*Dicentra formosa*
Epilobium angustifolium	*Epilobium ciliatum*	*Equisetum arven*	*Festuca* species
Hieracium albiflorum	*Hypochaeris radicata**	*Ilex aquifolium**	*Juncus effusus*
*Lactuca muralis**	*Leucanthemum vulgare**	*Luzula parviflora*	*Lycopodium clavatum*
Malus fusca	*Picea sitchensis*	*Rhamnus purshiana*	*Ribes laxiflorum*
Rubus parviflorus	*Salix hookeriana*	*Salix sitchensis*	*Sambucus racemosa*
Solidago canadensis	*Trisetum cernuum var. cernuum*	*Typha latifolia*	*Vaccinium ovatum*
Veronica beccabunga	*Bryum capillare*	*Ceratodon purpureus*	*Cladina mitis*
Cladonia chlorophaea	*Cladonia fimbriata*	*Cladonia gracilis*	*Cladonia phyllophora*
Cladonia pyxidata	*Cladonia* sp. A	*Cladonia* sp. B	*Conocephalum conicum**
Funaria hygrometrica	*Hygrohypnum ochraceum*	*Marchantia polymorpha*	*Oligotrichum aligerum*
Philonotis fontana	*Plagiothecium denticulatum*	*Pogonatum urnigerum*	*Pohlia nutans*
Polytricum commune	*Polytrichum formosum*	*Racomitrium varium*	*Rhytidiadelphus triquetrus*
Scapania sp.	*Sphaerophorus globosus*	*Ulota megalospora*	
Immature			
Alnus rubra	*Linnaea borealis*	*Listera cordata*	*Mahonia nervosa*
Prunus emarginata	*Ribes bracteosum*	*Trientalis latifolia*	*Cladina portentosa*
Claopodium bolanderi	*Dichodontium pellucidum*	*Lophocolea heterophylla*	*Mnium spinulosum*
Peltigera britannica	*Peltigera neopolydactyla*	*Plagiomnium insigne*	*Scapania undulata*
Stereocaulon tomentosum			
Regeneration and Immature			
Boykinia elata	*Rubus leucodermis*	*Salix* sp.	*Aulacomnium androgynum*
Bryum sp.	*Cladonia furcata*	*Cladonia transcendens*	*Claopodium crispifolium*
Dicranum scoparium	*Hypnum* sp.	*Jungermannia* sp.	*Lophocolea cuspidata*
Polytrichum juniperinum	*Racomitrium canescens*	*Racomitrium heterostichum*	*Rhytidiadelphus triquetrus*
Mature			
Goodyera oblongifolia	*Chiloscyphus polyanthos*	*Jungermannia leiantha*	*Mnium marginatum*
Old Growth			
Bazzania tricrenata	*Buxbaumia piperi*	*Herbertus aduncus*	*Hypnum dieckii*
Kurzia sylvatica	*Odontoschisma denudatum*	*Plagiothecium laetum*	*Porella cordaeana*
Radula bolanderi			
Mature and Old Growth			
Diplophyllum plicatum	*Mylia taylorii*		

4. Discussion

4.1 Species richness

Mueller-Dombois (1965) examined Douglas-fir and western hemlock forests on Vancouver Island and also found that regeneration sites were more species rich than forested successional stages due to the reemergence of forest species after logging and the rapid colonization of regeneration sites by a large number of shade-intolerant species absent from later successional stages. In this study, this pattern was particularly evident in western hemlock stands, where the canopy appeared to be very dense and excluded many species from the understorey on immature forested sites that were common on regeneration sites. Alternatively, the Douglas-fir canopy of eastern plots was observed to be less dense and more structurally diverse, with a greater number of large and small canopy gaps that result in higher light levels in the understorey and appeared to correspond to a greater number of understorey species. The higher numbers of species associated with Douglas-fir stands in comparison to western hemlock forests has also been reported by Stewart (1988) in Oregon. Similarly, Alaback (1982) has remarked on the depauperate understorey vegetation of western hemlock forests in Alaska.

4.2 Restricted species

Given the limited number of plots and the lack of pre-disturbance data for immature and mature stands, it is difficult to draw inferences regarding the presence or absence of individual species at a given successional stage. Many of the species that occurred in a single successional stage may have been chance occurrences of uncommon species. However, it is not surprising that the largest number of restricted species occurred on regeneration plots, given the extent to which these sites were colonized by herbaceous species absent on forested plots. It is also remarkable that four of the seven vascular species confined to eastern mature and old-growth stands were achlorophyllous species. These species *(Allotropa virgata, Hemitomes congestum, Hypopitys monotropa,* and *Monotropa uniflora)* are believed to be epiparasites that indirectly parasitize the roots of chlorophyllous plants through mycorrhizae connected to the roots of both achlorophyllous and chlorophyllous species (Björkman 1960; Furman and Trappe 1971). Little is known regarding the biology and ecology of these species, although achlorophyllous species are usually reported to be restricted to forested areas (Mueller-Dombois 1965; Schoonmaker and McKee 1988). The exclusion of achlorophyllous species from younger stands may result from unsuitable habitat conditions or an absence of the required mycorrhizae that may be associated only with the roots of older trees in mature and old-growth forests.

Some species that were restricted to a specific successional stage on one side of Vancouver Island were found in more than one successional stage on the other side of the island. For example, the moss *Buxbaumia piperi* was restricted to old-growth stands on western Vancouver Island, but occurred in immature, mature, and old-growth stands on the eastern side of the island. Similarly, Pacific yew *(Taxus brevifolia)* was restricted to older forests on the eastern side of the Vancouver Island, but occurred in regeneration, immature, and old-growth forests on western Vancouver Island. These results suggest that species characteristic of older successional stages may be ecosystem- or regionally specific and that the same species in other habitats or areas may have no value as characteristic species of older forests. Care must be taken in applying information from one ecosystem type to another.

It is worth mentioning the significantly higher number of introduced species that were found on the eastern plots compared to the western plots. The greater number of introduced species on eastern plots likely reflects the greater extent to which eastern Vancouver Island has become densely populated and altered by development, resulting in numerous and abundant seed sources of introduced species. Non-native species are now widely thought to represent a significant threat to biodiversity (Whelan and Dilger 1992; Simberloff 2000). It remains to be seen what the impacts on regional indigenous biodiversity will be due to the presence of the large number of introduced species on eastern Vancouver Island.

4.3 Cryptogams

We found that cryptogamic species accounted for more than half the total number of species on all forested sites. These numbers would be even higher if epiphytes had also been included, particularly in old-growth Douglas-fir stands, where lichens were often a significant component of the forest canopy. Although it did not necessarily support a high cryptogam cover, the importance of coarse woody debris to species richness is noticeable on both eastern and western plots (Figure 6). Similarly, rock and bedrock were also important, particularly in eastern plots, where a number of species were largely restricted to this substrate type, including ***Mnium spinulosum*** and ***Scapania americana***. These species were either rare or absent on western plots, where they appeared to have been replaced by less habitat-specific species, including ***Rhizomnium glabrescens*** and ***Scapania bolanderi***. These latter species were rare on rock substrates on eastern plots, but had become established on rock substrates in western plots—possibly because of the moister climatic conditions.

4.4 Implications for the management of coastal forests

The forests examined in this study reflect many of the conditions observed today on Vancouver Island, particularly on the eastern side of the Island where almost all of the old-growth Douglas-fir forests has been converted to second-growth stands, the landscape is highly fragmented and individual sites exhibit a variety of disturbances. With increasing forest fragmentation and a rapid increase in area dominated by regeneration and immature stands, many species will undergo rapid changes in abundance in response to these landscape changes. Species restricted to old-growth forests will remain limited to small, isolated fragmented stands and may decline, because the likelihood of becoming established in adjacent areas is severely hampered by a lack of suitable habitats. In contrast, those species restricted to younger stands will almost surely increase in abundance. The results of this study provide several challenges in managing these forests for biodiversity.

It is apparent that old-growth forests cannot be treated as a homogenous unit in management plans and that the age, composition and structure of vegetation must be considered in designing and implementing forest practices and conservation efforts to account for differences in old-growth forests between ecosystem types and geographical areas. The assemblage of species that may be restricted to a given old-growth stand likely differs in other ecosystems or regions: care must be taken when applying information about species distributions, patterns, and tolerances from one ecosystem type to another.

The two study areas in this investigation showed very different patterns of species distribution between successional stages. Forested stands on the east side of Vancouver Island that have several achlorophyllous species may indicate that the forests have reached the first stage of becoming "old growth", and these achlorophyllous species might be used as indicator species. These species were absent from all successional stages on the west side of the island, where better indicator species might be leafy liverworts such as ***Diplophyllum plicatum*** and ***Mylia taylorii***.

Although it is a common public perception that old-growth forests are considered valuable because they support a large number of species, the results of this study suggest that, with respect to plants, it is often recently disturbed sites that support the greatest number of species. However, most species observed on regeneration sites are widespread, ubiquitous and, on the eastern side of Vancouver Island, often introduced species that do not require protection or conservation efforts now or in the near future. Using species richness or other quantitative measurements of species diversity solely as a basis by which to direct conservation efforts is misguided, because they fail to distinguish between widespread or introduced species and uncommon or rare species. Likely, goals in conservation and management of species diversity could probably be better accomplished by taking into account species restricted to stands of different ages, particularly the older forested stands.

For example, if our interest is not on the landscape level but on the local forest-stand level, we know that fine-scale canopy gaps are important for species regeneration and maintaining biological diversity (Stewart 1986; Spies et al. 1990). Forest managers attempting to maintain biodiversity in old-growth stands, therefore, should retain those stands that are structurally diverse.

An important finding of this study was that cryptogamic species were a major component in all successional stages of forests on Vancouver Island and often equaled or exceeded the numbers of vascular species. Unfortunately, little research has focused on this lesser-known group. Because of the high sensitivity of nonvascular species to habitat conditions, it is recommended that clumps of old-growth trees be retained in managed forests to protect understorey bryophytes and epiphytic lichens, and to serve as a source of propagules to disperse species into nearby developing stands.
It is important in management practices to avoid or reduce disturbances on the substrates to maintain the assemblage of cryptogam species. Special care should be taken to preserve specific habitats, such as rock outcrops or large coarse woody debris which often support greater numbers of crypotgamic species than those found on humus. It was observed that although the same cryptogamic species were found on smaller-dimension logs in mature forests, many species reached their greatest development on large logs found in old-growth stands, where bryophyte colonies were larger and more abundant, possibly because of the longer period of time required for larger logs to decay compared to smaller logs.

Halpern and Spies (1995) outlined alternative silvicultural methods for ameliorating the impacts of forest harvesting on biodiversity. These methods encourage cutting and planting practices that promote structural complexity. Our results showed that the practice of clearcutting, at least in the drier forests types on the east side of Vancouver Island, seems to encourage the establishment of invasive non-native species. This was particularly noticeable in areas where substantial soil disturbance had occurred and there was little or no regeneration from the roots and rhizomes of forest-shrub species. In areas where the spread of exotic species is of concern or in areas where exotic species are threatening ecosystems or rare-plant populations, forest managers should be aware of and be encouraged to use harvesting regimes that reduce soil disturbance and damage to common species such as salal *(Gaultheria shallon)* that often resprout after logging. Although many of the invasive species disappear once canopy closure has occurred, their abundance on regeneration sites may delay the length of time in which crown closure occurs because of competition with regenerating conifers.

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Inset photos on cover, left to right:
Mylia taylorii - a liverwort species that was only found in old-growth forests on western Vancouver Island
Cytisus scoparius (Scotch broom) - an introduced weedy species common on regeneration sites on eastern Vancouver Island
Goodyera oblongifolia (rattlesnake-plantain) the only vascular species that was found only in older forests on western Vancouver Island
Allotropa virgata (candystick) - moss covered decaying log and the epiparasitic plant, *Allotropa virgata*

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