Forest fragmentation, structure, and age characteristics as a legacy of forest management

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Abstract. The combination of forest inventory and satellite-derived landscape composition and structure provides otherwise unavailable information on regional forest conditions and enables investigation of the cumulative effects of forest management over time. Forest pattern results from a range of both natural and anthropogenic factors. This study characterizes the forest pattern of Vancouver Island, British Columbia (>32,000 km^2) at the watershed scale, using new national datasets of Canadian forest composition and fragmentation, and relating these to forest inventory-derived age structure. Vancouver Island is extensively forested, possessing highly valuable and productive forests, and is managed to meet a range of stakeholder interests. Forest fragmentation metrics were derived from a satellite-derived, 25-m spatial resolution land cover map (i.e., grain) to represent patterns within 1 km analysis units (i.e., extent) for the entire forested area of Canada. We summarized forest fragmentation island-wide and compared trends between forest-dominated (>85% forest) and less-forested (<85% forest) watersheds. We also explored these patterns with partial canonical correspondence analyses to determine the independent and shared relationships of landscape composition, forest fragmentation, and spatial variables with forest age structure.

Less-forested watersheds are more fragmented than forest-dominated watersheds, as indicated by more (5.6 versus 2.7 per km^2) and smaller (36 versus 63 ha) forest patches, and a greater edge density (82 versus 55 m/ha). Of the 1283 watersheds examined, 91% were forest-dominated; island-wide trends are thus similar to those of the forest-dominated watersheds. Forest age is related to landscape composition and forest fragmentation, which collectively explain 27% and 53% of the age structure of all and less-forested watersheds, respectively. In both sets of watersheds, young forest stands (1-120 years) are associated with broadleaf forests, agreeing with successional expectations, and patchy forest distributions. For all watersheds, old growth forest stands (>240 years) are associated with dense coniferous forest, but also with early successional communities, smaller patch sizes, and greater edge densities, indicating fragmentation of these forests and reflecting strategies for managing old growth on the landscape. In contrast, watersheds with an abundance of mature forest (121-240 years) are compositionally similar to watersheds with old growth, but are much less fragmented. Our results indicate that although old growth forest stands on Vancouver Island have been retained, they are not typically found within a continuous forest matrix. Medium spatial resolution Earth observation products are now available for the entire forested area of Canada, providing valuable insight into spatial and temporal forest dynamics (i.e., succession, harvesting).

1. Introduction

A major aspect of forest pattern is fragmentation, which is a function of the amount and configuration of forest within a landscape. Fragmentation of forests may be caused by a variety of factors, including both natural processes, such as fires and insect infestation, and anthropogenic activities, such as logging and road building (Linke et al., 2007). Fragmentation can be considered as broadly (e.g.: forest vs. non-forest) or as subtly (e.g., between forest classes or ages) as desired; here we focus on gross fragmentation of forests in general by non-forested land covers. A forested landscape is understood to be fragmented when it contains a greater number of forest patches that are smaller and more isolated than those in an undisturbed reference landscape or reference time point. Biota may be less able to disperse to and/or persist in small, isolated patches (following island biogeography; MacArthur and Wilson, 1967). Additionally, fragmentation increases the dominance of edge habitat, which has diverse effects on the physical environment (Saunders et al., 1991) and, thus, consequences to the resident biota (e.g., Kupfer and Runkle, 2003) and natural disturbance regimes (Franklin and Formann, 1987).

The effects of harvesting and associated road networks on forest pattern have been well documented, with findings indicating that clear cutting and roads consistently decrease forest patch size and increase the number of forest patches and the amount of edge (Franklin and Formann, 1987; Ripple et al., 1991; Mladenoff et al., 1993). Forest removal also tends to simplify patch shapes (Mladenoff et al., 1993; Reed et al., 1996; Tinker et al., 1998), although the converse may occur when multiple cut blocks merge to form complexly-shaped aggregates (Ripple et al., 1991; McGarigal et al., 2001).

However, forest pattern extends beyond spatial structuring alone. Forest stand age is another crucial dimension of forest pattern. The forest age distribution within a landscape is a record of the local disturbance regime (both natural and anthropogenic) and is a key control on ecosystem function (Caspersen and Pacala, 2001). Forest age structure is strongly influenced by extractive use, which results in even age distributions up to the rotation age (i.e., the age at which a stand is considered mature and ready for harvesting), followed by a sharp decline in older age classes (Gustafson and Crow, 1996; Fall et al., 2004). This age distribution contrasts sharply with the negative exponential distribution of stand ages expected under many natural disturbance regimes (Frelich, 2002). Changes to forest age distributions are of concern because biodiversity and carbon cycling are closely linked to forest age: old forests provide critical habitat for threatened and endangered species (Berg et al., 1994) and immense carbon storage capacity (Harmon et al., 1990; Pregitzer and Euskirchen, 2004). There has been considerable interest and research on alternative forest management plans, whereby harvesting mimics natural disturbance and maintains natural age distributions and landscape structures (Franklin and Formann, 1987; Gustafson and Crow, 1996; Fall et al., 2004; Didion et al., 2007).

There are thus intuitive effects of forest management on both age structure and landscape structure, suggesting that there may also be a strong relationship between forest age and spatial pattern. Yet these factors have rarely been studied together and the spatial effects of forest harvesting on specific forest age classes are relatively unknown (but see McGarigal et al., 2001; Etter et al., 2005; Helmer et al., 2008). The overall goal of this communication is to characterize the forest patterns of watersheds on Vancouver Island, British Columbia and determine their interrelationships. To achieve this, we synthesize data from forest inventory and remotely-sensed land cover datasets to relate forest age structure to landscape composition, forest fragmentation, and spatial variables (i.e., watershed location and size). Our first objective is to summarize forest fragmentation for all watersheds considered in our analysis, and then compare the forest fragmentation of watersheds that have different levels of forest abundance. Our second objective is to determine the independent and shared relationships of landscape composition, forest fragmentation, and spatial variables with forest age structure. This research provides a valuable assessment of the current baseline conditions and correlations of forest age and landscape structure on Vancouver Island, contributing to our understanding of anthropogenic impacts to these landscapes. It also highlights the capabilities of several newly-available, national, remotely-sensed datasets and analysis tools that are novel to and merit wider application in landscape scale studies.

2. Materials and Methods

2.1. Study area

Vancouver Island is found at the southwestern corner of the province of British Columbia, Canada. It is approximately 460 km long and 80 km wide, with an area of 32,134 km^2. The island is characterized by a maritime climate with mild, wet winters, when temperatures rarely fall below 0^oC, and cool, dry summers (Coops et al., 2007). A mild climate, high amounts of precipitation, and suitable soils promote forest growth over much of Vancouver Island. With the exception of alpine areas, much of the island is occupied by forests dominated by Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), yellow cedar (*Chamaecyparis nootkatensis*), and Sitka spruce (*Picea sitchensis*) (Burns and Honkala, 1990), and has been for more than 12,000 years (British Columbia Ministry of Environment, Lands and Parks, 1999).

Vancouver Island is part of Canada's Pacific Maritime ecozone. The Pacific Maritime ecozone occupies 3% of Canada's area of forest, but accounts for 12% of Canada's wood volume (Power and Gillis, 2006). Since 1848, forest harvesting has been an important economic activity on Vancouver Island (British Columbia Ministry of Environment, Lands and Parks, 1999). Wildfires are well suppressed; harvesting, agriculture, and urban expansion are the primary agents of forest change and, in the latter case, land use conversion (Pew and Larsen, 2001). While 12.9% of Vancouver Island is occupied by protected areas, much of the island is managed in support of forest harvesting activities.

2.2. Data and input variables

2.2.1. Watersheds

British Columbia vector-based third order and higher watershed boundaries at a scale of 1:50,000 were obtained from the Government of British Columbia (Ministry of Sustainable Resource Management, 2004). This data represents 2093 watersheds on Vancouver Island. Watersheds larger than 50 ha were selected for analysis to ensure sufficient within-watershed land cover information (N = 1429). Of these, 146 watersheds were excluded from analysis because the land cover classification in these watersheds was incomplete as a result of substantial cloud contamination in the original satellite imagery, or because there were insufficient forest inventory data available in these areas, primarily in the private railroad concession in southeastern Vancouver Island. This omission perhaps improves our analyses and the consistency of the identified patterns as this area is more developed, drier, and thus less representative, in terms of disturbance regimes, landscape structure, and forest age distributions, of the island as a whole. In total, 1283 watersheds were retained to analyze forest patterns. Watersheds were divided into three sets: (1) a full set of all 1283 watersheds; (2) a subset of forest-dominated watersheds (where forests cover ≥ 85% of the watershed area, N = 1166); and (3) a subset of less-forested watersheds (where forests occur in < 85% of the watershed area; N = 117). The 85% forest threshold corresponds to the island-wide mean forest cover.

Spatial variables were derived from the watershed boundaries. Space was represented by a third order polynomial of the geographic coordinates (UTM northing and easting) of the centroid of each watershed (sensu Borcard et al., 1992; Table 1) and by the watershed area.

2.2.2. Land cover classification

Existing land cover data derived from Landsat-7 Enhanced Thematic Mapper Plus (ETM+) were used to represent landscape composition on Vancouver Island (http://www4.saforah.org/eosdlcp/nts_prov.html). Produced by the Canadian Forest Service, with support from the Canadian Space Agency and partnerships with all provinces and territories, the Earth Observation for Sustainable Development of Forests (EOSD) land cover dataset represents circa year 2000 (EOSD LC 2000) conditions and depicts 23 land cover classes over the forested ecozones of Canada at a spatial resolution of 25 m (Wulder et al., 2008a).

The EOSD LC 2000 classification of Vancouver Island is shown in Figure 1. Of the 23 possible EOSD land cover classes, 18 classes occur on Vancouver Island (Wulder et al., 2007), but only 16 classes were found in the watersheds considered in our analysis (Table 1). The coniferous-open (coniferous trees with a crown closure of 26-60%) class is the dominant class in over 90% of the watersheds on Vancouver Island. The EOSD LC 2000 product was used to generate information on both landscape composition and fragmentation for our analyses. Landscape composition was defined as the percent-by-area of each land cover class within each watershed.

2.2.3. Forest fragmentation metrics

A large number of landscape metrics have been developed to describe the composition and spatial structuring of habitat patches within a landscape, including patch size, shape, diversity, and co-occurrence, among others (McGarigal and Marks, 1995). While many metrics may be selected for a fragmentation study, not all metrics are useful in all types of landscapes or behave consistently across all levels of fragmentation or scales (Gergel, 2007). Thus, an appropriate rationale for metric selection is recommended (Li and Wu, 2004). From over 90 available metrics (Wulder et al., 2008b), we chose the metrics outlined in Table 2 to represent the nature of forest fragmentation on Vancouver Island. To calculate forest fragmentation, EOSD LC 2000 classes were first combined into broad forest, non-forest, and other (e.g., water, cloud) classes. Metrics were calculated over a grid of 1 km^2 (40 x 40 pixels) analysis units. The eight neighboring cells were used for metric calculation, and the EOSD pixels found along the borders of the 1km by 1km analysis units were not included in the analysis (i.e., were not considered edges). Further details on metric calculation are provided in Wulder et al. (2008b). To aggregate fragmentation metrics to the watershed analysis unit of our study, maximum, mean, and standard deviation values of the 1 km^2 cells within each watershed were determined (Table 1).

2.2.4. Forest inventory

Strategic forest inventory data were available for the majority of Vancouver Island (Leckie and Gillis, 1995). Forest stands were mapped as polygons with attributes describing stand characteristics such as age and composition. Forest inventory attributes were derived from a combination of photo interpretation and field validation. For each watershed, we determined the areal proportion for two distinct sets of age classes (Table 3): in the first set, stands were grouped into five age classes, following the recommendations of Gillis et al. (2003) for British Columbia forests; the second set of expanded age classes further divides stands into ten age classes commonly used in Canadian forest inventories (Leckie and Gillis, 1995).

2.3. Analysis

2.3.1. General trends in forest fragmentation

Summary statistics were computed to characterize the island-wide forest fragmentation for all watersheds. Forest fragmentation metrics of forest-dominated and less-forested watersheds were compared with ANOVAs. A criticism of many fragmentation studies is that they fail to characterize the effects of fragmentation independent of the amount of habitat in fragmented and unfragmented treatments (Fahrig, 2003). To address this, we also used ANCOVAs to assess trends in forest fragmentation between forest-dominated and less-forested watersheds (with analyses performed in STATISTICA 8.0 (StatSoft, Inc., Tulsa, OK, USA)). In this test, the proportion of a watershed that is forested was treated as a covariate. The question tested is then: How do the landscape configurations of forest-dominated and less-forested watersheds differ after controlling for any systematic effects of forest amount?

2.3.2. Partial canonical correspondence analysis

Partial canonical correspondence analysis (CCA; ter Braak, 1986; Borcard et al., 1992; Palmer, 1993) was used to relate forest age structure to landscape variables derived from EOSD data and to determine the independent and joint effects of landscape composition, forest fragmentation, and spatial variables on forest age. CCA is a constrained ordination technique that is widely used in community ecology. In typical applications, CCA is used to project the information content of a species-by-site matrix into fewer dimensions, each of which are defined to maximize their correlations with the input environmental gradients. CCA has begun to be applied to remotely sensed data, for example to relate community composition to spectral (Thomas et al., 2003; Schmidlein and Sassin, 2004; Malik and Husain 2008) or landscape variables (Cushman and McGarigal, 2004; Miller et al., 2004; Titeux et al., 2004; Watson et al., 2004; Brown et al., 2006; Barbaro et al., 2007; Davis et al., 2007; Pillsbury and Miller 2008; van Halder et al., 2008). CCA has also been used to impute forest inventory attributes from Landsat and geoclimatic (Ohmann and Gregory, 2002) and LiDAR data (Hudak et al., 2008). We know of no applications of CCA to investigate patterns of forest age.

CCA assumes unimodal relationships between variables, but is robust to violations of this assumption (ter Braak, 1986). We chose to use CCA because it is a multivariate technique, allowing the inclusion of all age information, rather than forcing us to distill the age variation within a watershed into a single, potentially ambiguous metric (i.e., mean age). It also directly relates age composition patterns to explanatory environmental variables (unlike an unconstrained ordination such as principal components analysis), and is thus readily interpretable. In the framework of a typical CCA in community ecology, our age classes were analogous to species, and the proportions of the watersheds in each age class were analogous to the species abundances.

Stepwise CCAs were performed for each dataset (landscape composition, fragmentation, and space) independently to determine the subsets of composition, fragmentation, and spatial variables that are most highly correlated to forest age distributions. These variable sets were then used in all possible combinations of partial CCAs. A partial CCA first statistically removes the effects of a given set, or sets, of variables (the covariates, or conditional variables) on the response variable set in order to then determine the "pure" effects of the variable set of interest (the constraining variable set). The outputs of these CCAs can be used to partition the independent and shared variation between each set of variables (Borcard et al., 1992; Cushman and McGarigal, 2002). For example, a CCA of age, constrained by composition, conditional on fragmentation and space, will determine the variation in age distributions uniquely explained by landscape composition; a CCA of age, constrained by fragmentation, conditional on space, will determine the variation in age distribution explained by fragmentation metrics independent of spatial variables, but which may have redundancies with landscape composition; and so forth.

Biplots of the age scores (c.f. species scores) and vectors representing the environmental variables were constructed from the partial CCAs of the independent contributions of landscape composition and fragmentation in order to graphically interpret the relationships between variables. In these plots, age classes are plotted at the centroids of their distribution in ordination space. Constraining variables are centered by their means at the origin of the plot and increase in the direction of their vector. The length of each vector indicates variable importance and vector direction indicates correlations between variables and both the canonical axes and other variables. A variable is highly correlated to axes and other variables that are largely parallel to its vector and uncorrelated to those that are perpendicular. The joint position of age classes and environmental variables in the ordination diagrams can be used to infer the importance of each variable to each age class (ter Braak, 1986). Age classes are strongly associated with variables that point in their general direction in ordination space. Watershed (site) scores can also be plotted in an ordination diagram (now a triplot), but for clarity, we have not done so. Instead, watershed scores were mapped in a GIS. These watershed score maps can be interpreted by cross-referencing relative values with their position in the species-environment biplot. Analyses were conducted in the open source statistical software package R (http://www.r-project.org), using the add-on package vegan (Oksanen et al., 2008).

2.3.3. Patch-to-watershed scaling

In order to confirm the relationships observed between forest age structure and forest fragmentation of watersheds and to elucidate the scaling between forest stand attributes and emergent properties at the landscape scale, we calculated area and shape metrics (fractal dimension, shape index, perimeter:area ratio; McGarigal and Marks (1995)) for the forest inventory polygons. Differences between age classes were assessed with Kruskal-Wallis nonparametric tests.

3. Results

3.1. General trends in forest fragmentation

Vancouver Island is dominated by forest (Table 4). On average, 85% of the area of each watershed is covered by forest. Watersheds typically have 3 large forest patches per square km with an average area of 60 ha. Only 117 watersheds (9%) had less than 85% forest cover. Consequently, the island-wide trends in forest fragmentation are very similar to those of the forest-dominated watersheds (Table 4). In contrast, and not surprisingly, less-forested watersheds were more fragmented, with less (68%) and greater variability in forested area. Furthermore, less-forested watersheds had more and smaller forest patches. Interestingly, the proportion of patches that was forested is similar for both watershed groups. Likewise, the standard deviation of forest patch size is uninfluenced by forest cover, indicating that forest patches are consistently smaller in less-forested watersheds, with few to no remnant, large forest patches. Watershed area did not differ between forest-dominated and less-forested watersheds, and therefore does not influence the trends in patch size. Finally, less-forested watersheds have a much greater edge density.

The trends in forest fragmentation metrics for these two watershed groups are quite different, however, when we control for the amount of forest area (Table 5). The differences in mean patch size and edge density for forest-dominated and less-forested watersheds are no longer significantly different. Furthermore, the differences between the proportion of patches that are forested and the variability of patch size have gained significance: for a given amount of forest area, less-forested watersheds have a greater proportion of forested patches and less variability in patch size. Less-forested watersheds still contained more forest patches, but the difference with forest-dominated watersheds is less notable.

3.2. Partial canonical correspondence analyses

3.2.1. All watersheds

Both of the forest age classifications yielded similar patterns. The broader age classes resulted in slightly stronger relationships between age and landscape structure, likely as a result of the larger per-class sample sizes associated with these broader classes. Only the results of the analyses using the five broader age classes are presented, but interpretations are robust for either age grouping used.

Forest age structure on Vancouver Island was related to 8 forest fragmentation metrics, 14 land cover classes, and 6 spatial variables (variables and Monte Carlo permutation test p-values listed in Table 6). Individually, forest fragmentation, landscape composition, and spatial variables accounted for 4.5%, 25.2%, and 15.6% of the variation in forest age distributions; however, there was substantial overlap between these components (Figure 2a), and not all variables remained significant when including other components as covariables. Specifically, fmarea_STD, frarea_MAX, frarea_MEAN, fprop_STD, and watershed area did not provide unique information and were excluded from the final models.

Collectively, 35.8% of the variation in forest age distribution on Vancouver Island could be related to forest fragmentation, landscape composition, and spatial variables. Note that there is negative shared variation between the three components and between spatial variables and forest fragmentation metrics. Although counterintuitive, negative shared variation is possible and occurs when variables conditional on one another model a response better than those variables alone (Økland, 2003). Forest age was most strongly related to landscape composition. The unique contribution of landscape composition to forest age is plotted in Figure 3. The first four canonical axes were significant ($p < 0.05$). Axis one separates young forests (regeneration and immature; 1-120 years) on the right, from mature and old growth forests in the center, from the non-forest age on the left. This corresponds well with the EOSD LC 2000 composition: Abundances of all forest classes are either positively correlated or uncorrelated with axis one (except for treed wetlands) while all non-forested and non-vegetated classes are negatively correlated with this axis. Axis two further separates age classes within the broad categories defined by axis one; age is positively associated with this axis. Axis two also has strong correlations with the proportion of dense coniferous vegetation (positive) and the proportion of herbaceous vegetation (negative) in a watershed. Thus, the abundance of dense coniferous forest in a watershed is strongly associated with the abundance of older age classes. Conversely, broadleaf, mixed woods, and sparse conifer forests are all associated with abundant younger forests. The patterns arising along axes three and four are not as readily interpreted (Figure 3b); however, they do reveal that the oldest forests are associated with abundant non-forested and other early successional cover: Recently logged areas, as indicated by a greater abundance of herbs, shrubs, and the regeneration age class, fall out to the left of axis three, as does the old growth age group. Axis 4 is especially sensitive to the mature forest age class and the rock and rubble, and wetland shrub land cover classes.

Forest fragmentation metrics correlated relatively weakly with forest age structure on Vancouver Island, and were largely redundant with composition (Figure 2a). The first fragmentation canonical axis was significant ($p < 0.05$), and axes two and three were marginally significant ($p < 0.1$). A biplot of age classes and fragmentation variables along the first two axes is given in Figure 4. Axis one is a continuum of forest patch structure within a watershed, separating watersheds characterized by large, compact patches and intermediate forest ages on the left from those with small patches and a greater edge density, and very young and very old forests on the right. Axis two is sensitive to the heterogeneity among the 1 km^2 analysis units within a watershed. Watersheds with patchy forest distributions (i.e., a high standard deviation of the proportion of forest area) and at least locally high edge densities are associated with negative values of axis two.

Watershed scores, corresponding to the position of each watershed within these ordinations, were mapped over Vancouver Island and are shown in Figure 5. Interpretations of these maps follow the above interpretations of the axes. Watersheds with large, negative values for the first composition axis, and thus relatively high abundances of non-vegetated land cover, are clustered in the mountainous interior of Vancouver Island (site A in Figure 5) and in agricultural areas to the southeast (Figure 5, site B). Watersheds with large positive scores on this axis, indicating greater proportions of young and broadleaf forests, occur near Quatsino Sound (Figure 5, site C) and around Rock Bay to the northeast (Figure 5, site D); these same watersheds also receive large negative scores on fragmentation axis two, indicating that they are patchily forested and contain highly fragmented areas. Relatively large, positive values for composition axis two and fragmentation axis one, which are strongly associated with watersheds with abundant old growth stands, dense coniferous forests, small patches, and high edge densities, are concentrated in protected areas, especially Brooks Peninsula Recreation Area (Figure 5, site E), and Pacific Rim National Park and Carmanah Walbran Provincial Park (Figure 5, site F). Large negative values of composition axis three, associated with regenerating forest and herbaceous vegetation and shrubs, are more likely in watersheds near the coast and concentrated in the north-center of the island (Figure 5, site G).

3.2.2. Scale effects

Relationships between age class and fragmentation were also investigated at the stand level with the forest inventory polygons, and partially confirm the watershed-level patterns (data not shown). Old growth and mature stands have the highest and lowest mean fractal dimensions, and thus the greatest and least patch shape complexity, respectively ($p < 0.05$), which corresponds to the patterns of edge density for these age classes at the watershed scale. (This holds true for other patch shape metrics as well.) Stand- and watershed-level patterns of patch size, however, are contradictory. At the stand level, old growth forests occur in the largest patches, on average, while stands of mature forest are the smallest ($p < 0.05$).

3.2.3. Less-forested watersheds

Landscape variables were more closely associated with forest age structure in the subset of less-forested watersheds than over all watersheds; 7 land cover classes, 4 fragmentation metrics, and

4 spatial variables collectively accounted for 61% of the variation (Table 7). As with the analysis of all watersheds, landscape composition was the strongest correlate, followed by spatial variables and forest fragmentation, and considerable variation was shared between these variable sets (Figure 2b). The independent effects of composition yielded two significant canonical axes (Figure 6). As with the analysis of all watersheds, axis one separates the non-forested age from forest ages and is positively associated with forested land covers, and negatively associated with non-forested classes. Axis two appears to be a gradient from cover by herbaceous vegetation and broadleaf forests to coniferous and wetland cover types. In contrast to the island-wide pattern, where mature forests are associated with dense coniferous cover, mature forests in less-forested watersheds tend to be associated with broadleaf species.

Forest fragmentation could be related to a small portion of the variance in age structure in less-forested watersheds; one canonical axis was marginally significant. The regeneration age class was associated with greater forest abundance and greater within-watershed variability of edge density, while immature forests were associated with lower forest abundance. Mature and old growth classes showed no real trend, suggesting that these age groups are either associated with mean values of these variables or that they were evenly distributed across these watersheds (Figure 7).

4. Discussion

The age class distribution of forests on Vancouver Island is variable, with the western coast having greater rainfall and a potential for long periods between stand replacing disturbances. Lertzman et al. (1996) concluded that for hemlock forest on the west coast of Vancouver Island, area-wide stand-replacing disturbances are uncommon. Instead, for this wet maritime ecosystem gap processes dominate and the average turnover time for stands ranges between 350 and 950 years. While not necessarily applicable island-wide due to differing forest types and moisture conditions, to act as a foil we plot age distributions that would result from these rotation periods (350 and 950 years) alongside the observed age frequencies from the forest inventory in Figure 8. Vancouver Island has more young forest and slightly less mature and old growth forest than would be expected under the natural disturbance regimes posited by Lertzman et al. (1996), which is consistent with age patterns expected where forest harvesting is occurring. Of note, the amount of old growth forest observed is in accord with that under a 350 year rotation. In this study, we sought to further understand the mechanisms influencing forest age distribution and its spatial variation using landscape composition and forest fragmentation information derived from a remotely-sensed land cover product.

Partial canonical correspondence analyses were successful at describing the variation in forest age, explaining 36-61% of the variation in forest age structure. This is a novel application of CCA, which is typically used for community description, at a novel scale. However, multivariate problems are common across all levels of organization and we strongly recommend the use of CCA to explore multivariate correlations at the landscape scale. Moreover, the site (watershed) scores from CCA can be input into a GIS to provide information-rich maps of composite variables (e.g., Figure 5). Findings in this study highlight the parallels between stand age distributions, landscape composition, and forest fragmentation on Vancouver Island. All of these characteristics are sensitive to natural and anthropogenic disturbance regimes. Thus, their individual and collective patterns can shed light on regional forest management.

4.1. Landscape composition and forest succession

Relationships we identified between forest age and landscape composition reinforce our understanding of forest succession and development processes. We observed that, at the watershed scale, younger forests are associated with broadleaf and sparse coniferous forest types, while older forests are associated with dense coniferous forest types. This finding agrees with the forest succession trajectories associated with Coastal Western Hemlock Zone forests, such as the majority of Vancouver Island forests, where deciduous trees are represented in many seral communities (Franklin and Dyrness, 1988). This agrees with Wimberly and Ohmann (2004), who observed increases in broadleaf and sparse forests at the expense of large conifer forests in response to extractive forest management. The transition from broadleaf to conifer and sparse to dense forests over time reflects stand development, following harvest, for example, although the exact relationships also depend on propagule pressure, productivity (Franklin et al., 2002), and stocking protocols (Kennedy and Spies, 2005).

4.2. Forest fragmentation

We found that old growth is associated with greater forest fragmentation. The partial ordination of forest age on forest fragmentation shows that old growth forests are more abundant in watersheds with smaller, more irregular patches. Taken together with the association of this age class with early seral communities in the ordination by landscape composition (Figure 3b), these results suggest that fragmentation of old growth stands is likely to be due to harvesting activities in the same watershed. When analyses were restricted to less-forested watersheds, old growth forests were not strongly associated with any of the forest fragmentation metrics. Regenerating forests, in both watershed groups, were associated with within-watershed heterogeneity, which may reflect the patchwork nature of historic forest harvesting patterns. Interestingly, comparing Figures 3a and 4 indicates that although watersheds with abundant mature and old growth forests are compositionally similar, they have very different fragmentation characteristics. In contrast to old growth stands, mature stands are strongly associated with less fragmented forests.

Increased fragmentation of old growth forests relative to mature forests is also supported by the contradictory trend of relative patch size of these ages between the watershed and stand levels. This pattern likely arises from the differences in patch delineation at the two scales. Forest inventory polygons are defined as homogenous forest units; forest patches in the watershed-level analysis are an aggregation of all forest types and, thus, contain any number of forest inventory stands. The reversal of mature and old growth patch area when scaling from the stand to the landscape indicates that though mature forest stands may themselves be small, they occur within larger forested patches at the watershed scale. Conversely, while individual old growth stands are relatively large, they are also isolated in a non-forested matrix. This raises very interesting questions about the effects of a non-random distribution of edge types and edge permeability across stand ages.

Our results are consistent with existing studies of the landscape structure of forest ages, however, all other such studies have been conducted at the patch scale, and it is unclear how previous results would scale up to the landscape. Mladenoff et al. (1993) observed that the old growth type was the most fragmented forest class in a disturbed landscape. They also note that anthropogenic land cover change substantially simplified patch shapes; patch shape of the old growth type most closely approximates the high shape complexity of old growth patches in a natural landscape. McGarigal et al. (2001) document that logging and roads reduced the total area and the patch size of mature forest. We similarly observed that old growth forests are strongly associated with smaller patches and with greater edge densities (i.e., are more fragmented), which may indicate either increased forest fragmentation as a result of management (more small patches will result in a greater edge density than fewer large patches), or may simply be a reflection of the naturally more complex shapes associated with old growth forest patches.

In contrast, our results only partly agree with those of Etter et al. (2005), who found that forest age is positively associated with the amount of surrounding forest and that, when aggregating to a coarse forest/non-forest classification, regenerating forest adjacent to remnant mature stands increases patch size. Both of these lines of evidence suggest that, although fragmented, old forests in their system are embedded within a greater forested matrix. Although we found that old growth forest on Vancouver Island *is* associated with the amount of dense conifer forest in a landscape (which may be the signal of the old growth forest itself), additional lines of evidence from the relationships between abundant old growth and landscape composition and from the patch-to-watershed scaling reinforce the correlations observed with the fragmentation metrics, all of which suggest that old growth forest occurs in the areas of greatest fragmentation: Old growth is associated with non-forested and early seral patches co-occurring in the same watershed and tends to be found in isolation rather than as part of a larger forest matrix. In part, this reflects forest management strategies for retention and management of old growth biodiversity targets on the landscape (Klenner et al., 2000).

4.3. Landscape composition versus forest fragmentation

Both our inspection of general trends in landscape metrics between forest-dominated and less-forested watersheds and our detailed CCAs of forest age allowed us to identify the unique, overlapping, and potentially contradictory effects of landscape composition and forest fragmentation on Vancouver Island. Comparisons of the ANOVA and ANCOVA of forest fragmentation metrics between forest-dominated and less-forested watersheds on Vancouver Island indicate that reduced forest abundance has reduced patch sizes and increased edge density, and, conversely, that fragmentation (i.e., changes in patch shape and configuration, but independent of forest amount) has increased the proportion of forested patches and reduced the variability of patch size, when standardizing for forest abundance. Both of these processes have contributed to the larger number of forested patches in less-forested watersheds.

Partial CCAs revealed substantial overlap between landscape composition and forest fragmentation variables and their related influences on forest age distributions. This can be expected as many of the forest fragmentation variables are simple calculations from the landscape composition dataset (e.g., % forested area). Previous studies of biodiversity have noted that fragmentation metrics have relatively low explanatory power independent of land cover, and that the unique contribution of these metrics is generally dwarfed by that of landscape composition (Cushman and McGarigal, 2004; Barbaro et al., 2007). Possibly using more complicated metrics that encapsulate the shape and juxtaposition of landscape elements, rather than patch and area tallies, will increase the independent explanatory power of fragmentation variables. Indeed, the fragmentation variables that dropped out of the CCA analysis when composition was included were predominantly associated with the proportion of forest within a watershed. Those retained in the CCA emphasized patch structure (fmarea_MEAN, fdense_MEAN, fdense_MAX) and variability within a watershed (frarea_STD), information that is not present in the aspatial landscape composition variables.

Another possibility for the limited relationship between fragmentation and forest age structure is the limited range of forest fragmentation that occurs on Vancouver Island. Nearly all watersheds are dominated by forest (i.e., 91% of Vancouver Island watersheds have >85% forest cover, and 96% have >50% forest cover). Many researchers have found that the importance of fragmentation and landscape structure to ecological processes is strongly mediated by habitat abundance (Andrén, 1994; Collingham and Huntley, 2000; King and With, 2002; Matlack and Monde, 2004; but see Cushman and McGarigal, 2003). Most Vancouver Island watersheds are well above any of the habitat loss thresholds identified in the literature as being necessary to display a fragmentation effect. Furthermore, although a mosaic of forest ages suggests fragmentation within a forested area, the generalized forest, non-forest, and other categories that were used in the calculation of the fragmentation metrics do not allow us to characterize patterns amongst forest types. Even when we repeated the above analyses on the subset of less-forested watersheds (with less than 85% forest cover), which would be expected to be more likely to highlight the influence of landscape configuration, fragmentation was not disproportionately more important (Figure 2b). In fact, although forest fragmentation explains more of the total inertia in forest age structure in less-forested watersheds compared to all watersheds (2.4% vs. 1.6%), it actually accounts for slightly less of the explained inertia (4.0% vs. 4.5%). Working in a similar system, Cushman and McGarigal (2003) also found that the effects of fragmentation were not restricted to landscapes with low forest abundance.

5. Conclusions

In this research we have characterized the general trends in forest patterns in Vancouver Island watersheds. Remotely sensed land cover products have a demonstrated capacity to provide valuable information on forest pattern. Vancouver Island is extensively forested, and is composed of a mosaic of different forest ages. Most watersheds are characterized by a small number of large forest patches. More fragmented watersheds are also those with relatively less forest cover. As a result, most Vancouver Island watersheds are above typical habitat loss thresholds identified in the literature as being necessary to display a fragmentation effect.

Forest age structure at the watershed level is linked to both landscape composition and configuration, and these relationships are indicative of ecological processes and forest management practices. On Vancouver Island, forest age primarily reflects landscape composition, which indicates the typical successional development of stands as they age. Additionally, old growth forests island-wide tend to occur in fragmented watersheds and are associated with seral communities such as broadleaf forests and with regenerating stands. Old growth forests also occur in watersheds that characteristically have smaller patches and greater edge densities. Furthermore, old growth forests are often found in isolated patches rather than as part of a larger mosaic of continuous forest, reflecting specific management strategies and the on-going history of harvesting on Vancouver Island.

Medium spatial resolution Earth observation products are now available for Canada's entire forested area (with over 600 million hectares mapped). These data allow us to characterize landscape composition and configuration, providing valuable insight into spatial and temporal forest dynamics (i.e., succession, harvesting). The findings in this study highlight the parallels between stand age distributions, landscape composition, and forest fragmentation on Vancouver Island. While we investigated the inter-relationships between forest management and subsequent landscape patterns on Vancouver Island, a myriad of additional opportunities to address issues of regional or national scope remain to be undertaken.

Acknowledgements

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Table 1. Full suite of fragmentation, composition, and spatial input variables.

Fragmentation metric	Land cover class	Spatial
fpatch_MEAN	water	X
fpatch_STD	snow/ice	Y
fpatch_MAX	rock/rubble	X^2
fprop_MEAN	exposed land	Y^2
fprop_STD	shrub low	XY
fprop_MAX	wetland shrub	X^2Y
fmarea_MEAN	wetland herb	XY^2
fmarea_STD	herb	X^3
fmarea_MAX	wetland treed	Y^3
frarea_MEAN	coniferous dense	ws_area
frarea_STD	coniferous open	
frarea_MAX	coniferous sparse	
fdense_MEAN	broadleaf dense	
fdense_STD	broadleaf open	
fdense_MAX	broadleaf sparse	
	mixedwood sparse	

Table 2. Selected forest fragmentation metrics.

Metric	Description	Reference
f_rarea	Relative area (%)	Turner et al. (2001)
f_patch	Number of forest patches	Li et al. (2005)
f_prop	Proportion of forest patches (%)	
f_marea	Mean patch size (ha)	McGarigal and Marks (1995)
f_sarea	Standard deviation of patch size (ha)	Cumming and Vervier (2002)
f_dense	Edge density (m/ha)	Li et al. (2005)

Table 3. Age class definitions.

<table>
<tr><th>Age range (years)</th><th>Age class (Gillis et al., 2003)</th><th>Expanded age class (Leckie and Gillis, 1995)</th></tr>
<tr><td>0</td><td>none</td><td>0</td></tr>
<tr><td>1-20</td><td>regeneration</td><td>1</td></tr>
<tr><td>21-40</td><td rowspan="5">immature</td><td>2</td></tr>
<tr><td>41-60</td><td>3</td></tr>
<tr><td>61-80</td><td>4</td></tr>
<tr><td>81-100</td><td>5</td></tr>
<tr><td>101-120</td><td>6</td></tr>
<tr><td>121-140</td><td rowspan="2">mature</td><td>7</td></tr>
<tr><td>141-240</td><td rowspan="2">8</td></tr>
<tr><td>241-250</td><td rowspan="2">old growth</td></tr>
<tr><td>251+</td><td>9</td></tr>
</table>

Table 4. Forest fragmentation trends for Vancouver Island watersheds. All watersheds intersecting the forest inventory, larger than 50ha, and uncontaminated by cloud in the EOSD dataset are considered (n = 1283). Fragmentation metrics were calculated for 1 km^2 subunits and averaged to watersheds. Values are the mean ± standard deviation [range] of these watershed averages. Forest-dominated watersheds (≥ 85% forest cover, n = 1166) and less-forested watersheds (< 85% forest cover, n = 117) were compared with ANOVA and significance is reported.

Variable	All watersheds	Forest-dominated watersheds	Less-forested watersheds	ANOVA p
f_rarea (%)	85.3 ± 13.6 [4, 100]	87.1 ± 11.7 [14, 100]	67.9 ± 18.6 [4, 99.6]	< 0.0001
f_patch (n)	2.9 ± 2.6 [0.8, 30]	2.7 ± 2.2 [0.9, 25.5]	5.6 ± 4.1 [0.8, 30]	< 0.0001
f_prop (%)	36.6 ± 21.8 [3.8, 100]	36.7 ± 22.1 [3.8, 100]	35.8 ± 18.4 [6.5, 93.8]	N.S.
f_marea (ha)	60.3 ± 27.9 [0, 100]	62.7 ± 27.1 [0, 100]	36.1 ± 24.1 [0, 98.8]	< 0.0001
f_sarea (ha)	15.7 ± 12.1 [0, 65]	15.7 ± 12.3 [0, 65]	15.3 ± 9.2 [0, 43.3]	N.S.
f_dense (m/ha)	57.5 ± 45.3 [0, 279.3]	55.1 ± 45.6 [0, 279.3]	82.2 ± 34.1 [4.4, 172]	< 0.0001
ws_area (ha)	2310.6 ± 3856.4 [61.2, 48999.2]	2286.1 ± 3956.0 [61.2, 48999.2]	2554.6 ± 2667.2 [106.2, 12525.7]	N.S.

Table 5. Forest fragmentation trends at the watershed level across Vancouver Island, controlling for forest amount. These are thus the differences of "pure" fragmentation. Least square means of fragmentation metrics, adjusting for % forest, are given for forest-dominated watersheds (≥ 85% forest cover, n = 1166) and less-forested watersheds (< 85% forest cover, n = 117). Watersheds were compared with ANCOVA, and significance is reported.

Variable	Forest-dominated watersheds	Less-forested watersheds	ANCOVA p
f_rarea (%)	85.6 ± 13.2	83.2 ± 77.8	N.S.
f_patch (n)	2.9 ± 2.7	3.8 ± 4.3	0.0293
f_prop (%)	35.6 ± 23.8	47.0 ± 38.1	0.0029
f_marea (ha)	60.2 ± 28.9	61.0 ± 46.2	N.S.
f_sarea (ha)	16.2 ± 13.3	10.7 ± 21.2	0.0096
f_dense (m/ha)	57.8 ± 48.7	54.9 ± 77.8	N.S.

Table 6. Landscape variables that significantly contribute to CCAs of forest age over all Vancouver Island watersheds. Variables were not significant when including other datasets as covariates, and were excluded from final models are indicated with an *.

Fragmentation metric	p	Land cover class	p	Spatial variable	p
frarea_STD	0.005	broadleaf dense	0.005	XY^2	0.005
fdense_MEAN	0.005	snow ice	0.005	X^2Y	0.005
fmarea_MEAN	0.005	water	0.005	X	0.005
fdense_MAX	0.005	broadleaf open	0.005	X^3	0.005
fmarea_STD*	0.005	herbs	0.005	Y	0.005
frarea_MAX*	0.010	shrub low	0.005	ws_area*	0.040
frarea_MEAN*	0.005	coniferous dense	0.005		
fprop_STD*	0.005	coniferous sparse	0.005		
		wetland treed	0.005		
		mixedwood sparse	0.005		
		wetland shrub	0.005		
		rock rubble	0.015		
		broadleaf sparse	0.010		
		exposed land	0.020		

Table 7. Landscape variables that significantly contribute to CCAs of forest age over Vancouver Island watersheds with <85% forest cover.

Fragmentation metric	p	Land cover class	p	Spatial variable	p
fdense_STD	0.005	coniferous open	0.005	XY^2	0.005
frarea_MEAN	0.005	broadleaf dense	0.005	Y	0.005
fprop_STD	0.015	wetland shrub	0.005	ws_area	0.035
frarea_MAX	0.025	wetland treed	0.005	X^2Y	0.045
		broadleaf open	0.005		
		herb	0.005		
		mixedwood sparse	0.025		

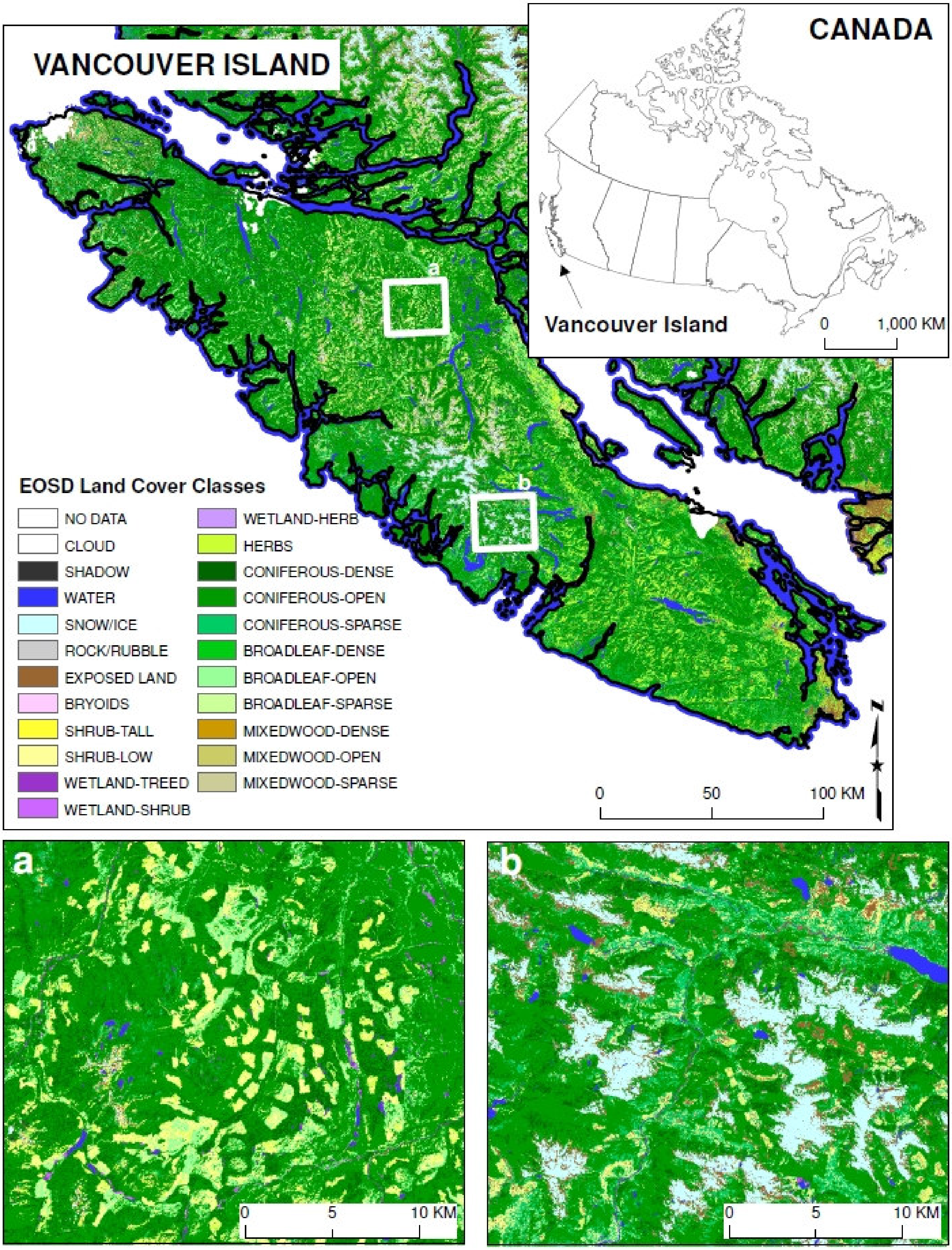


Figure 1. EOSD land cover classification of Vancouver Island.

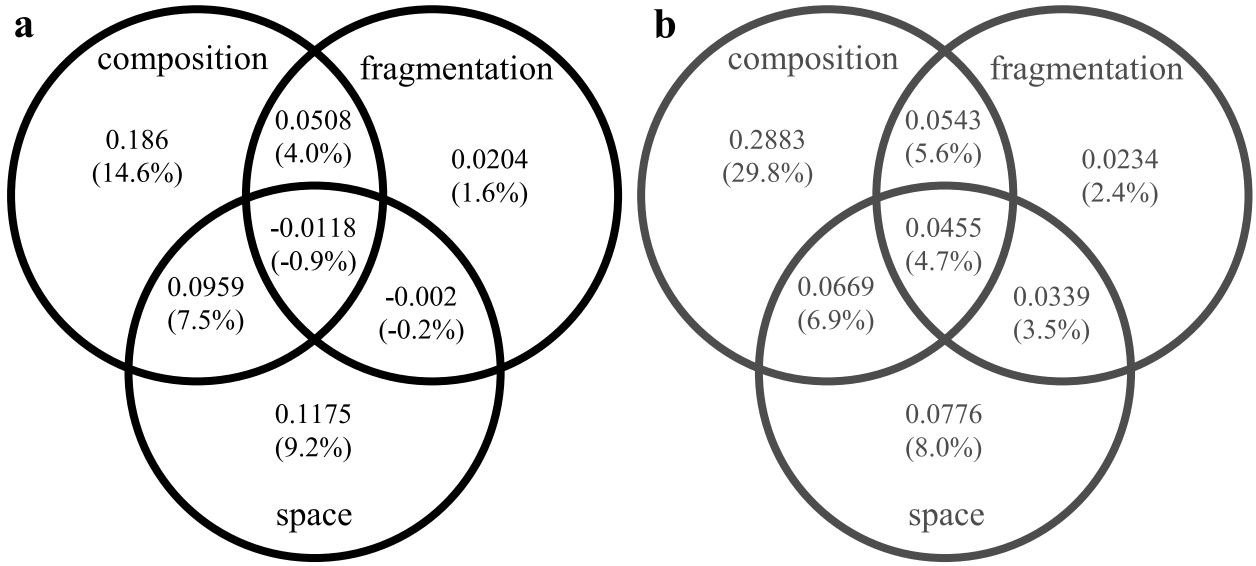
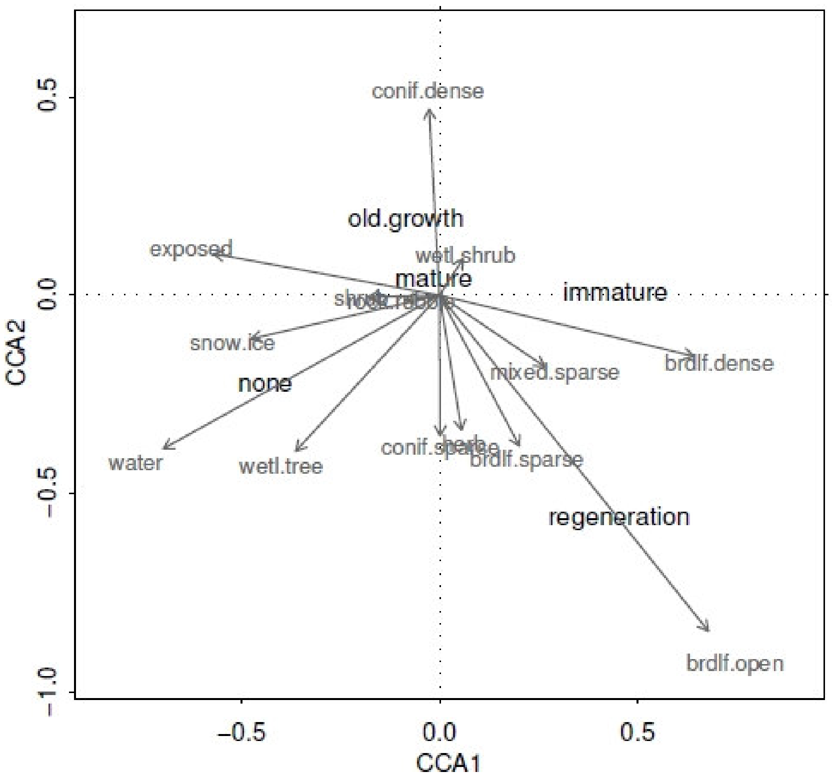


Figure 2. Partitioning of variation in forest age distributions between landscape composition, landscape fragmentation, and spatial variables for a) all candidate Vancouver Island watersheds and b) watersheds with forest cover < 85%.



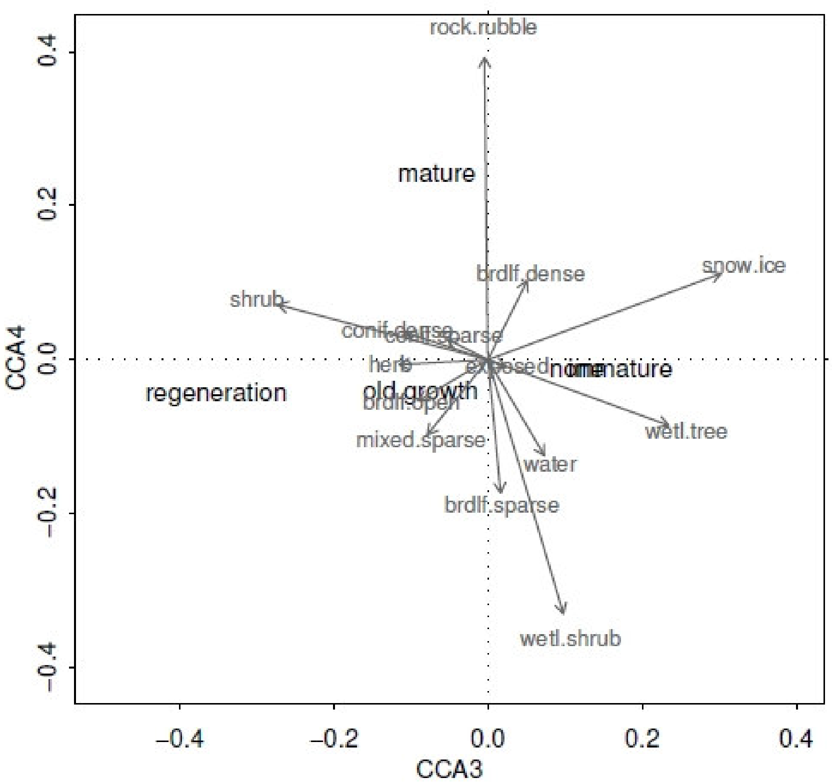


Figure 3. Partial ordination of forest age constrained by landscape composition, independent of the effects of fragmentation and space. Panels a) and b) plot the age scores and environmental gradients for canonical axes 1 & 2 and 3 & 4, respectively.

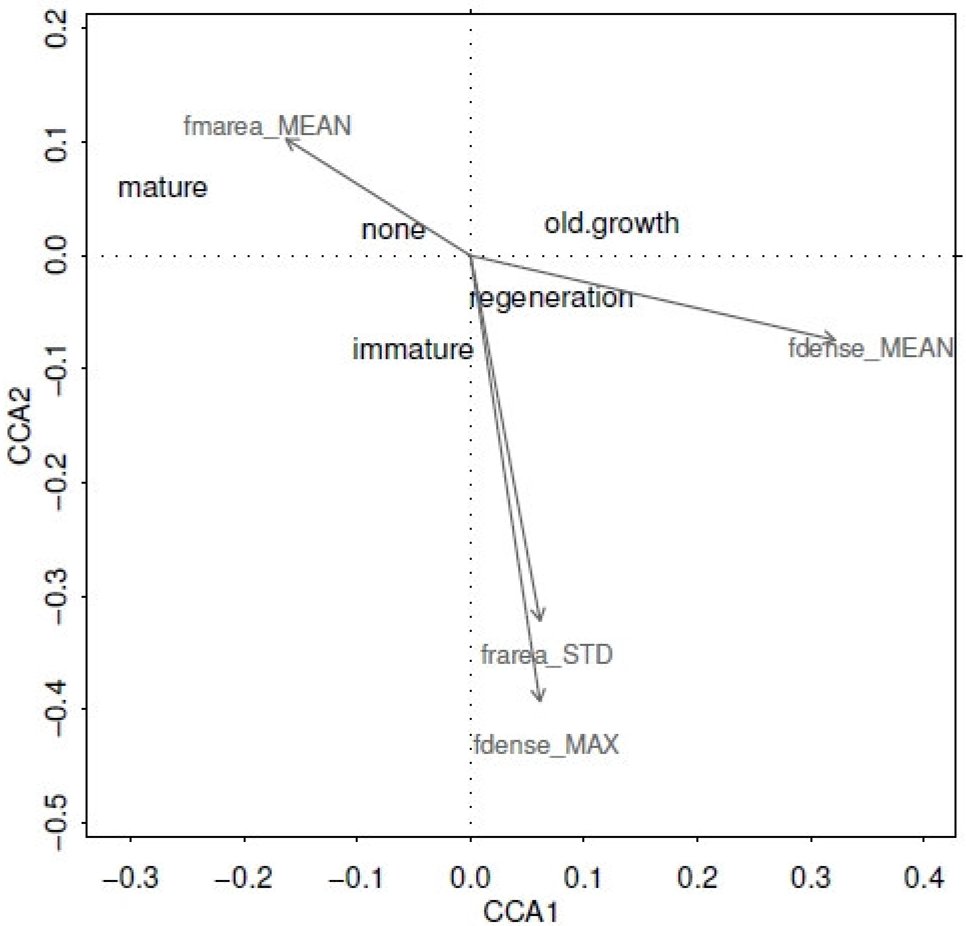


Figure 4. Partial ordination of forest age constrained by fragmentation, independent of the effects of composition and space. Age class scores and environmental gradients for canonical axes 1 and 2 are plotted.

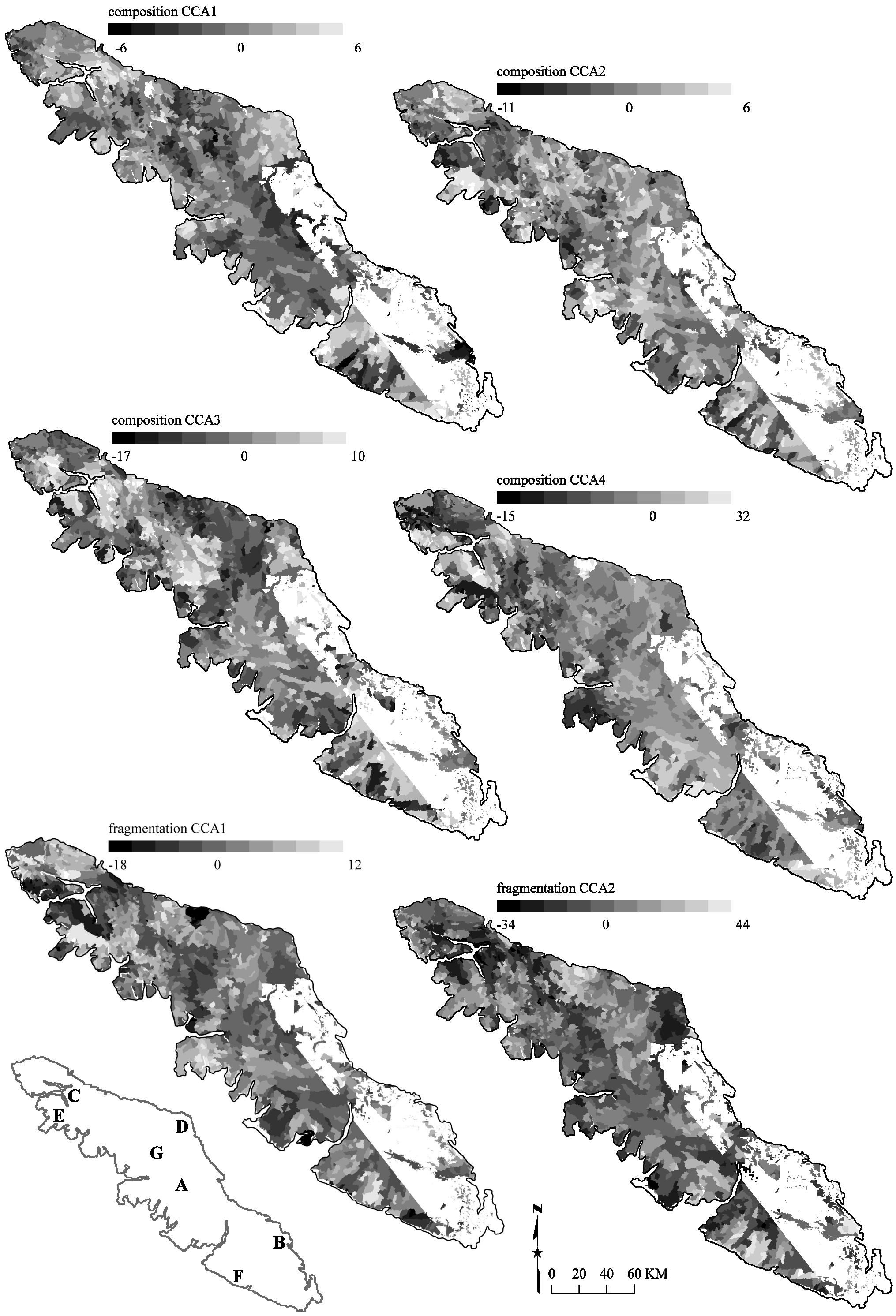


Figure 5. Watershed scores for the 4 composition and 2 fragmentation canonical correspondence axes mapped over Vancouver Island. To interpret relative values, please refer to Figures 2 and 3. The large white cut-out in southeastern Vancouver Island is an area with no forest inventory coverage for which analyses could not be carried out.

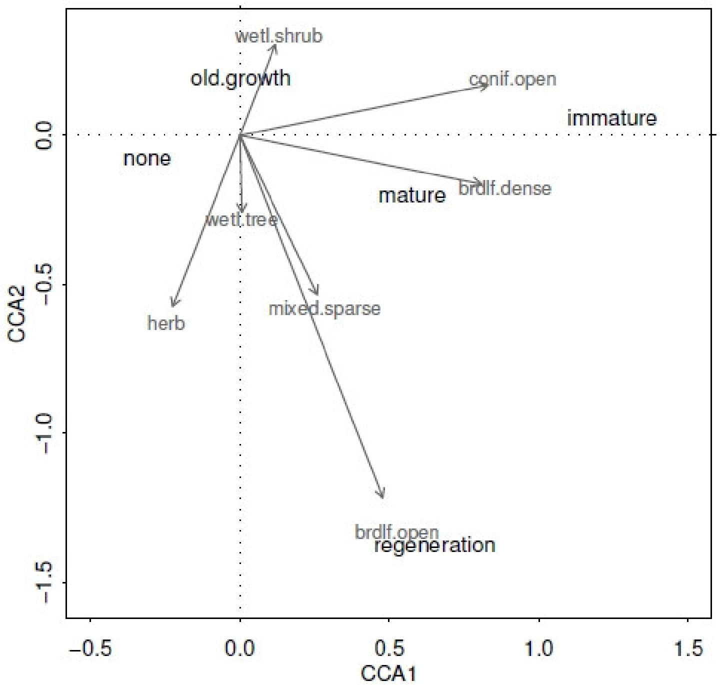


Figure 6. Partial ordination of forest age constrained by landscape composition, independent of the effects of fragmentation and space, for only watersheds less than 85% forested. Age scores and environmental gradients are plotted for canonical axes 1 and 2.

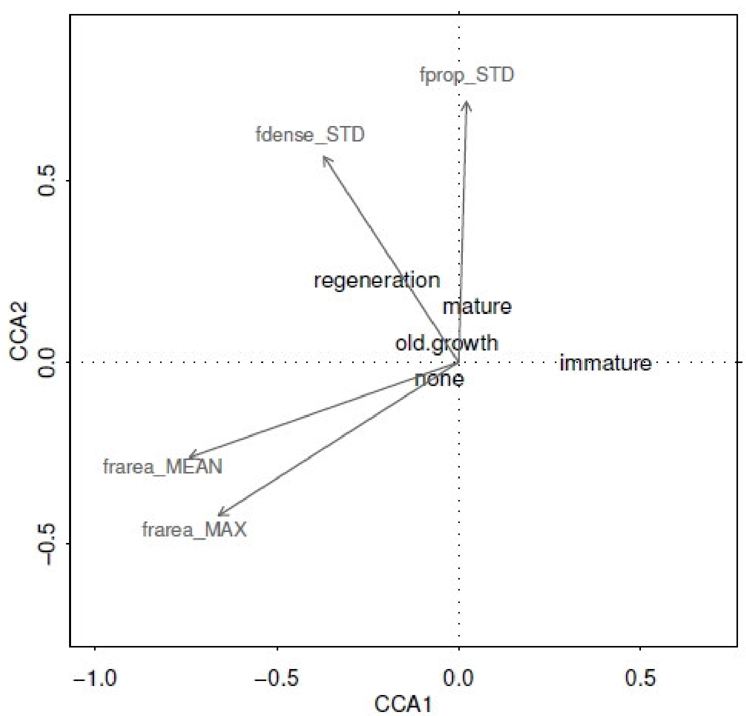


Figure 7. Partial ordination of forest age constrained by fragmentation, independent of the effects of composition and space, for only watersheds less than 85% forested. Age scores and environmental gradients are plotted for canonical axes 1 and 2. Note that only axis 1 is significant.

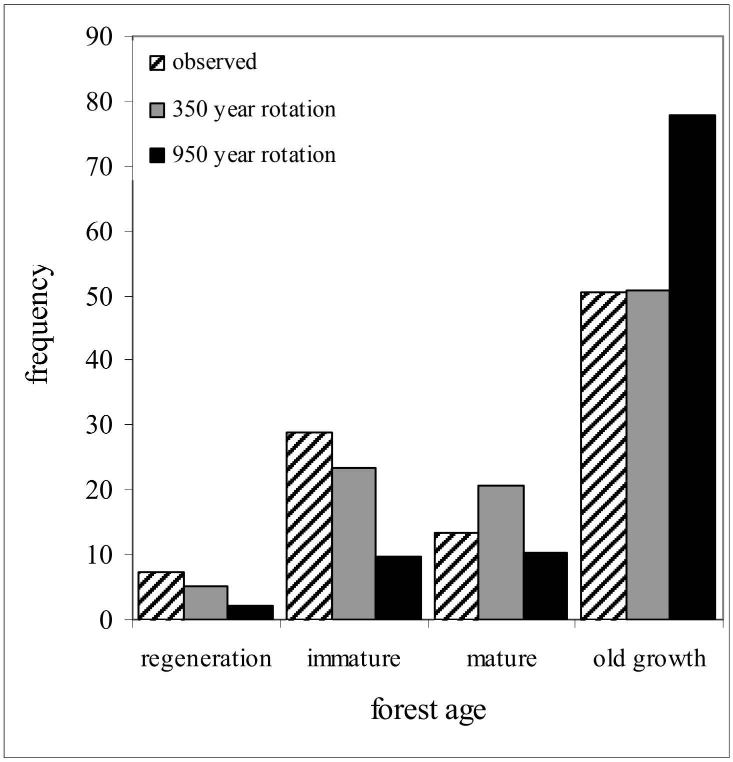


Figure 8. Vancouver Island forest age distributions, observed and expected under natural disturbance regimes (estimated from Lertzman et al. 1996).