SERAL STAGE, SITE CONDITIONS, AND THE VULNERABILITY OF UNDERSTORY PLANT COMMUNITIES TO FOREST HARVESTING

by

Jason Richard Smith
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Name: Jason Richard Smith

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Examining Committee:

          Chair: Jennifer Passmore

Dr. Kenneth Lertzman
Senior Supervisor
Associate Professor of Resource and Environmental
Management

Dr. Alton Harestad
Supervisor
Professor of Biological Sciences

Date Defended/Approved: May 19, 2005

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ABSTRACT

Understanding how composition and structure of vegetation responds to disturbance is essential to predicting and managing the impacts of forest harvesting on plant communities. My analyses showed that the wet, temperate rainforests of coastal British Columbia exhibit trends in diversity across a successional sequence similar to those found in Douglas-fir forests to the south. As well, I was able to highlight the importance of considering the response of individual species. I identified 12 species that were associated with old-forest. Furthermore, I found these late-seral associates exhibited similar environmental preferences to one another. Specifically, the typical plot containing a late-seral associate was drier than the typical plot for most other species. If forest managers want to maintain species' distributions across the landscape, a shift has to be made from focussing solely on aggregate measure of diversity, to considering the impacts of management activities on species that are especially vulnerable to disturbance.

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1 INTRODUCTION

Sound management of forest biodiversity requires a solid understanding of stand dynamics. The age of a forest stand (or time-since-disturbance) has been recognized since the early days of plant ecology as a key determinant of the vegetation community found at a particular location on the landscape (Cowles 1899, Cooper 1913, Clements 1916). Since then, changes in vegetation composition across a successional sequence have been documented for a wide range of ecosystems, leading to the development of some broadly applicable mechanisms of succession (e.g., Eglar 1954, Connell and Slatyer 1977, Noble and Slatyer 1980, Tilman 1985). In the last few decades, ecologists have focused increasingly on applying what we have learned about succession to the management of vegetation communities (Alaback 1982, Niering 1987, Roberts and Gilliam 1995, Franklin et al. 2002). The mitigation of forest-harvesting impacts has been at the forefront of these investigations.

Most studies of forest succession consider community development following a perturbation that completely eliminates the previous stand (Connell and Slatyer 1977) – a stand replacing disturbance. Forest harvesting in western North America and many other parts of the world typically involves the removal of an entire stand of trees, resulting in the regeneration of an even-aged stand (Wilson and Wilson 2001). This even-aged model has been the basis of much research into forest dynamics (e.g., Eglar 1954, Habeck 1968, Elliott et al. 1997). Thus, the lessons learned from studies of forest succession after stand-initiating

disturbances can be very useful when trying to understand the ecological consequences of forest harvesting.

Much research on successional patterns and outcomes in forests has emphasised tree species (e.g., Habeck 1968, Oliver and Larson 1996). Thus, we have a good understanding of how the tree community changes in relation to time-since-disturbance (Roberts 2004). However, in forests of coastal Oregon, Washington and British Columbia the species composition of trees present in the overstory is relatively constant over successional time, with the only significant change being the shift in some old forests from the dominance of long-lived pioneer species such as Douglas-fir to shade-tolerant species such as Western Hemlock (Franklin and Dyrness 1973, Franklin and Hemstrom 1981). In the wetter forests of coastal British Columbia this late-seral shift is absent, with tree species composition remaining relatively constant through time (Wells 1996). For these coastal forests the understory herb and shrub layers are often more diverse than the tree layer. They can undergo substantial shifts in species composition, with different species dominating in early, mid and late-seral stages (Klinka et al. 1985, Spies 1991). Unlike research on the tree layer, most studies of the herb layer across successional stages have focussed on either community level properties, such as various indices of diversity (e.g., Long 1977, Schoonmaker and McKee 1988, Qian et al. 1997), or the response of species groups (e.g., Halpern 1989, McKenzie et al. 2000).

Although we have begun to understand shifts in understory diversity across a successional sequence, many important changes in the plant community are missed by not considering the identities of species present in each seral stage. For example, community-level diversity indices, metrics incorporating richness, evenness and/or abundance, have been criticised for not discriminating between residual and invasive species (Halpern and Spies 1995, Roberts and Zhu 2002).

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Furthermore, Brosofske et al. (2001) found that communities in northern Wisconsin differed in composition but not in diversity (as measured by richness and H′), which emphasises the importance of considering species identity rather than just abundance and distribution. The entire species complement of a forest could turn over, but if the richness and distribution of species in the new community is the same as the old, most diversity indices would indicate no change (McLachlan and Bazely 2001, Moola and Vasseur 2004). In addition, evidence is mounting that species richness alone does not provide a good assessment of ecosystem functioning (Wardle et al. 1997), or community organisation (Aubert et al. 2003); thus, the presence of many species alone does not necessarily equate to good conservation value. However, even methods that take into account species identity, such as ordination, can miss the important responses of some individual species. This omission is especially likely if sensitive species comprise a small proportion of the vegetation, either in richness or abundance.

Many studies have identified individual species as occurring with greater abundance or frequency in old forest versus earlier seral stages (e.g., Schoonmaker and McKee 1988, Spies 1991, Wulf 1997, Hermy et al. 1999). Much of this work has been done in Europe and eastern North America in the context of ancient forest remnants embedded in a matrix of agricultural land (Wulf 1997, Hermy et al. 1999, Moola and Vasseur 2004). Given the sharp contrast between these two land types, it is not surprising that a large number of late-seral associates and dependents have been identified. In the temperate rainforests of western North America the landscape contrast between old forest and the surrounding matrix is generally not as extreme. Patches of old forest are more typically surrounded by younger regenerating stands that can mitigate edge effects (Matlack 1993, Oliver and Larson 1996). Nonetheless, several studies have

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identified plant species associated with late-seral stands (Schoonmaker and McKee 1988, Tappeiner and Alaback 1989, Spies 1991, Lindh and Muir 2004), and some authors have even identified late-seral obligates (Schoonmaker and McKee 1988, Ryan et al. 1998).

To date, very little information is available on successional shifts in understory plant species composition for the very wet, maritime Western-Hemlock forests of coastal British Columbia. These forests typically have very long disturbance intervals, with large-scale fires recurring every few hundred to several thousand years (Lertzman et al. 2002, Gavin et al. 2003a) The composition of plant communities has thus developed in a context where a large proportion of the landscape consists of late-seral forest, and early seral patches are generated infrequently in space and time. Although mammal species sensitive to large-scale disturbance have been identified in these forests (Bunnell 1995), very little research has been published that identifies plant species associated with late-seral forest. The one study available found only one vascular plant species that was limited to late-seral stands (Ryan et al. 1998). However, some plant species are able to persist under less than ideal conditions before eventually being eliminated (e.g., Jules 1998), leading to a delayed response of species composition to changes in the landscape (Lindborg and Eriksson 2004). Ryan *et al.* (1998) did not look for this pattern. In addition, even if a species is not eliminated from a particular seral stage, a reduced frequency of occurrence could have conservation implications. If the species is unable to recover prior to the next harvest, its frequency of occurrence could be further reduced. Consecutive reductions, over several rotations, in a species' distribution and frequency across a landscape are important if we wish to minimize management impacts on natural communities.

My overall objective in this paper is to facilitate ecologically sound management by improving our understanding of how the constituent species of plant communities respond to forest harvesting. Specifically, I identify species and communities that may be vulnerable in terms of their ability to recover following stand-replacing disturbances, such as forest harvesting. I use a three-fold approach to explore relationships between seral stage and occurrence of plant species, using vegetation plot data from the very wet, maritime Western-Hemlock forests of coastal British Columbia. First, I identify late-seral associates by looking for species that occur with greater frequency in late-seral forests versus younger stands, and show no indication of recovery prior to the stand reaching rotation age. Second, I look at patterns of richness and species composition for all species and for late-seral associates across a seral stages. Third, I examine site characteristics such as soil conditions and canopy cover to explain observed patterns. I discuss these analyses with regard to ecological interpretations and implications for forest management.

2 METHODS

2.1 Data source

My analyses were conducted using a pre-existing dataset developed by Weyerhaeuser's British Columbia Coastal Group for the purpose of Terrestrial Ecosystem Mapping (TEM; BC Ministry of Forests and BC Ministry of Environment Lands and Parks 1998) and forestry planning. The dataset consists of 581 four hundred metre-squared plots collected from seven of Weyerhaeuser's planning areas on the coast of southern British Columbia (BC; Figure 1). For each plot, percentage cover by species for vascular and non-vascular plants was recorded, in addition to environmental characteristics including structural stage, soil moisture, soil nutrient status, and canopy cover. The ecosystem type of each plot was classified at the site series level, according to BC's Biogeoclimatic Ecosystem Classification (BEC) system (Pojar et al. 1987, Meidinger and Pojar 1991). Data collection methods followed standard B.C. government procedures (BC Ministry of Forests and BC Ministry of Environment Lands and Parks 1998).

Within the BEC system there are several levels of ecosystem classification. Broad ecological groups are based primarily on climatic attributes such as temperature and precipitation regimes. The finest scale climatic group in this system is the variant. Within variants, ecosystems are delineated according to site-level attributes, including soil moisture and nutrient regimes (Meidinger and Pojar 1991). The most commonly used BEC unit at this level is the site series. The dataset I used comes from variant 1 of the very wet, maritime subzone of the

Coastal Western Hemlock Zone (CWHvm1; Figure 1). The CWHvm1 has a climate that is wet and mild, and a well-developed understory with a sparse herb-layer (Green and Klinka 1994). Throughout my analyses, I delineate ecosystem types within the CWHvm1 by site series, which are indicated by a number between 01 and 14 (Figure 2). Site series 01 denotes *zonal* ecosystems, which occur on sites with soil moisture and nutrient levels that are intermediate for the BEC variant. Otherwise, larger numbers generally indicate wetter, richer ecosystems (Banner et al. 1993). For more detail on the characteristics of specific site series please consult the BC Government Field Identification Guides (Banner et al. 1993, Green and Klinka 1994).

Structural stage describes a plot according to the age of the stand, as well as physiognomic characteristics including stand density, tree height, understory development and canopy structure (BC Ministry of Forests and BC Ministry of Environment Lands and Parks 1998). I use the structural stage of a stand as synonymous with seral stage (Table 1). Because structural stage can account for variation in rate of succession at different sites, it is a better estimator of seral stage than stand age alone (Wells et al. 1998, Franklin et al. 2002). Structural stage classification accounts for many of the features indicated in the literature as important in the development of late-seral communities. These include stand density and species composition, vertical and horizontal canopy heterogeneity, understory development, snags and coarse woody debris (Franklin et al. 1981, Franklin and Spies 1991, Spies and Franklin 1991, Tappeiner et al. 1997, Franklin et al. 2002).

2.2 Data preparation

Although rare species are an important component of ecosystems, their sporadic occurrence in ecological sampling makes them uninformative in

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analyses intended to detect general trends in species composition. Their inclusion in analyses intended to extract patterns related to broad changes in environmental attributes may result in these patterns being obscured (McCune and Grace 2002). I therefore eliminated species that occurred in only a single plot from all multivariate analyses. This resulted in the removal of 70 of 259 species from analyses of all structural stages, and the removal of 50 of 114 species from analyses of old forest plots. Using a rarity threshold of less than two occurrences is very conservative and may leave a lot of noise in the data. McCune and Grace (2002) recommend removing species that occur in less than 5% of plots. However, I did not want to obscure any meaningful variation in community structure through excessive trimming of the dataset.

I conducted all analyses of species composition using presence-absence data rather than abundance values. Because my primary aim is to assess species persistence in the landscape, either as community constituents or as future sources of propagules (Bailey et al. 1998), I judged the frequency of occurrence across plots to be more relevant than abundances within plots. In addition, when heterogeneity among plots is high, most of the useful information is captured by presence-absence (McCune and Grace 2002). In NMS multivariate analysis, Bailey (1996) found little difference in ordinations produced with abundance data and frequency data. Furthermore, I restricted the dataset to vascular, non-tree species as defined by Pojar and MacKinnon (1994).

2.3   Late-seral association

Late-seral species have been defined according to a range of criteria, based on abundance and/or frequency of occurrence in different seral stages (e.g., Spies 1991, FEMAT 1993). Because all analyses were done with presence-absence data, I based my definition of late-seral association on a species' frequency of

occurrence in seral stages along a successional sequence, starting at old-growth, through harvest and regeneration to young forest. My intention in defining late-seral species is to identify species that may be negatively affected by typical harvesting regimes, so I chose a successional sequence starting at old-forest to mimic the successional path of a stand about to be harvested. I did not include mature forest in the successional sequence, because under a typical management rotation stands are targeted for harvest when they reach maturity.

I identified a species as a late-seral associate if its frequency of occurrence in young forest was less than half that in old-growth and the species did not recover to greater than half its old-growth frequency in the successional sequence from old-growth through young forest. I used a graph portraying the frequency of occurrence for individual species in each structural stage to assess whether a species was a late-seral associate according to the definition provided above (e.g., Figure 4). To visually evaluate differences in species occurrence between seral stages I computed the standard error of a species' frequency in each seral stage using a bootstrap re-sampling technique with 1000 iterations (Efron and Tibshirani 1991). I implemented this bootstrap error computation in Microsoft Excel using Visual Basic for Applications.

I limited assessment of late-seral associates to species from one of two groups. First, I considered species identified by the Forest Ecosystem Management Assessment Team (FEMAT 1993). Their list of "old-growth associates" is based on the contemporary literature and the opinions of experts from the region. It is the closest thing to a published list of late-seral associates for my study area. Second, I considered any additional species in my dataset that occurred with greater frequency in old-growth stands versus stands younger than mature.

2.4 Statistical methods

2.4.1 Data structure

Most of my statistical analyses assume that sample units are randomly sampled and independent of one another. However, the locations of plots used in my analyses were not randomly determined. Rather, plot locations were chosen to best represent the community being sampled, an approach referred to as "subjective without pre-conceived bias" (Mueller-Dombois and Ellenberg 1974, Pojar et al. 1987). Furthermore, the plots are not truly independent because they are from seven discrete study areas (Figure 1). Nonetheless, I feel justified in my approach for several reasons. First, I was able to confirm that soil nutrient and moisture regimes were fairly evenly represented among structural stages (Figure 3), which indicates the dataset is not biased for the environmental characteristics I consider. Second, I have been cautious in interpretation of my results; I explicitly scope my discussion and conclusions to account for biases introduced by the limitations of my dataset. Third, my acknowledgment of the dataset's limitations allows the reader to assess for themselves the validity of inferences I draw from my analyses. Fourth, my analyses necessitate a large dataset, which requires a huge investment of time and money that is typically not available for ecological research; sometimes we have to make do with what we have. Finally, management applications of my results will likely use the same type of data I use.

Prior to all analyses, I applied a Shapiro-Wilk test for normality. The majority of the data were not normally distributed, so I used non-parametric tests throughout my analyses. I applied all statistical tests of significance using

an alpha level of 0.05, unless otherwise indicated. In addition, for all analyses comparing groups of plots I eliminated groups containing less than three plots.

2.4.2   Multivariate analyses

There are many methods of assessing differences in species composition among plant communities. For example, various diversity indices have been used to differentiate plant communities among seral stages (e.g., Schoonmaker and McKee 1988, Halpern and Spies 1995). However, many compositional shifts cannot be detected with basic diversity measures. I used multivariate statistics to examine differences in community composition among both site series and structural stages. Specifically, I applied non-metric multi-dimensional scaling (NMS; Kruskal 1964) to examine patterns of species composition among groups, and multi-response permutation procedure (MRPP; Mielke et al. 1976, Berry et al. 1980, 1983) to test for differences in species composition. These analyses were applied to old forest plots, as well as the entire dataset.

NMS is an ordination technique that takes the arrangement of plots in n-dimensional species space, where n is the total species richness of the sample, and summarizes this arrangement in a small number of dimensions. The specific number of dimensions chosen is based on how similar the distances are between plots in ordination space, versus the distances in n-dimensional species space. This is done by computing a metric called *stress* which describes the degree of difference in the order of plots when they are ranked by distance in species space versus ordination space. Low stress indicates that the ordination maintains the relationships among communities and species. NMS is a very useful method for comparing species composition of plots, and for illustrating similarity and differences in species composition between plots. The advantage of NMS over

other ordination techniques is that it does not make any assumptions about normality or the relationship between plots and environmental characteristics (McCune and Grace 2002). This independence from environmental parameters makes NMS especially useful for relating patterns of community composition to site conditions.

I used the "slow and thorough" autopilot settings provided in PC-ORD (McCune and Mefford 1999) with Sorenson's distance measure for all my NMS analyses. I rigidly rotated the ordination results to maximize the correlation of axis 1 with the richness of late-seral associates. This rotation facilitated interpretation of the ordination results. By maximizing the correlation of late-seral richness with a single axis, I could easily interpret which other attributes were related to the richness of late-seral associates. In addition, the rotation minimizes the correlation of the other two axes with late-seral richness. Therefore, any data structure associated with these two axes is independent of the plots' late-seral richness.

I used the position of plots in ordination space to calculate the "typical" position of a plot containing a given species, for all species. The position of this typical plot is specified by the average position of all plots containing the species. I was then able to look for patterns in the species composition of plots containing late-seral species, and compare the site conditions of plots containing late-seral species with site conditions in all other plots.

MRPP tests whether *a priori* groups of plots differ in species composition by comparing the average similarity of plots within these groups to the average similarity of plots in all possible permutations of the groups (Berry et al. 1983). The agreement statistic output by MRPP (A) describes the average within group homogeneity relative to the average homogeneity of all possible groups (McCune and Grace 2002). An A greater than zero indicates within group

homogeneity is greater than expected by chance, while an A equal to one means all plots within a group are identical. When A is zero, homogeneity within groups equals that expected by chance. A is less than zero when groups are more heterogeneous than expected. In community ecology A is often below 0.1 even when significant, and an A greater than 0.3 is generally considered quite high (McCune and Grace 2002). All my MRPP analyses used a rank transformed similarity matrix, computed with Sorenson's similarity coefficient. Groups were weighted, using the formula n/sum(n), to compensate for variation in group size.

All multivariate analyses were conducted in PC-ORD 4.25 (McCune and Mefford 1999).

2.4.3 Univariate analyses

I calculated the average species richness and the average late-seral species richness of each site series for old forest, and for all structural stages combined. I also determined these richness statistics for each structural stage. I defined species richness as the average number of species per plot. I then applied a Kruskal-Wallis test (Kruskal and Wallis 1952) to detect differences in species richness among site series, and among structural stages. If a significant difference was found, I applied a multiple comparison procedure for non-parametric data to detect which pairs of structural stages or site series differed in species richness (Dunn 1964, Zar 1999).

To explain what makes some plots higher in late-seral species than others, I compared the canopy cover of plots rich in late-seral associates and plots with no late-seral associates. I made this comparison within each structural stage, and used a Kruskal-Wallis test to detect significant differences. I defined a plot as rich in late-seral associates if its richness value was more than 1.5 times the inter-

quartile range above the upper quartile of the late-seral richness distribution for the given structural stage.

I used Spearman's rho (r_s) for computing correlations between environmental parameters and axis scores of the NMS ordinations. It is a ranked correlation coefficient and thus appropriate for non-normal data (Zar 1999). For all comparisons, I have provided graphs indicating central tendency and variation to allow visual assessment of differences in distributions (e.g. Figure 12).

All univariate analyses were conducted in SPSS 13.0 (SPSS 2004), with the exception of Dunn's (1964) multiple comparison procedure which was done in a custom Excel spreadsheet designed by myself.

3 RESULTS

3.1 Identification of late-seral associates

I found 29 species that occurred more frequently in old forests than in younger stands. FEMAT (1993) identified 27 of the species in my dataset as old-growth associates (Table 2). However, of the combined 38 species in these two groups, only twelve species met my definition of "late-seral associate" (Figure 4), which was based on a 50% decline in frequency of occurrence from old to young forest, and no appreciable indication of recovery. Species that I rejected as late-seral associates exhibited a variety of occurrence patterns across seral stages, from species that were exclusively found in young forest to species with less definite patterns (Figure 5).

The late-seral associates I identified showed a few different responses to seral stage. For instance, *Listera* sp. and *Goodyera oblongifolia* were mostly absent from any seral stage but old forest. *Clintonia uniflora, Coptis asplenifolia,* and *Rubus pedatus* declined sharply across the seral sequence from old forest through harvest and subsequent stand development. *Gymnocarpium dryopteris* and *Vaccinium alaskaense* declined more gradually. *Streptopus lanceolatus, Vaccinium ovalifolium,* and *Moneses uniflora* initially declined but began to re-appear further on in young-mature stands. *Orthelia secunda* and *Oplopanax horridum* showed less definite patterns, but still exhibited the general pattern of occurrence I used to define late-seral associates.

The typical plots containing each late-seral species were aggregated in both the NMS ordination of all plots and the ordination of old forest plots. For the ordination of all seral stages, I saw the greatest separation along NMS axes 1 and 2 (Figure 6). When old forest plots were considered separately late-seral species were still cluster together, with most of the separation evident along NMS axis 1, with some clustering towards the upper end of axis 3 (Figure 7).

Most late-seral associates occur across a range of sites along gradients of soil moisture and nutrients (Figure 8). This is especially true for *Streptopus lanceolatus* and both *Vaccinium* species. However, *Clintonia uniflora, Goodyera oblongifolia, Moneses uniflora,* and *Listera* sp. are limited to three or fewer site series. These site series represent ecosystems that have very poor-medium nutrient regimes, and xeric-subhygric moisture regimes (Figure 2). None of the four species that exhibit high specificity to a particular ecosystem type occurs in nutrient-rich, or especially wet site series.

3.2 Understory species composition

The patterns of similarity in species composition among different plots were well represented by a three-dimensional NMS ordination (Figures 9 and 10). Three dimensions adequately represented the structure of the original dataset (i.e., low stress), while providing a sufficient reduction in dimensionality to be interpretable. Increased dimensionality resulted in minimal reductions in stress. A Monte Carlo test confirmed that this solution was better than that obtained using a randomized version of the plot by species matrix. The 3-D ordination solution explains 76% of the variation in similarities among plots in the original data matrix, with 21% explained by the first axis, 18% by the second, and 37% by the third.

The first axis (NMS 1) represented a gradient from species poor to species rich sites, with both late-seral species richness ($r_s = 0.68$, $P < 0.001$) and species richness ($r_s = 0.49$, $P < 0.001$) positively correlated with axis 1 (Table 3). The centroid of old forest plots was separated from the rest of the seral stages along this axis (Figure 9), although there was a great deal of variability the position of individual plots for all seral stages. Site series were well distributed along axis 1, with richer/wetter site series occurring further right along the axis (Figure 10).

The second axis (NMS 2), the weakest in explaining variation in the original dataset, was negatively correlated with species richness overall ($r_s = -0.52$, $P < 0.001$), but did not have any correlation with late-seral species richness ($r_s = -0.05$, $P = 0.20$) (Table 3). In addition, axis 2 was positively correlated with canopy cover ($r_s = 0.57$, $P < 0.001$). The herb and shrub/herb seral stages occupy almost identical positions along this axis, while the point clusters of the other seral stages are highly overlapping further right on the axis. The seral stage centroids are roughly arranged in a successional sequence along axis 2, with the exception of old forest which occurs at approximately the same position as young forest. Site series 11, 12 and 14 occur grouped at the lower end of axis 2, with the rest of the site series clustered further up in a fairly tight group.

The third axis (NMS 3) was the strongest in terms of explaining the original data structure. This axis is also negatively correlated with species richness ($r_s = -0.51$, $P < 0.001$), and represents a declining soil nutrient gradient ($r_s = -0.60$, $P < 0.001$) (Table 3). Old forest occurs furthest along axis 3, but there is a great deal of overlap among all seral stages. I could not discern any particular pattern along this axis with respect to site series.

MRPP analysis confirmed that plots within structural stages are more similar than plots among structural stages ($A = 0.12$, $P < 0.001$). Thus, the structural stages have distinct community compositions, even when ecosystem

types are lumped at a coarse resolution (i.e., BEC variant). The differences among structural stages were even more apparent when only plots from site series 1 were considered (A = 0.18, $P < 0.001$).

The earliest two structural stages occur in very close proximity in three-dimensional ordination space, indicating very similar species composition (Figure 9). MRPP analysis of the herb and shrub/herb stages confirms their similarity (A = 0.001, $P = 0.32$). Pole/sapling, young forest, and mature plots also exhibit very similar species compositions. Their separation from other seral stages is evident from herb and shrub/herb stages along axis 2 and from old forest along axis 1. MRPP indicates that differences in species composition among these three mid-seral stages are minor (A = 0.02, $P < 0.001$). Old forest plots are set apart from other plots in ordination space. The compositional differences between old forest plots and other structural stages were confirmed by MRPP analysis, with the mature stage the most similar and the shrub/herb stage the most different (Table 5). The greatest differences in species composition of adjacent structural stages occurred between shrub/herb and young forest, and between mature and old forest (Table 6).

Site series differ in species composition as indicated by the grouping of plots in ordination space (Figure 10). The greater similarity within site series versus between site series was supported by MRPP (A = 0.23, $P < 0.001$). Site series 7, 8 and 9 have very similar species compositions (A < 0.01, $P = 0.26$). The wetter, richer site series 11 to 14 generally stand out from the other site series.

3.3 Understory species composition in late-seral plots

The patterns of similarity in species composition among late-seral plots were also well represented by a three-dimensional NMS ordination. Three dimensions adequately represented the structure of the original dataset (i.e., low

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stress), while providing a sufficient reduction in dimensionality to be interpretable (Figure 11). Increased dimensionality resulted in minimal reductions in stress. A Monte Carlo test confirmed that the solution was better than that obtained using a randomized version of the plot by species matrix. The 3-D ordination solution explains 79% of the variation in similarities among plots in the original data matrix, with 27% explained by the first axis, 33% by the second, and 19% by the third.

Two of the three axes were strongly correlated with species richness (Axis 1: $r_s = 0.54$, $P < 0.001$; Axis 3: $r_s = -0.69$, $P < 0.001$) (Table 4). Axis 1 was also strongly correlated with late-seral species richness ($r_s = 0.80$, $P < 0.001$). The drier site series tended to occur left on axis 1, with site series 3 and 4, the driest ecosystems, occurring furthest to the left. The second axis represented a fairly strong soil nutrient gradient ($r_s = 0.61$, $P < 0.001$), while the third axis was positively correlated with soil moisture ($r_s = 0.45$, $P < 0.001$). Canopy cover did not explain the patterns of similarity seen among old forest plots, because none of the axes were significantly correlated with canopy cover ($r_s < 0.17$, $P > 0.05$).

In general, site series that were similar in soil and moisture regime had similar species composition (Figure 11). I did not observe any other obvious clusters of site series in ordination space.

3.4 Understory species richness

Both species richness and late-seral richness are influenced by seral stage (Figure 12). Species richness followed a "U-shaped curve" (Wells et al. 1998) across the successional sequence, with maximum values in early-seral forests, minimum values in mid-seral forests, and old forests exhibiting an intermediate level of species richness. Late-seral species were also at minimal richness in mid-

seral forests, with intermediate richness in the youngest stands, and, as expected, maximum richness in old forest.

In all seral stages, several outlier plots had much higher richness of late-seral associates than the bulk of the distribution (Figure 12). For plots where species richness was greater than 1.5x the inter-quartile range above the upper quartile, canopy cover was lower than for plots without late-seral associates, in pole/sapling, young forest and old forest stands (Figure 13). However, this difference in canopy cover was statistically significant only for plots in young forest (Kruskal-Wallis test, $P < 0.05$; no correction for multiple comparisons).

Species richness and richness of late-seral associates varied across site-series (Figure 14). In general, wetter and higher-nutrient site series had higher species richness. Site series followed a similar pattern for old forest plots, with the exception that the wettest site series characterised by bogs and swamps, had relatively low numbers of late-seral associates. Zonal sites (i.e., site series 01), which are typically the most common sites on the landscape, had relatively low overall species richness but were intermediate in richness of late-seral associates. When I considered SMR independent of other site factors, wetter plots had higher species richness, with a slight decline in the very wettest sites (Figure 15). However, this decline was only significant for late-seral associates. Both overall species richness and late-seral richness increased with increasing SNR (Figure 16).

4 DISCUSSION

4.1 Defining late-seral associates

4.1.1 Species associated with late-seral stands

Several of the species I identified as late-seral associates have been shown in other studies to be more abundant or frequent in old forests than in younger forests. These include *Clintonia uniflora* (Halpern and Spies 1995), *Goodyera oblongifolia* (Schoonmaker and McKee 1988, Halpern 1989, Ruggiero et al. 1991, Halpern and Spies 1995, Ryan et al. 1998, Lindh and Muir 2004), *Moneses uniflora* (Moola and Vasseur 2004), *Coptis asplenifolia* (Lindh and Muir 2004), *Orthelia secunda* (Roberts and Zhu 2002, Selmants and Knight 2003), *Listera cordata*, (Klinka et al. 1985, Halpern and Spies 1995), *Vaccinium alaskaense* (Klinka et al. 1985), and *Vaccinium ovalifolium* (Klinka et al. 1985). In addition, all late-seral associates identified in my analyses were listed as "old-growth associates" by the Forest Ecosystem Management Team (FEMAT 1993), with the exception of *Oplopanax horridum* (Table 2). Thus, my results provide empirical support for FEMAT's list of old-growth associates, which is primarily based on expert opinion.

Some species that I did not identify as late-seral associates have been found in other studies to be most abundant in old forests (Klinka et al. 1985, Schoonmaker and McKee 1988, Halpern 1989, Ruggiero et al. 1991, FEMAT 1993, Halpern and Spies 1995, Roberts and Zhu 2002, Lindh and Muir 2004, Moola and Vasseur 2004). There are a few reasons why my analyses did not indicate these

species to be late-seral associates. First, the flora of the other study areas may respond differently than the flora of my study area, to seral shifts in environmental attributes. Plants are plastic in their response to specific environmental attributes depending on the other biotic and abiotic conditions in which they are growing (Schlichting 1986, Callaway et al. 2003). For example, some species have varying degrees of shade tolerance depending on site (Carter and Klinka 1992) and climatic conditions (Wright et al. 1998). The studies that found late-seral associations for species where I did not were conducted in ecosystems with less rainfall and/or more pronounced summer droughts than my study area. Second, some species identified in the literature as late-seral associates did not occur with sufficient frequency in my dataset to make a proper assessment. These include the myco-heterotrophic species *Monotropa uniflora, Monotropa hypopithys*, and *Corallorhiza maculata* (Schoonmaker and McKee 1988, Halpern and Spies 1995), which require conditions typical of late-seral forests, such as a thick litter layer and shade (Leake 1994). Third, with the exception of Halpern and Spies (1995), I could find no studies from western North America that empirically consider changes in the occurrence of individual species across a full successional sequence, from newly-established to old-growth forest. The studies that do consider late-seral association are non-empirical and either base their assessment on expert opinion (FEMAT 1993), or leave the reader to make their own assessment based on the data provided (e.g., Klinka et al. 1985, Schoonmaker and McKee 1988).

Other research done in the temperate coastal rainforests of western North America identified some of my late-seral species as not being associated with old forest (e.g. *Vaccinium alaskaense, Clintonia uniflora* Schoonmaker and McKee 1988, *Goodyera oblongifolia* Bailey et al. 1998). There are a few possible reasons for this discrepancy. First, individuals may have re-colonised disturbed sites from

adjacent late-seral forest. Although late-successional herbs are typically poor dispersers (Dzwonko and Loster 1992, Matlack 1994, Brunet and von Oheimb 1998, Bossuyt et al. 1999, Ehrlen and Eriksson 2000), close proximity to a propagule source may facilitate some colonisation once suitable conditions return to the regenerating stand. It is not always clear whether the authors controlled for distance to an old-forest edge. Second, with the exception of Ryan et al. (1998) I could find no studies conducted in the very wet, maritime ecosystems of coastal North America. As mentioned previously, a species response to seral stage can depend on broader environmental parameters. Third, if a wide range of climates is considered within one study, any patterns of late-seral association may be masked by variation among sites. For instance, Bailey et al. (1998) found no difference in species composition between late-seral and regenerating stands when they lumped stands from different study sites. However, within a study site, the species composition of late-seral stands consistently stood out from thinned and unthinned regenerating stands.

4.1.2 Mechanisms of late-seral association

Ecosystem stability has been described in terms of resistance, the amount an ecosystem changes following disturbance, and resilience, the time to recover the original ecosystem following disturbance (Pimm 1984, Halpern 1988). Stability may not be an emergent property of the ecosystem, rather it may be strictly a product of the resistance and resilience of individual species (Halpern 1988). Thus, the stability of a species' presence on a particular site can be thought of in the same way as an ecosystem's, with resistance indicated by ability of the species to persist following disturbance, and resilience indicated by how quickly the species can re-colonise if eliminated from a site by disturbance. Late-seral associates are unstable because they are, by definition, heavily

impacted by stand-replacing disturbances. Thus, late-seral associates can be defined according to their levels of resistance and resilience. I put forward three attributes of a species response to disturbance that will be displayed by late-seral associates.

Low Resistance 1. The species depends on some attributes of old forest not present in at least one of the other seral stages. Such attributes could include pattern of canopy cover (Hermy et al. 1999), soil conditions (Hermy et al. 1999), or the presence of specific mycorrhizal fungi (Bidartondo and Bruns 2002). The majority of species I identified as late-seral associates prefer sites with most of these attributes (Pojar and MacKinnon 1994). For example, *Goodyera repens*, a congener of the late-seral associate *G. oblongifolia*, uses its association with mycorrhizal fungi to extract carbon from decomposing litter (Alexander and Hadley 1985). Because this relationship is only important when the plant is immature, the lack of appropriate fungal species in earlier seral stages may prevent recruitment of new individuals into the population.

Low resistance 2. The species is unable to persist through unfavourable conditions present in the regenerating forest, a further indication of low resistance. Two traits known to be associated with variation in persistence are seed size and shape (Thompson et al. 1993), and vegetative reproduction (Cook 1985, Eriksson 1994, Levine and Feller 2004). Research in the forests of the US Pacific Northwest indicates that understory species generally have a low presence in the seed bank (Halpern et al. 1999), so persistence would likely have to be vegetative. For example, a study in the deciduous forests of Denmark found that herbaceous species with a high degree of lateral spread are more common in old forests (Graae and Sunde 2000). Some of the late-seral associates I identified (or their congeners) do have known mechanisms of vegetative persistence. *Listera caurina* uses large below-ground resources to persist through

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the low-light conditions created by dense coniferous forests (Lezberg et al. 1999). Nonetheless, I found *Listera* sp. to have a strong association with old forests, suggesting either that it is unable to mobilize this mechanism of persistence in young forests, or that the stored resources are insufficient to overcome the period of unfavourable conditions. For most species in my study areas there is little understanding of what conditions are unfavourable, let alone what the minimum conditions are for persistence. To understand the processes influencing late-seral associations, further autecological research is required to better understand mechanisms of persistence.

Low resilience. Once suitable conditions return to a stand, a species that was previously eliminated from the stand is slow to re-colonize, indicating a lack of resilience. Dispersal limitation has been shown to be an important distinguishing attribute of late-seral plants, which can impact their ability to re-colonize regenerating stands (Brunet and von Oheimb 1998, Hermy et al. 1999, Verheyen and Hermy 2001a, b, Honnay et al. 2002). Across a range of forest types, the number of late-seral species in regenerating stands is negatively correlated with the distance of those stands from old forest, with migration rates of individual late-seral species generally less than 1 metre/year (Matlack 1994, Meier et al. 1995, Brunet and von Oheimb 1998, Bossuyt et al. 1999, Butaye et al. 2001, Dzwonko 2001, Jacquemyn et al. 2001). Even where appropriate growing conditions for a late-seral associate have returned to a regenerating stand, late-seral species can still be absent due to dispersal limitation (Brunet et al. 2000, Ehrlen and Eriksson 2000, Verheyen and Hermy 2001b, Butaye et al. 2002). Dispersal ability can be estimated qualitatively from dispersal mechanism (Dzwonko and Loster 1992); zoochores are generally good dispersers, anemochores are moderate dispersers, and myrmecochores and barochores are usually very poor dispersers (Matlack 1994). Based on fruit and seed

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morphology, the late-seral associates I identified are a mix of zoochores (6), anemochores (3), and barochores (3). Thus, there is no apparent bias towards poor dispersers, although I do not know how this distribution of dispersal mechanisms compares to the distribution among the rest of the flora. However, two of the anemochores are orchids that grow close to the ground, which may make them very poor dispersers (Murren and Ellison 1998, Arditti and Ghani 2000, Machon et al. 2003, Chung et al. 2004). Because the six zoochores are likely good dispersers, other factors, such as sensitivity to site conditions, are likely driving their association with old forest.

The U-shaped frequency response across the successional sequence, by late-seral associates (Figure 4), could be explained as a disassociation with mid-seral forests, rather than as an association with late-seral forests (mid-seral disassociation). For example, some of the species I considered are known to be relatively abundant in both clearcuts and old stands, but much less abundant in young forests. These species include *Vaccinium alaskanse*, *Coptis asplenifolia*, and *Rubus pedatus* (Tappeiner and Alaback 1989). This mid-seral disassociation is postulated to be a response to the low light-levels common in mid-seral forests (Tappeiner and Alaback 1989, Frazer et al. 2000). However, even if mid-seral disassociation is the mechanism for reduced frequency of occurrence in mid-seral forests, the species I selected as late-seral associates did not recover in the "mature forest" structural stage. The continued absence of these potential mid-seral disassociates in mature forests suggests a lack of resilience, possibly due to dispersal limitation, which justifies their classification as late-seral associates. Also, because none of the old forest plots had been logged previously, it is unclear how long it would take for late-seral associates to re-colonise old forests.

4.2 Dynamics of the understory community across seral stages

4.2.1 Species richness

The U-shaped pattern of species richness across the successional sequence, from an herb-dominated community to old forest (Figure 12), can be explained by shifts in available resources. Many studies support the peak in species richness I observed in early-seral stands (Long 1977, Schoonmaker and McKee 1988). This early-seral peak in species richness is likely due to the combination of residual species held over from the previous stand and invasive species exploiting the flush of light, space and nutrient resources following harvesting. The relatively high richness of late-seral associates in early seral stages (Figure 12) supports the hypothesis that residual species are a factor contributing to early-seral richness. The low species richness I observed in mid-seral forests is also corroborated by the literature, where the paucity of species is primarily attributed to the dense canopy of trees limiting light resources in the understory (Alaback 1982, Halpern and Spies 1995, Wells 1996). As mature forests age, the overstory becomes horizontally heterogeneous with the development of canopy gaps, understory light-levels increase, and coarse woody debris levels rise (Franklin et al. 2002). In response to these environmental shifts and greater habitat diversity (Dumortier et al. 2002) species richness increases, including the richness of late-seral associates. Perhaps coincidentally, in my study the increase in median species richness between mature and old forest matched the increase in late-seral species richness between these two stages.

4.2.2 Species composition

Although the species composition of plots did vary by structural stage, there was considerable overlap in the composition of some stages. The high degree of overlap between the herb and shrub/herb stages indicates that, from a compositional standpoint, these two communities are identical and cannot be distinguished by species composition. Their separation into separate structural stages is likely due to the influence of silvicultural considerations in delineating these stages. MRPP analyses indicated the three mid-seral stages (i.e., pole/sapling, young forest, and mature) had different species composition, but that the differences were minor, suggesting it may be appropriate to combine these stages when considering vegetation composition. Late-seral plots stood out from the other seral stages in both the ordination and MRPP analyses, signifying that these forests have a distinct species composition. Similar patterns of species composition exist among seral stages in drier CWHdm forests of British Columbia, although in these forests the composition of each stage is more distinct (Klinka et al. 1985).

The large amount of overlap in species composition among seral stages may be due to variation resulting from the wide region sampled. For example, Bailey et al. (1998) considered plots taken from an even wider range of ecosystem types and geographical locations, and found minimal differences in species composition between seral stages. It is worth noting that all my comparisons between structural stages consider only species composition. Substantial shifts in species abundances, which would be transparent to these analyses, may be occurring among structural stages. Such shifts are important aspects of succession from a forest management perspective, especially when considering wildlife habitat (e.g., Felix et al. 2004, Michelfelder 2004).

The influence of site characteristics on species composition is strong, as indicated by the high correlation between soil properties (SMR and SNR) and ordination axes, even when all seral stages are lumped together. This suggests that a sizeable number of species are able to live, and reflect site differences, under the wide range of light and competition regimes present in different seral stages. These species respond more to conditions associated with landscape position than finer scale structural features such as canopy cover, coarse woody debris, and habitat heterogeneity. This muted response of overall community composition to environmental changes associated with succession is not surprising considering that I identified only a small proportion of the total flora as late-seral associates.

4.2.3 Late-seral associates

The pattern of late-seral species richness across the successional sequence fits with our understanding of the life-history of plant species associated with old forest. These species are typically long-lived (Whitford 1949, Noble and Slatyer 1980, Cook 1983) and adapted to persisting in low-resource conditions (Grime 1977, Whittaker and Levin 1977, Hermy et al. 1999, Graae and Sunde 2000). This ability to tolerate adversity explains why late-seral associates still occur frequently in early-seral stands, despite the dramatic change in environmental conditions during and after the disturbance that initiated the new stand. However, the reproductive capacity of late-seral associates may be hampered in a non-suitable environment, which explains their gradual decrease in frequency, moving from early to mid-seral stands (Franklin et al. 1981, Arsenault and Bradfield 1995). Individuals persisting as legacies from the previous stand begin to die, and minimal recruitment is occurring to replace them (e.g., Jules 1998, Lienert and Fischer 2003).

While I considered changes in species frequencies across multiple seral stages, many studies that identify late-seral species only consider species that have high abundance in old forests and low abundance in all other seral stages. For example, Moola and Vasseur (2004) use Indicator Species Analysis to identify late-seral associates, which excludes any species able to persist for even a short time in clearcuts. Schoonmaker and McKee (1988) do not identify *Goodyera oblongifolia* as impacted by forest-harvesting even though its abundance decreased by two orders of magnitude following logging. Ryan et al. (1998) only consider species that are completely restricted to old-growth stands as late-seral species. Failure to consider early-seral persistence when defining late-seral associates could have consequences when managing for species diversity. For example, a delay in the extirpation of species from a stand may create an "extinction debt" (Tilman et al. 1994), which could lead to the impact of forest harvesting on late-seral plant communities being underestimated during the early post-harvest period.

4.3 Drivers of old forest community composition

4.3.1 Composition of all understory species

When I considered old forest plots separately from other plots, species composition was more associated with soil moisture and nutrient regimes than when I considered all seral stages together, as indicated by the higher correlations of SMR and especially SNR with ordination axes. Conversely, species composition was more associated with canopy cover among plots from all seral stages than among old forest plots. These differences in the ecosystem attributes associated with species composition suggest that different mechanisms structure the understory of regenerating forests and old forests. For example, old

forest communities may be temporally stable in many attributes such as humidity and temperature regime, so all that is left to vary at a specific site are edaphic factors. In contrast, environmental conditions are dynamic in regenerating forests, as stand density, tree height and tree species shift through time (Wells 1996, Franklin et al. 2002). Thus, understory community composition in young stands is primarily driven by overstory conditions which affect light levels (Klinka et al. 1996, Frazer et al. 2000, McKenzie et al. 2000), and competitive interactions resulting from the differential response of species to changing environmental conditions (Connell and Slatyer 1977, Halpern 1989, McKenzie et al. 2000).

In old forests, vegetation dynamics are driven largely by the shifting distribution of canopy gaps altering light conditions on the forest floor (Spies 1991). However, in the forests I studied this process of gap dynamics occurs over a long time span relative to changes in canopy composition across earlier seral stages (e.g., Lertzman and Krebs 1991, Lertzman et al. 1996). The relative stability of light conditions in old forest allows vegetation to respond to physical characteristics of the site (Brosofske et al. 2001), such as soil drainage patterns (Hanley and Brady 1997). Therefore, late-seral vegetation composition is primarily a response of species to site conditions, and ability to tolerate stresses associated with the late-seral environment (Grime 1977, Hermy et al. 1999), including slowly shifting light regimes. While I observed minimal response in species composition to the light environment, it is likely that shifts in abundance and dominance are occurring among constituents of the understory community. This latter phenomenon has been observed among tree species in higher elevation forests of coastal British Columbia (Lertzman 1992).

Vegetation composition is known to be related to edaphic factors such pH, moisture and nutrients (Pregitzer and Barnes 1982, Bridge and Johnson 2000,

Ferris et al. 2000, Brosofske et al. 2001, Dumortier et al. 2002, Adkison and Gleeson 2004, Lookingbill et al. 2004). In general, wet and nutrient-rich sites support more species than dry, nutrient poor sites (e.g., Lapin and Barnes 1995). My data support this relationship; species richness increased with both wetter SMR and more nutrient-rich SNR. However, Lapin and Barnes (1995) found that dry-rich sites had higher species richness than wet-poor sites, indicating that nutrient level is a primary driver of species richness with moisture regime playing a secondary role. The inverse relationship is apparent in my data, where patterns of species richness among site series are dominated by SMR, with SNR driving richness patterns within similar moisture regimes (Figure 14). In old forests of south-western Washington State, soil moisture, in association with a particular climate, was a good predictor of understory richness (Brockway 1998). My results indicate that site series classification may be similarly used to predict the species richness of a site.

4.3.2   Composition of late-seral associates

Overall species richness and richness of late-seral associates showed similar responses to edaphic conditions, but some differences were apparent. Both richness measures increased with SMR and site series, but the relationship was weaker and non-monotonic for late-seral associates, with a peak at moderate-high soil moisture. This result is corroborated by ordination results which indicate that, on average, late-seral associates occur in drier plots than many species (Figures 6 and 7), although, because of the strong species richness-moisture relationship, these "drier plots" are still mesic. Furthermore, late-seral associates in deciduous forests of Europe were found to prefer mesic, nutrient-rich soils (Hermy et al. 1999). Late-seral associates that are most restricted in terms of site conditions prefer even drier, and less nutrient-rich sites than the

average late-seral associate (Figure 8). Therefore, although wetter sites typically have higher species richness, they are not necessarily the best sites for late-seral associates.

4.4 Management implications

4.4.1 Ecosystem and structural stage classification in B.C.

The role of the biogeoclimatic classification system (BEC) in British Columbia has expanded considerably since its inception. Initially, ecosystem classification was used primarily for silvilcultural purposes, such as selecting the ideal tree species to plant on a site and specifying site preparation measures (Green et al. 1984, Coates and Haeussler 1987). Over the last decade, with increasing emphasis on conserving biodiversity (e.g., Park and McCulloch 1993, B.C. Ministry of Forests and B.C. Ministry of Environment Lands and Parks 1995), and the expanding adoption of ecosystem-based management (e.g., Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, Coast Information Team 2004), the BEC system is being used as a proxy to manage broad assemblages of species from a wide range of taxa (e.g. as a coarse filter approach to conservation in managed forests). Such use of ecosystem types as surrogates for species composition has been criticized in the literature for not capturing coherent assemblages of species across a range of taxa (e.g., Mac Nally et al. 2002). However, because site series are primarily based on the climax vegetation of the site (Pojar et al. 1987, Meidinger and Pojar 1991), it is has been deemed reasonable to assume that the BEC system serves as an effective surrogate for the species composition of late-seral plant communities.

My analyses indicate that site series do reflect cohesive assemblages of understory species in old forests. Site series are also adequate surrogates for

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species composition when all seral stages were considered together, which is surprising because the BEC system is based on late-seral composition. However, the great degree of overlap among site series suggests there are many factors influencing late-seral species composition that are not addressed in the BEC system. Nonetheless, much of this overlap reflects different degrees of resolution in distinguishing communities along the nutrient-moisture gradient, not an inherent flaw in the system. For example, there is a particularly high degree of overlap among the richer, wetter site series. Thus, site series do have utility in capturing assemblages of vascular plants, but their use in predicting species composition should be done with caution. Further refinement of the system, and identification of factors contributing to variation among plots within a site series, would greatly increase the utility of the BEC system for specification of biodiversity surrogates.

Structural stage classification has mixed utility for describing distinct plant communities, in terms of composition, along a successional sequence. MRPP analyses indicated that the herb and shrub/herb stages are nearly indistinguishable. In addition, mid-seral stages, from pole/sapling to mature forest, were very similar in species composition (Table 1). Thus, from a compositional perspective only three seral communities existed in the data set I examined: early-seral stands, mid-seral stands, and old forest. However, it is likely that stand structure continues to develop for several hundred years following large-scale disturbances in temperate rainforests of western North America (Lertzman 1995, Franklin et al. 2002). Thus, the "old forest" structural stage may contain more than one discrete plant community. However, I lumped communities at the BEC variant level for comparisons of composition between seral stages. Therefore, differences among young stands, and among mid-seral stands, may be obscured by variation in composition among plots within each

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seral stage. Nonetheless, the structural stage classification system needs to be refined if it is to reflect the response of the understory community to stand conditions. Specifically, there should be greater resolution for older stands, and when describing vegetation composition perhaps decreased resolution for younger stands.

4.4.2 Silvicultural prescriptions

Traditional forest management practices usually involve harvesting early in the "mature forest" structural stage, when the stand's mean annual increment (MAI) is at or approaching its peak (Pearse 1967, Chang 1984, Curtis 1995). Because late-seral associates will not have typically re-colonised stands at this stage, harvesting would eliminate these species from large portions of the managed landscape. One solution is to increase the rotation age of the stand, which would maintain late-seral associates over a larger proportion of the landscape by allowing them to re-colonise prior to the next harvest. Brunet and von Oheimb (1998) recommend increasing the rotation length to match species migration rates, ensuring re-colonisation of harvest areas and continued viability of populations of late-seral associates across the managed landscape. This type of approach is especially relevant for present-day CWHvm1 ecosystems where the proportion of the landscape currently in an early- to mid-seral condition is likely larger than the historical precedent, due to rotation lengths that are much shorter than the historical disturbance return interval (Lertzman et al. 2002, Gavin et al. 2003a, b). However, my analyses indicate that many late-seral associates are absent throughout the mature structural stage, which can extend up to 250 years (Table 1). Currently, rotation ages in the CHWvm1 are generally less than 120 years (e.g., BC Ministry of Forests 1999, 2003). An appropriate reduction in harvest frequency would drastically affect timber supply and is

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likely not a tenable option for the majority of the landscape. However, longer rotations are consistent with other management objectives such as carbon sequestration (Diaz-Balteiro and Romero 2003, Venn 2005) and wildlife habitat (Curtis and Carey 1996, Thompson et al. 1999, Taylor et al. 2003), so they may be useful under certain circumstances.

Retaining patches of old forest in a cutblock is another way to facilitate re-colonisation of poor dispersers following forest harvesting. Such patches can act as "lifeboats" for species requiring late-seral conditions, and sources of inocula for these species once suitable conditions return to the surrounding forest (Franklin et al. 1997). Current management practices often require conserving patches of forest protecting riparian areas, stabilising slopes, and maintaining habitat for endangered species. In addition, many logging operations on the coast of British Columbia are moving towards a "retention" silvicultural system, where patches of forest are left uncut within a cutblock to maintain late-seral structure and species (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, Mitchell and Beese 2002, Beese et al. 2003). If the patches are appropriately positioned, the average dispersal distance for re-colonising species can be significantly reduced compared to a standard cutblock. Another consideration when choosing the location of retained patches is the identity of species in the community within the patch. If the objective of the patch is to serve as a lifeboat for late-seral associates, it is important to place retention patches in site series known to be rich in late-seral associates. Furthermore, knowledge of how late-seral associates are distributed among site series can inform broader-scale planning, to ensure that late-seral associates are adequately protected throughout the landscape.

4.5 Study limitations and future work

This study provides one of the first data-based assessments of understory dynamics and late-seral association for the wet forests of coastal British Columbia. However, broad application of my results should be entertained cautiously, due to the sampling protocols that were employed in gathering these data. First, plots were sampled from a small subset of the CWHvm1 ecosystem, which extends from south-western Vancouver Island up to the central coast of the BC mainland. However, the BEC system is based upon the principle of "ecological equivalence" (Bakuzis 1969), which states that different sites with the same physical characteristics will have the same climax vegetation (Pojar et al. 1987). Although factors such as site-history and climatic variability can influence vegetation composition, site series of the BEC system are designed to consistently express the composition of the potential climax vegetation for a site (Pojar et al. 1987). Therefore, the BEC system allows for cautious extrapolation of compositional patterns on late-seral sites in my study area to other parts of the CWHvm1. Second, plot selection was not random, but rather based on a sampling protocol that is "subjective without pre-conceived bias" (Mueller-Dombois and Ellenberg 1974). Specifically, plots are placed in a relatively homogeneous stand, in terms of soil and vegetation characteristics, where site conditions are typical of the broader ecosystem the plot is intended to represent (Mueller-Dombois and Ellenberg 1974, Pojar et al. 1987). Thus, my results are applicable to locations expressing the typical conditions of a site series, but less applicable to locations that occur along the transition between two site series, and locations that do not fit into the site series classification system such as wetlands and rocky outcrops.

My sample size was inadequate to fully address harvesting impacts on late-seral plant communities. First, there were several site series that were either not represented in my analyses, or were represented by a small number of plots. Second, I was unable to address impacts on ecosystem types not described by standard site series designations. Third, there are several late-seral species identified elsewhere in the literature that either did not appear in the dataset, although they are known to occur in the area, or occurred with such low frequency that I had to exclude them from my analyses. Acquiring additional plot data can be very expensive, but reasonable options exist. For example, Terrestrial Ecosystem Mapping projects require collection of appropriate data, and these projects are continually conducted across the province. Better coordination of such data collection efforts may yield a substantial amount of new data with a minimum incremental cost.

I identified a suite of species that occur with reduced frequency in early- to mid-seral forests, but was not able to definitively state the mechanisms by which this reduction in frequency occurs. Because the likelihood of a given species occurring at a particular site depends on whether its niche requirements are met, understanding the life-history attributes of species identified as late-seral associates can inform the choice of appropriate mitigation or restoration actions. For most herbaceous species of the temperate rainforests of western North America, very little is known about their life histories. Further research into the habitat requirements and demography of these species is required. In addition, because dispersal ability as been shown to be a primary factor affecting how quickly late-seral associates recover following forest harvesting, we need to better understand how these vulnerable species disperse. This knowledge would allow us to assess the impact of different harvesting configurations on the re-colonisation of late-seral associates.

5 CONCLUSION

My study reveals some important conclusions about the understory communities of British Columbia's coastal western-hemlock forests, including:

- Some understory species show strong associations with late-seral forests, and may be threatened by logging.

- Understory dynamics follow successional trajectories of richness and composition similar to the better studied Douglas-fir forests to the south.

- The composition of old forest communities does not recover over the duration of a typical management rotation.

- Structural stage and site series have value as surrogates for understory composition, but refinement is required in how communities are divided.

I was able to extend understanding of how vegetation communities are influenced by time-since-disturbance, both in terms of richness and composition of species. Furthermore, I demonstrated the importance of considering individual species, by identifying species that are especially vulnerable to forest harvesting. However, my results also highlight how little is understood about the mechanisms that drive shifts in the frequency and abundance of species across a successional sequence. We have to start focussing biodiversity research on vulnerable species, in addition to broader diversity trends, if we want to continue logging while maintaining species across their original distribution in the landscape.

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7 APPENDIX – SPECIES LISTS

7.1 Species used in multivariate analyses

Acer glabrum
Achlys triphylla
Adenocaulon bicolor
Adiantum aleuticum
Agrostis sp.
Alnus viridis
Anaphalis margaritacea
Aquilegia formosa
Aruncus dioicus
Athyrium filix-femina
Blechnum spicant
Boschniakia hookeri
Boykinia occidentalis
Bromus sp.
Carex canescens
Carex deweyana
Carex echinata
Carex hendersonii
Carex laeviculmis
Carex mertensii
Carex obnupta
Carex sp.
Cinna latifolia
Cirsium sp.
Claytonia sibirica
Clintonia uniflora
Coptis aspleniifolia
Corallorhiza maculata
Cornus canadensis
Cornus stolonifera

Deschampsia cespitosa
Dicentra formosa
Drosera rotundifolia
Dryopteris expansa
Eleocharis sp.
Elymus glaucus
Empetrum nigrum
Epilobium angustifolium
Epilobium ciliatum
Epilobium glaberrimum
Equisetum sp.
Eriophorum sp.
Fauria crista-galli
Festuca rubra
Galium trifidum
Galium triflorum
Gaultheria shallon
Gentiana sceptrum
Goodyera oblongifolia
Gymnocarpium dryopteris
Heracleum maximum
Hypericum anagalloides
Hypochaeris radicata
Juncus effusus
Juncus ensifolius
Kalmia microphylla
Lactuca muralis
Ledum groenlandicum
Linnaea borealis
Listera sp.

Lonicera involucrata
Luzula sp.
Lycopodium annotinum
Lycopodium clavatum
Lysichiton americanus
Mahonia nervosa
Maianthemum dilatatum
Melica subulata
Menziesia ferruginea
Microseris borealis
Mitella sp.
Moneses uniflora
Myrica gale
Nuphar lutea
Oenanthe sarmentosa
Oplopanax horridus
Orthilia secunda
Oxycoccus oxycoccos
Petasites frigidus
Physocarpus capitatus
Platanthera dilatata
Platanthera huronensis
Platanthera stricta
Poaceae
Polypodium glycyrrhiza
Polystichum munitum
Prosartes hookeri
Pteridium aquilinum
Ranunculus sp.
Rhamnus purshiana
Rhynchospora alba
Ribes sp.
Rosa gymnocarpa
Rosa nutkana
Rubus idaeus
Rubus leucodermis
Rubus parviflorus
Rubus pedatus
Rubus spectabilis
Rubus ursinus

Salix sp.
Sambucus racemosa
Sanguisorba officinalis
Scirpus sp.
Spiraea douglasii
Stachys chamissonis
Stellaria sp.
Streptopus amplexifolius
Streptopus lanceolatus
Tellima grandiflora
Thalictrum occidentale
Tiarella trifoliata
Tolmiea menziesii
Torreyochloa pauciflora
Trautvetteria caroliniensis
Triantha glutinosa
Trientalis borealis
Trientalis europaea
Trillium ovatum
Trisetum canescens
Vaccinium alaskaense
Vaccinium ovalifolium
Vaccinium ovatum
Vaccinium parvifolium
Veratrum viride
Viola sp.

7.2 Rare species (single occurrence, not used in multivariate analyses)

Achillea millefolium
Actaea rubra
Allium cernuum
Angelica arguta
Angelica genuflexa
Angelica lucida
Anthoxanthum odoratum
Arctostaphylos uva-ursi
Artemisia sp.
Asarum caudatum
Asplenium trichomanes
Aster sp.
Botrychium multifidum
Carex anthoxanthea
Carex aquatilis
Carex lyngbyei
Carex macrocephala
Carex pauciflora
Carex sitchensis
Cerastium sp.
Chimaphila umbellata
Comarum palustre
Corallorhiza striata
Corydalis scouleri
Deschampsia elongata
Digitalis purpurea
Dulichium arundinaceum
Epilobium sp.
Fragaria chiloensis
Fritillaria camschatcensis
Galium sp.
Glyceria elata
Gnaphalium sp.
Hemitomes congestum

Hieracium albiflorum
Hordeum brachyantherum
Juncus mertensianus
Lathyrus nevadensis
Menyanthes trifoliata
Montia parvifolia
Oxalis oregana
Parnassia fimbriata
Pedicularis bracteosa
Penstemon davidsonii
Phegopteris connectilis
Phyllodoce empetriformis
Pinguicula vulgaris
Plantago lanceolata
Platanthera sp.
Potentilla anserina
Potentilla villosa
Prenanthes alata
Rubus arcticus
Rubus chamaemorus
Scutellaria galericulata
Senecio vulgaris
Sisyrinchium idahoense
Sorbus scopulina
Stenanthium occidentale
Streptopus streptopoides
Taraxacum officinale
Trichophorum cespitosum
Trisetum spicatum
Trollius albiflorus
Urtica dioica
Vaccinium uliginosum
Veronica anagallis-aquatica
Veronica beccabunga

Veronica scutellata
Vicia americana
Asplenium viride
Calamagrostis canadensis
Caltha leptosepala
Carex brunnescens
Carex lenticularis
Carex utriculata
Circaea alpina
Dactylis glomerata
Danthonia intermedia
Dodecatheon jeffreyi
Dodecatheon pulchellum
Elymus hirsutus
Erigeron peregrinus
Erythronium oregonum
Festuca subulata
Galium aparine
Gentiana douglasiana
Heuchera sp.
Holcus lanatus
Holodiscus discolor
Maianthemum stellatum
Monotropa hypopithys
Monotropa uniflora
Osmorhiza berteroi
Plantago macrocarpa
Prunella vulgaris
Saxifraga sp.
Selaginella wallacei
Senecio triangularis
Sorbus sitchensis
Symphoricarpos albus
Trifolium sp.
Typha latifolia
Vaccinium vitis-idae

8 TABLES AND FIGURES

Table 1: Description of stand structural stages. Time-since-disturbance is for a typical stand and can vary depending on ecological conditions. Based on description in B.C. Ministry of Forests and B.C. Ministry of Environment Lands and Parks (1998).

Structural Stage	# of Plots	Description	Time-Since-Disturbance	Key Features
2	20	Herb	< 20 years	primarily herbs, few invading shrubs or trees
3	147	Shrub/Herb	<20 – 40 years	shrubs, seedlings, advance regeneration
4	88	Pole/Sapling	<40 years	trees > 10 m, densely stocked
5	124	Young Forest	40 – 80 years	self-thinning stage, differentiation in canopy layer
6	72	Mature Forest	80 – 250 years	understory re-established, canopy opens, sub-canopy of shade-tolerant species
7	130	Old Forest	> 250 years	structurally complex, vertical and horizontal diversity in canopy

Table 2:   Species considered and species selected as old-growth associates. "FEMAT" refers to species specified as old-growth associates in FEMAT (1993). "> Occurrence in Old Forest" refers to species who have a higher frequency of occurrence in old forest than other structural stages. A "late-seral associate" meets the criteria specified in this publication.

Species	FEMAT	> Occurrence in Old Forest	Late-Seral Associate
Achlys triphylla	X	X	
Adiantum aleuticum	X		
Bromus sp.		X	
Cinna latifolia		X	
Clintonia uniflora	X	X	X
Coptis asplenifolia	X	X	X
Corallorhiza maculata	X	X	
Cornus canadensis		X	
Dicentra formosa		X	
Disporum hookeri	X	X	
Dryopteris expansa	X		
Empetrum nigrum		X	
Goodyera oblongifolia	X	X	X
Gymnocarpium dryopteris	X		X
Linnea borealis		X	
Listera sp.	X	X	X
Lysichiton americanum	X		
Mahonia nervosa		X	
Malus fusca		X	
Melica subulata	X		

Table 2:   continued

Species	FEMAT	> Occurrence in Old Forest	Late-Seral Associate
Menziesia ferruginea	X	X	
Mitella brewerii	X		
Moneses uniflora	X	X	X
Oplopanax horridum		X	X
Orthelia secunda	X	X	X
Rubus pedatus	X	X	X
Streptopus amplexifolius	X	X	
Streptopus roseus	X	X	X
Taxus brevifolia	X		
Tiarella trifoliata	X	X	
Trautvetteria caroliniensis		X	
Trillium ovatum	X		
Vaccinium alaskaense	X	X	X
Vaccinium ovalifolium	X	X	X
Vaccinium parvifolium	X	X	
Viola glabella	X		

Table 3: Spearman correlation co-efficient between plot characteristics and axes from NMS ordination on plots from all structural stages.

Variable	NMS 1	NMS 2	NMS 3
Soil Moisture Regime	0.39*	-0.26*	-0.26*
Soil Nutrient Regime	0.08	0.02	-0.60*
Species Richness	0.49*	-0.52*	-0.51*
Late-seral Species Richness	0.68*	-0.05	0.01
Canopy Cover	-0.19*	0.57*	0.04

*indicates $P < 0.001$

Table 4:   Spearman correlation co-efficient between plot characteristics and axes from NMS ordination on plots from old forest.

Variable	NMS 1	NMS 2	NMS 3
Soil Moisture Regime	0.40*	-0.02	-0.45*
Soil Nutrient Regime	0.27	0.61*	-0.39*
Species Richness	0.54*	0.12	-0.69*
Late-Seral Species Richness	0.80*	0.01	-0.02
Canopy Cover	-0.04	0.16	0.12

*indicates $P < 0.001$

Table 5:   MRPP comparison of structural stage 7 (old forest) with other structural stages. The A-statistic indicates the degree to which plots within a group are more similar than plots between groups. See methods for details on MRPP and structural stages.

Structural Stage	Chance Corrected Within-Group Agreement (A)	P
2 vs. 7	0.05	$\ll 0.001$
3 vs. 7	0.10	$\ll 0.001$
4 vs. 7	0.07	$\ll 0.001$
5 vs. 7	0.08	$\ll 0.001$
6 vs. 7	0.04	$\ll 0.001$

Table 6: MRPP comparison of temporally adjacent structural stages. The A-statistic indicates the degree to which plots within a group are more similar than plots between groups. See methods for details on MRPP and structural stages.

Structural Stage	Chance Corrected Within-Group Agreement (A)	P
2 vs. 3	< 0.01	0.32
3 vs. 4	0.07	≪ 0.001
4 vs. 5	0.01	0.003
5 vs. 6	< 0.01	0.06
6 vs. 7	0.04	≪ 0.001
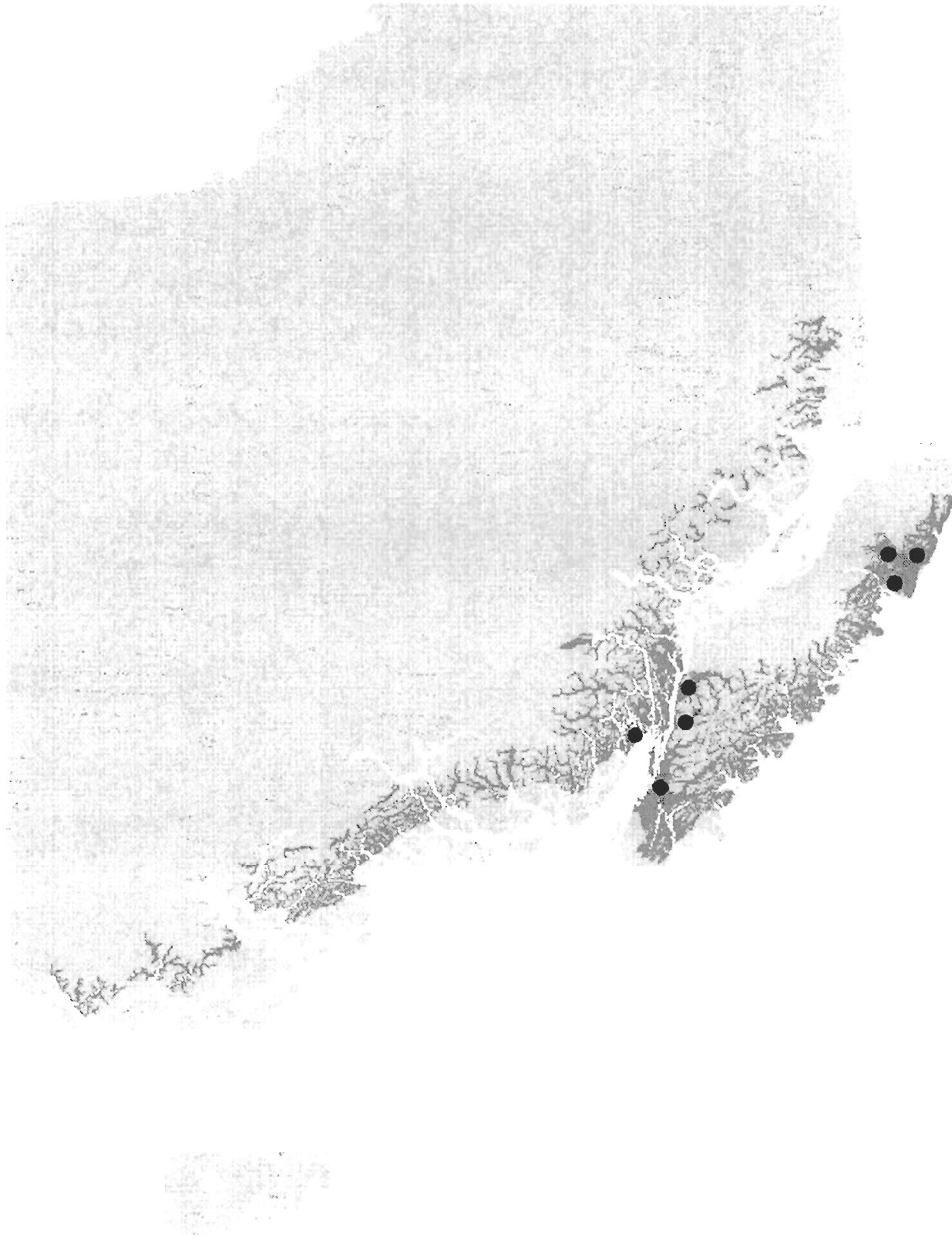
Figure 1: Map of southern British Columbia, Canada. Dark grey area indicates extent of the CWHvm1 BEC variant. Black dots indicate the centre of the distribution of vegetation plots for each of the seven study areas. Map source: http://www.for.gov.bc.ca/hre/becweb/subsite-map/provdigital-01.htm, by permission.
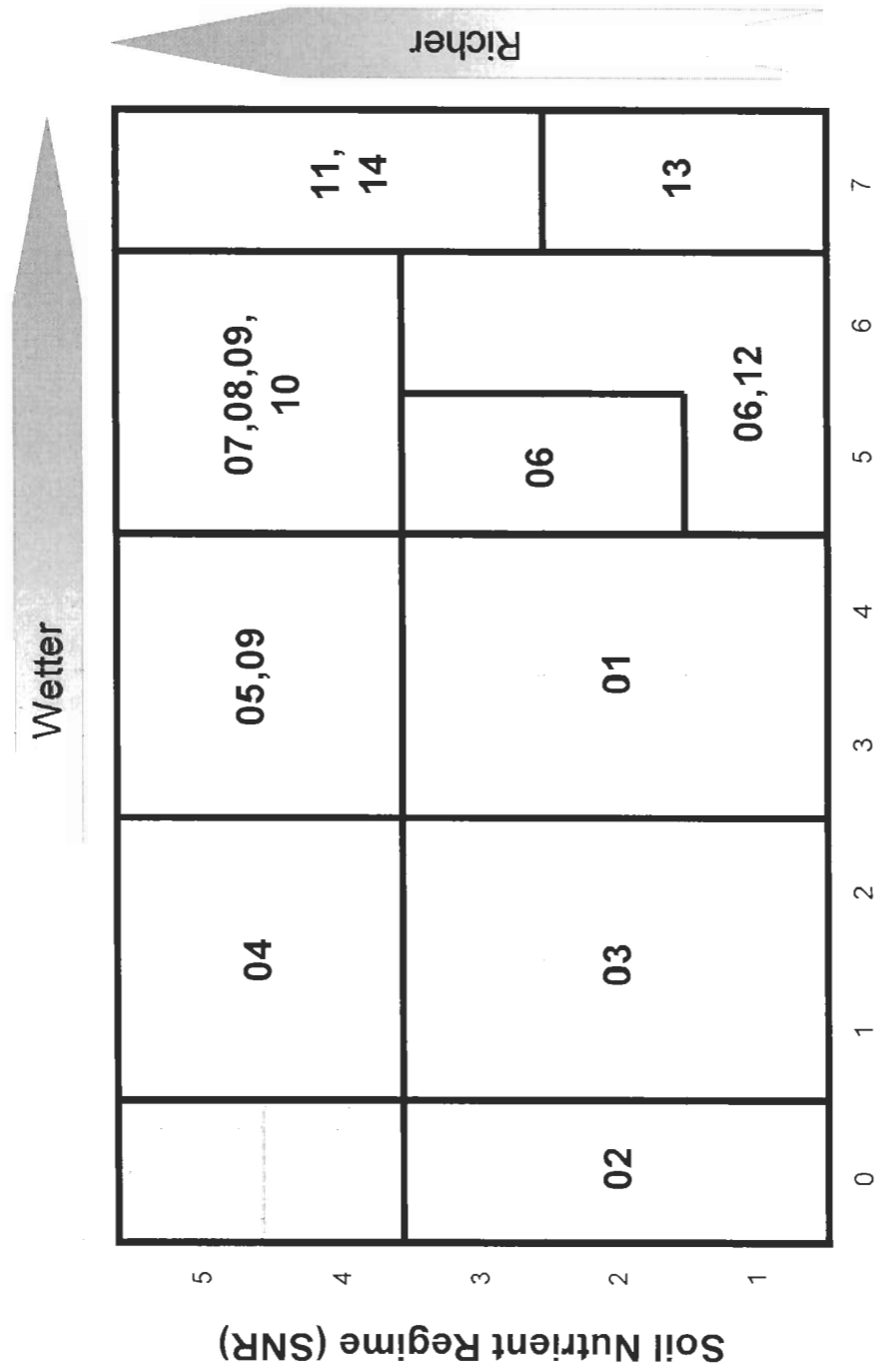
Figure 2: Edatopic grid describing the soil moisture and nutrient regimes of different site series. Site series are defined by soil conditions, slope position, and climax vegetation community. Site series 01 indicates mesic, mid-slope sites, where the vegetation composition reflects the broader, regional climate. Site series 09, 10, and 11 are floodplain sites from high to low fluvial bench respectively. (Modified from Banner et al. 1993, Green and Klinka 1994, by permission).
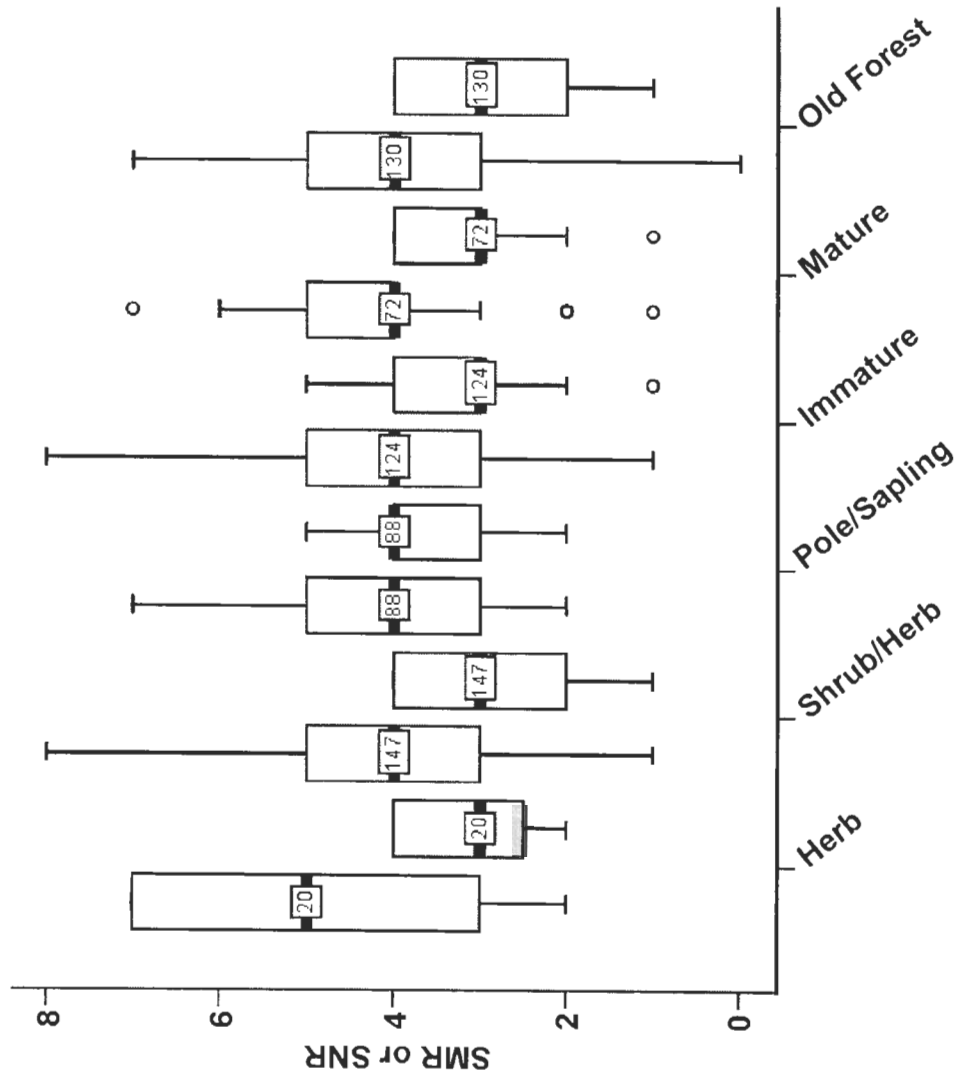
Figure 3: Range of soil moisture regime (SMR; white bars) and soil nutrient regime (SNR; grey bars) for plots in each structural stage. Larger values indicate wetter/more nutrient rich plots. The number of plots sampled is indicated in the box overlaying the median bar. Note that each outlier marker may indicate multiple outliers due to overlap.
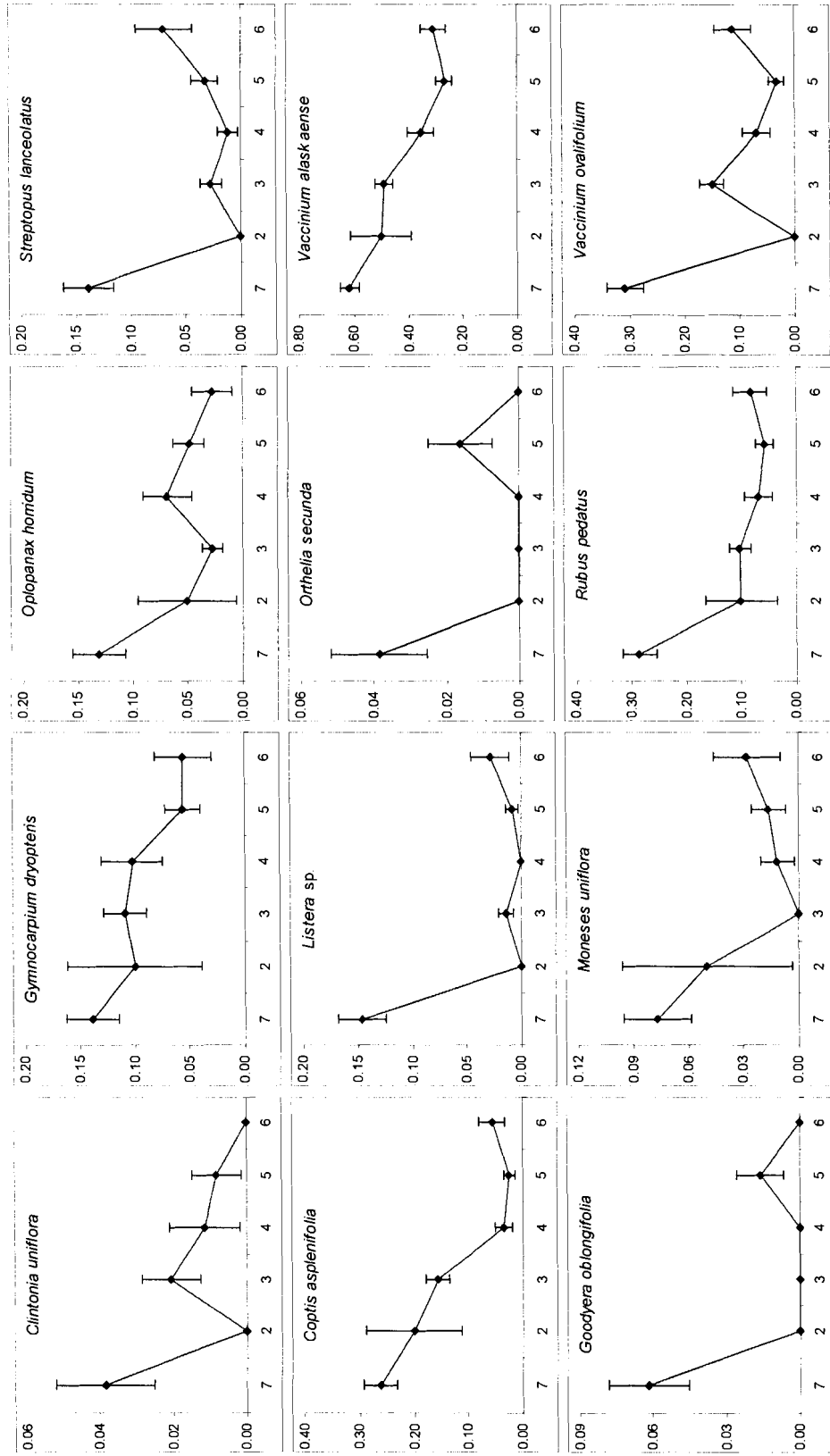
Figure 4: Frequency of occurrence for old-growth associates, in each structural stage. Structural stage 7 = Old Forest, 2 = Herb, 3 = Shrub/Herb, 4 = Pole/Sapling, 5 = Young Forest, 6 = Mature Forest. The x-axis is arranged along a typical successional sequence starting in old forest through harvest and re-growth. Errors bars are ±1 SE based on a bootstrap estimate.

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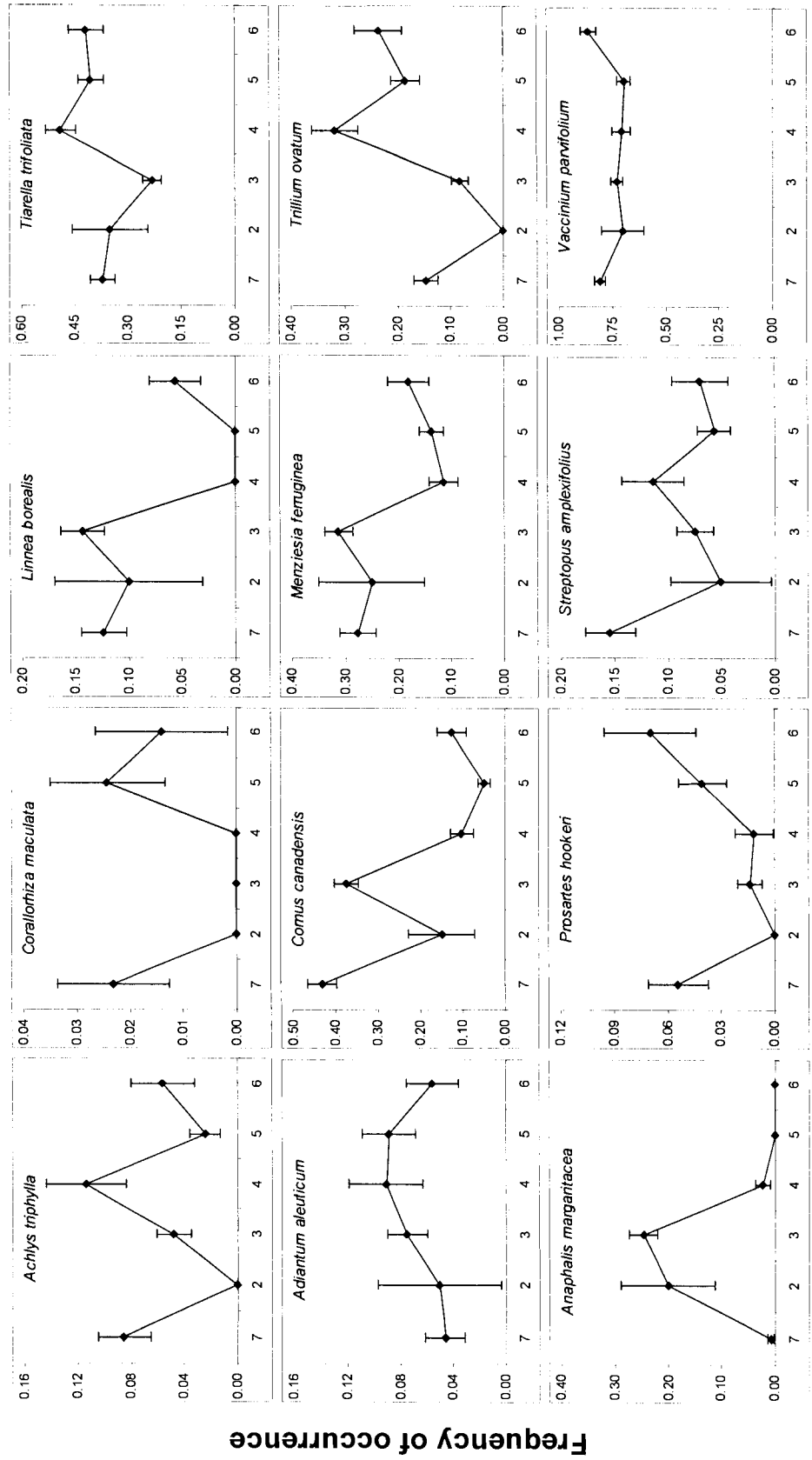
Figure 5: Frequency of occurrence for selected species that are not old-growth associates, in each structural stage. Structural stage 7 = Old Forest, 2 = Herb, 3 = Shrub/Herb, 4 = Pole/Herb, 5 = Young Forest, 6 = Mature Forest. The x-axis is arranged along a typical successional sequence starting in old forest through harvest and re-growth.
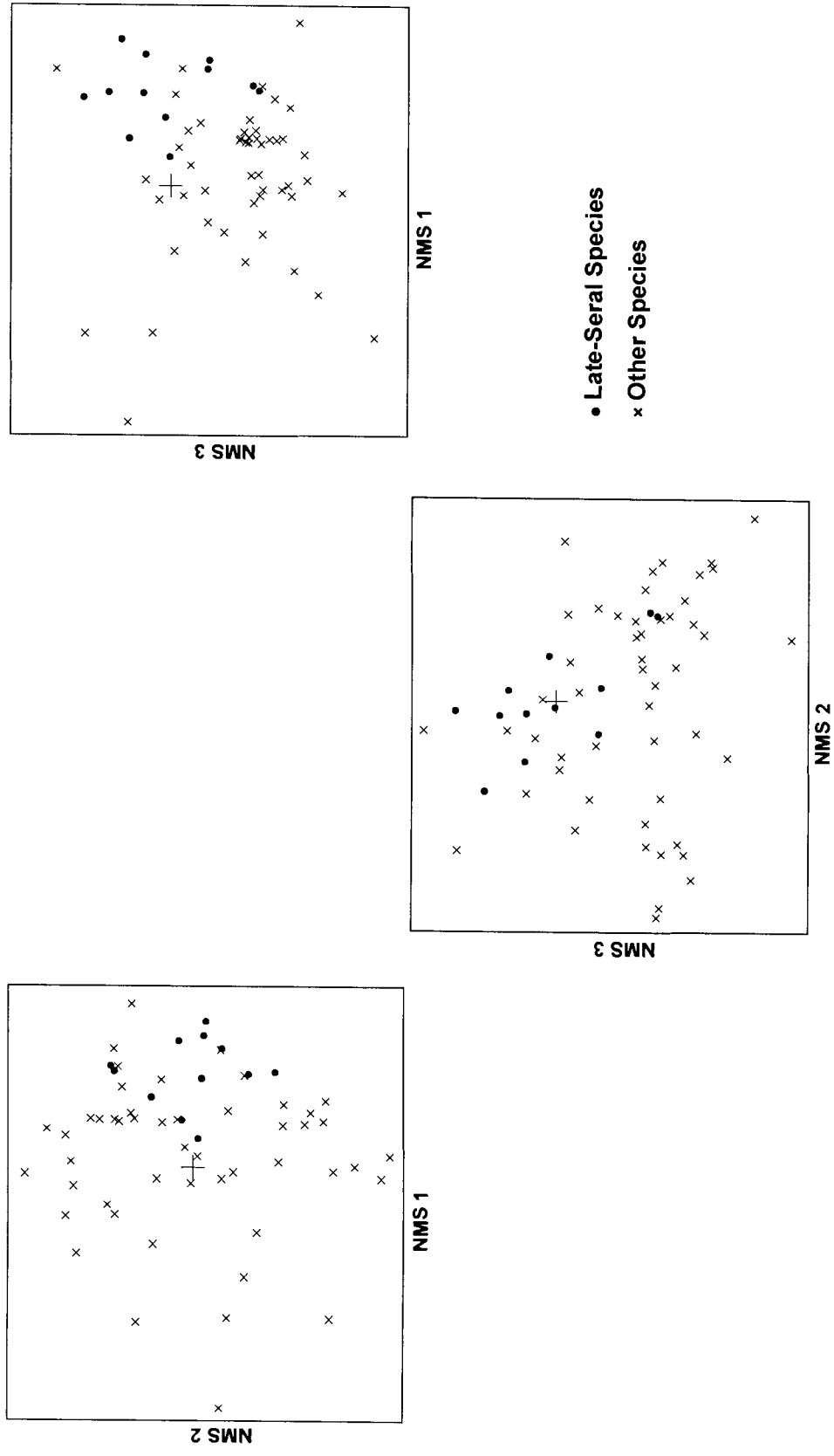
70
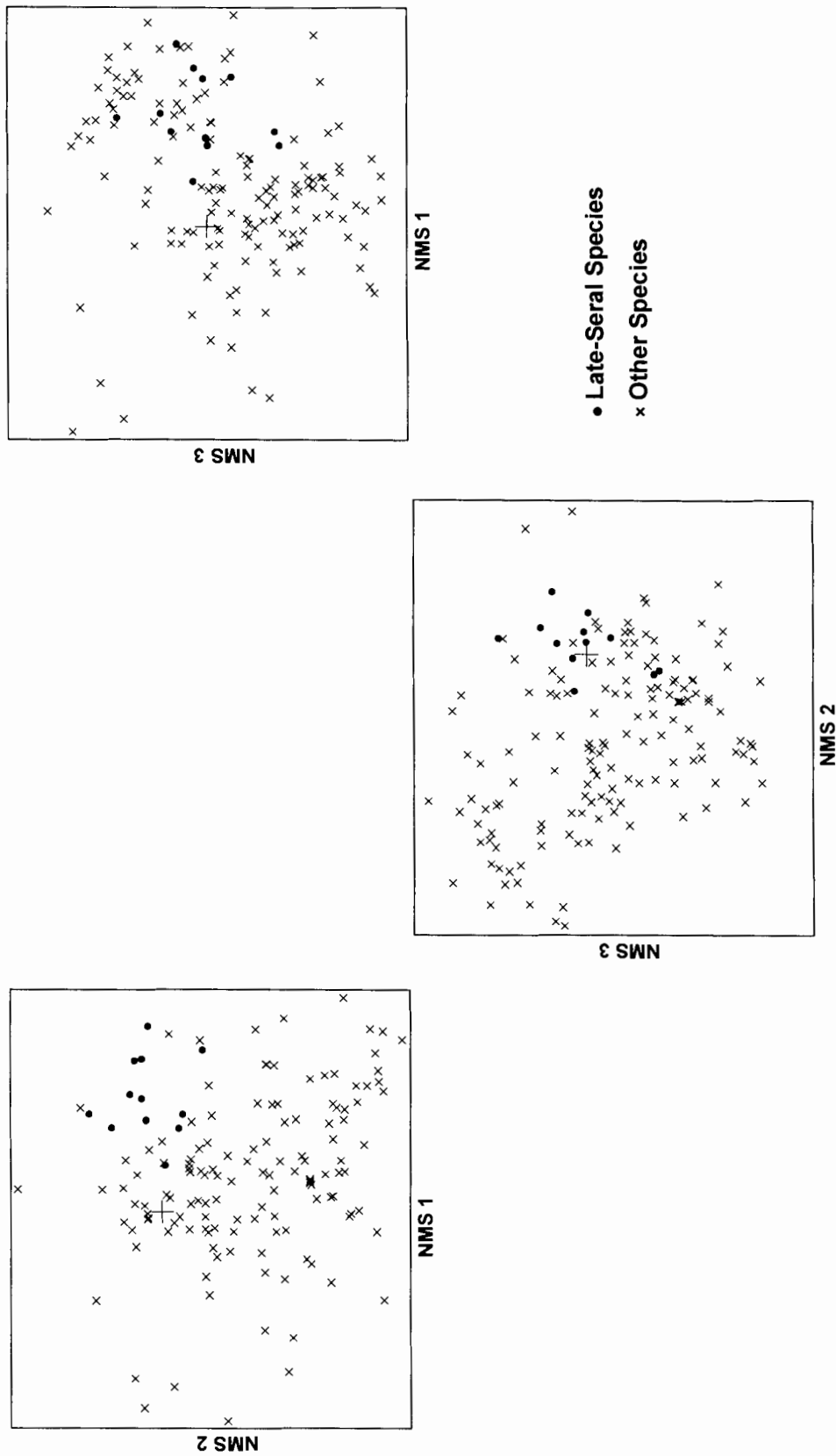
Figure 6: Position in non-metric multidimensional scaling (NMS) reduced species space of a "typical" plot containing each species, for plots from all structural stages. The position of each point is calculated by taking the average position on each axis of all the plots in which the species is found. Each point in the plot represents an individual species. Points are differentiated according to whether the species was identified as a late-seral associate.

Figure 7: Position in non-metric multidimensional scaling (NMS) reduced species space of a "typical" plot containing each species, for plots from structural stage 7. The position of each point is calculated by taking the average position on each axis of all the plots in which the species is found. Each point in the plot represents an individual species. Points are differentiated according to whether the species was identified as a late-seral associate.

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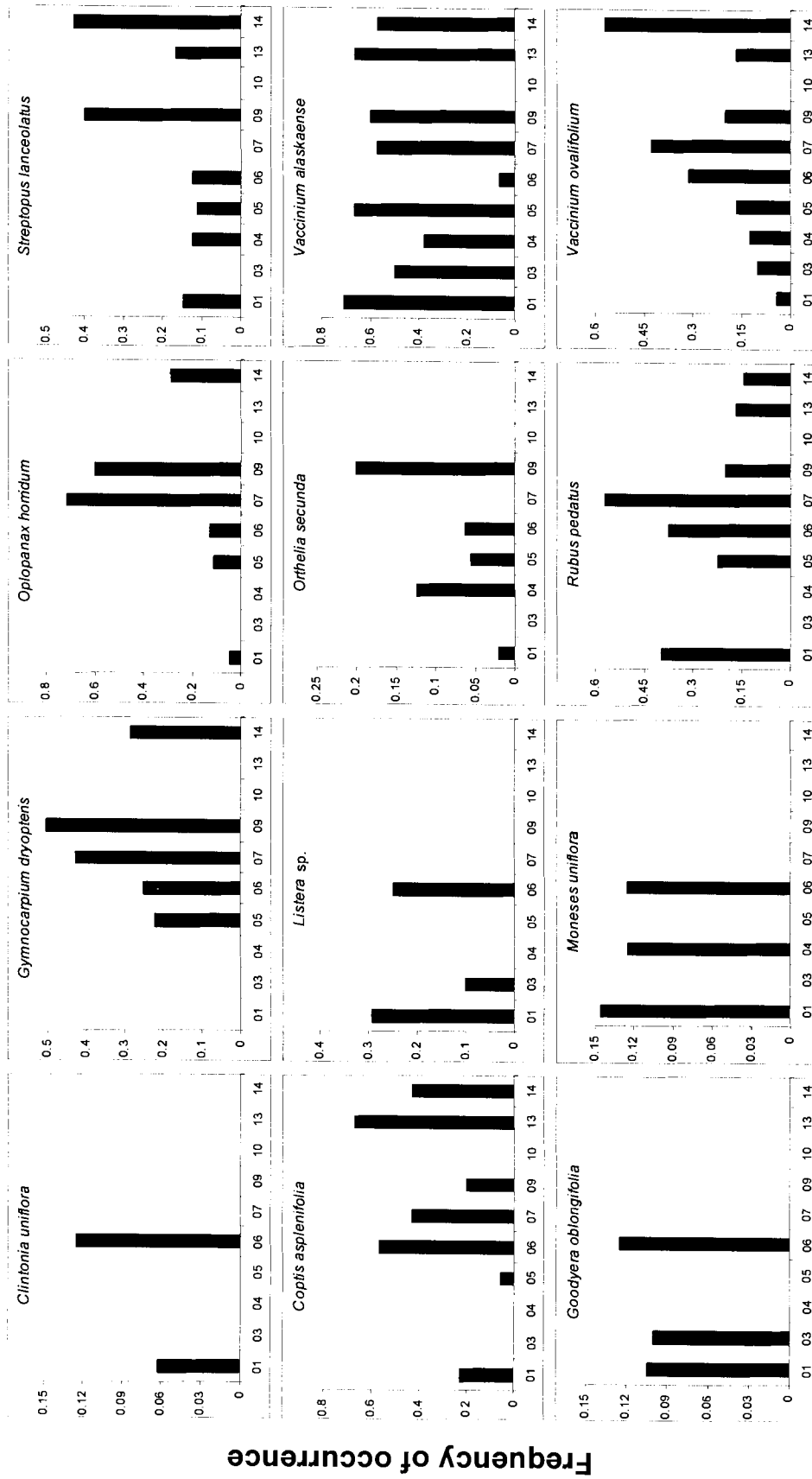
Figure 8: Frequency of occurrence in old forest plots, by site series, for late-seral associates. This figure indicates the range of site conditions in which a species can be found.
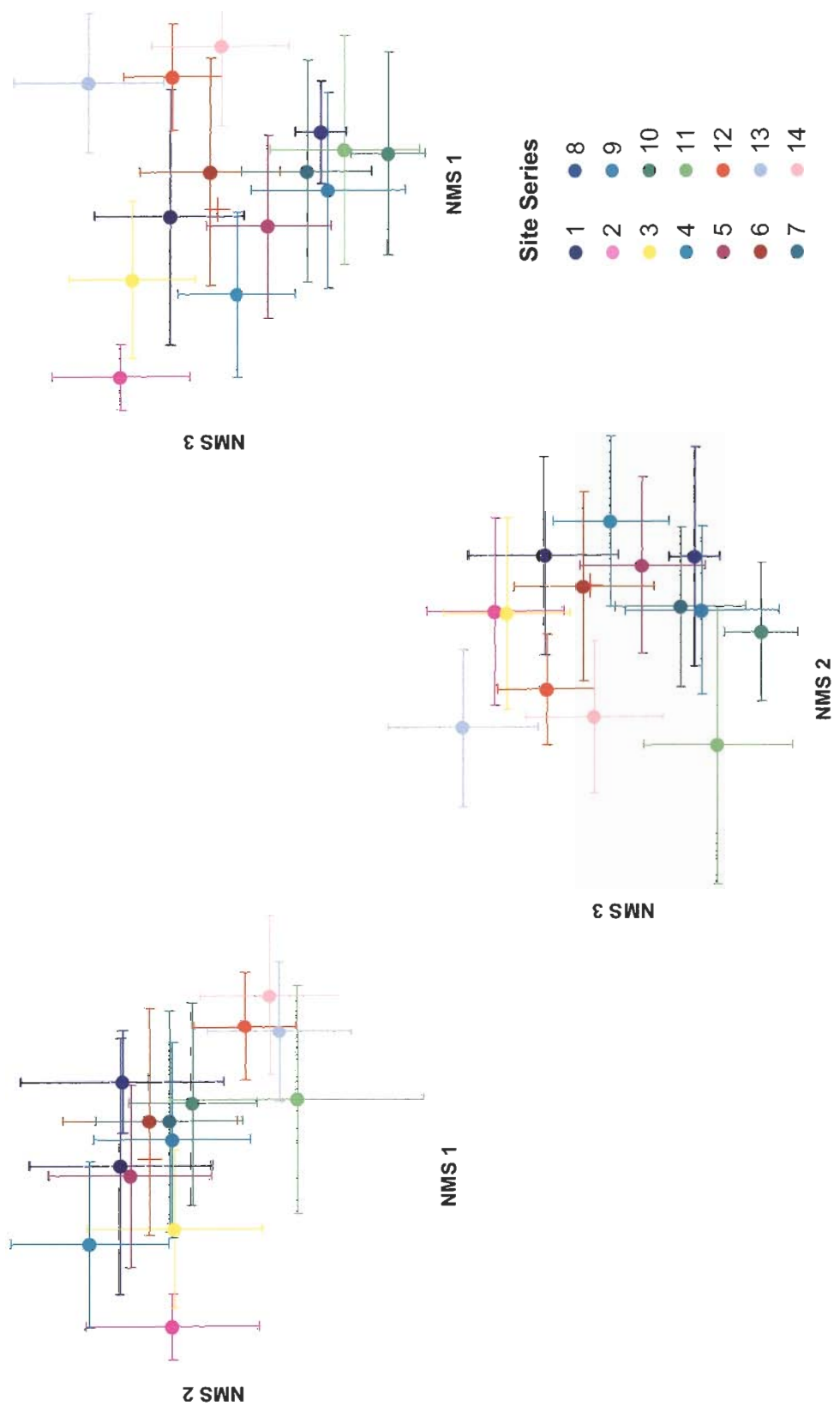
73
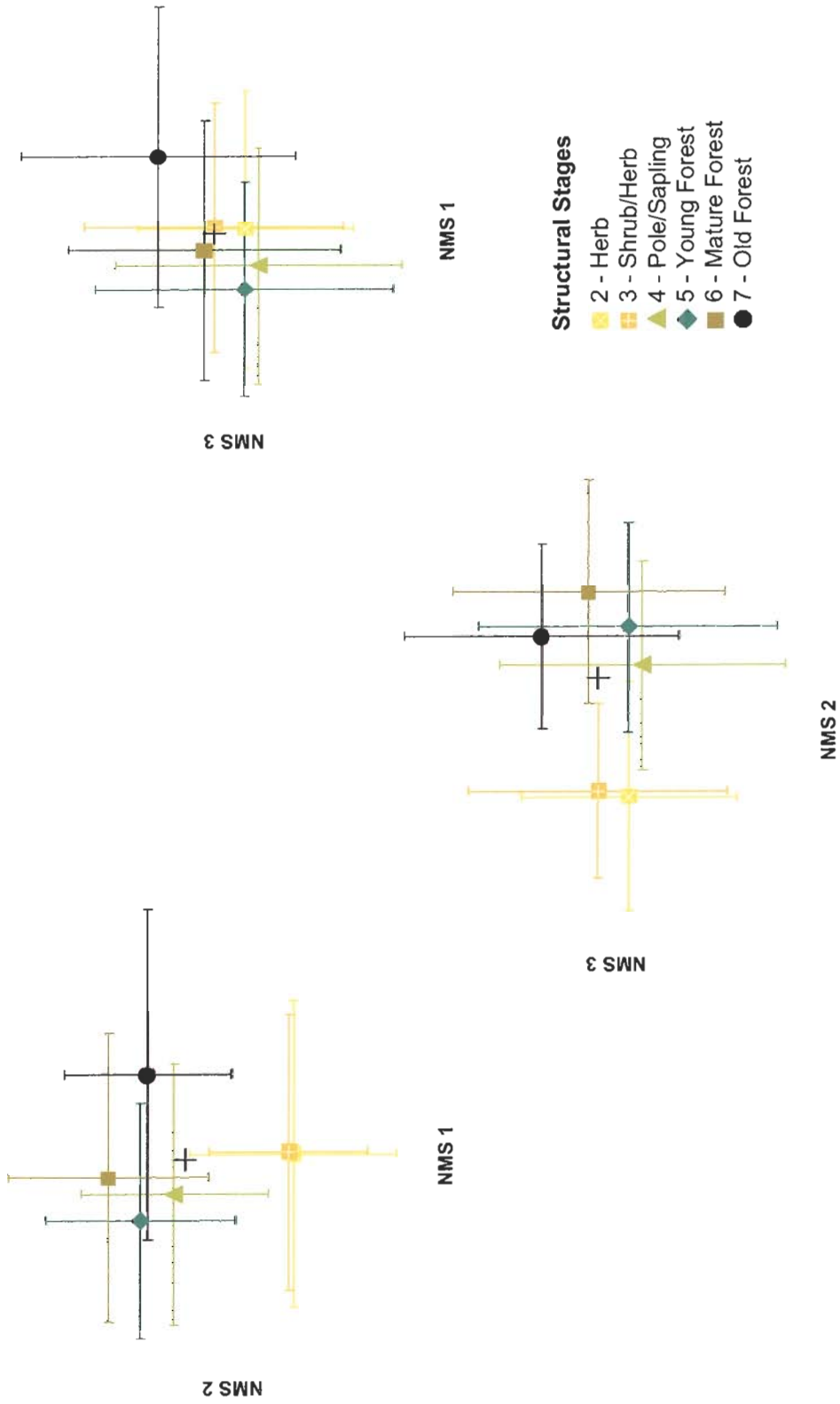
Figure 9: Summary of non-metric multidimensional scaling (NMS) ordination scores in species space, for all plots. Dots indicate the centroid of the plot cluster for each structural stage. Bars indicate the amount of spread in the plot cluster, calculated as ±1 SD from the centroid. Greater overlap between plot clusters in 3-D ordination space indicates higher similarity in species composition of the structural stages represented by the point clusters.

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Figure 10: Summary of non-metric multidimensional scaling (NMS) ordination scores in species space, for all plots. Dots indicate the centroid of the plot cluster for each site series. Bars indicate the amount of spread in the plot cluster, calculated as ±1 SD from the centroid. Greater overlap between plot clusters in 3-D ordination space indicates higher similarity in species composition of the site series represented by the point clusters.
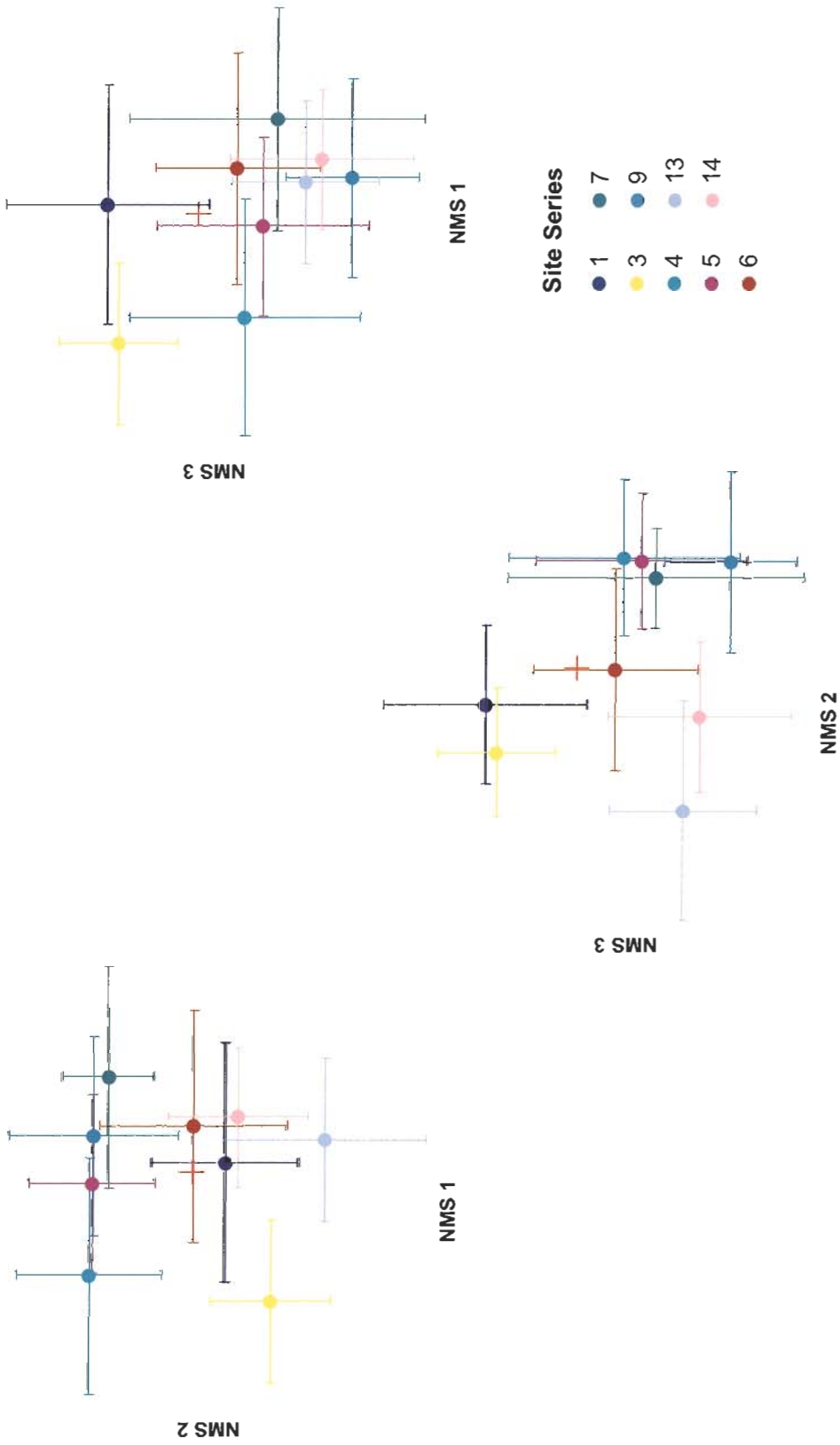
Figure 11: Summary of non-metric multidimensional scaling (NMS) ordination scores in species space, for old plots only. Dots indicate the centroid of the plot cluster for each structural stage. Bars indicate the amount of spread in the plot cluster, calculated as ±1 SD from the centroid. Greater overlap between plot clusters in 3-D ordination space indicates higher similarity in species composition of the site series represented by the point clusters.
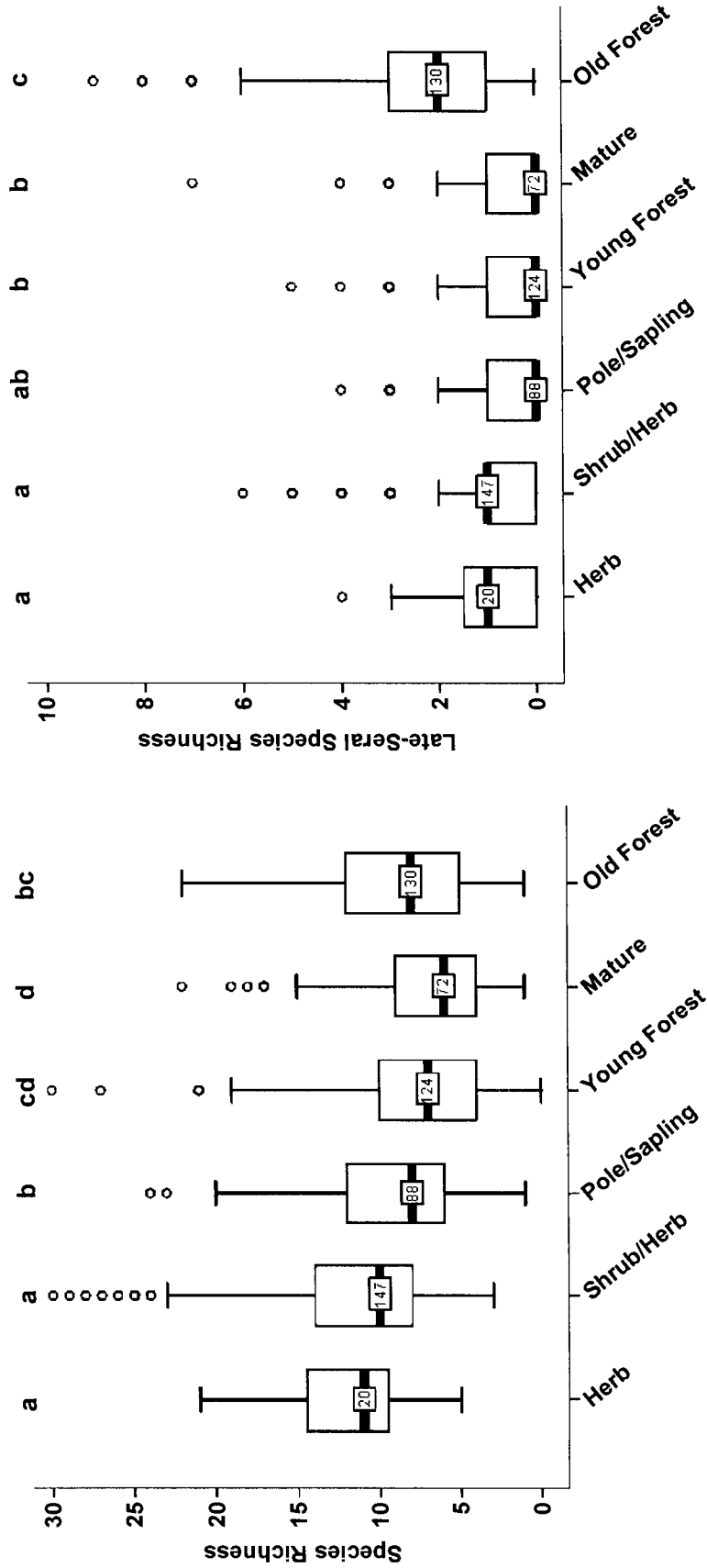
Figure 12: Range of species richness in plots by structural stage, for all understory species and late-seral species. Both figures indicate a U-shaped response along the successional sequence, although scaling of the y-axis to incorporate outliers obscures this pattern. Numbers on the median line indicate the sample size for each group. Different lower case letters indicate structural stages with significantly different species richness ($P <$ 0.05). Note that each outlier marker may indicate multiple outliers due to overlap, and that figures have different scales on the y-axis.
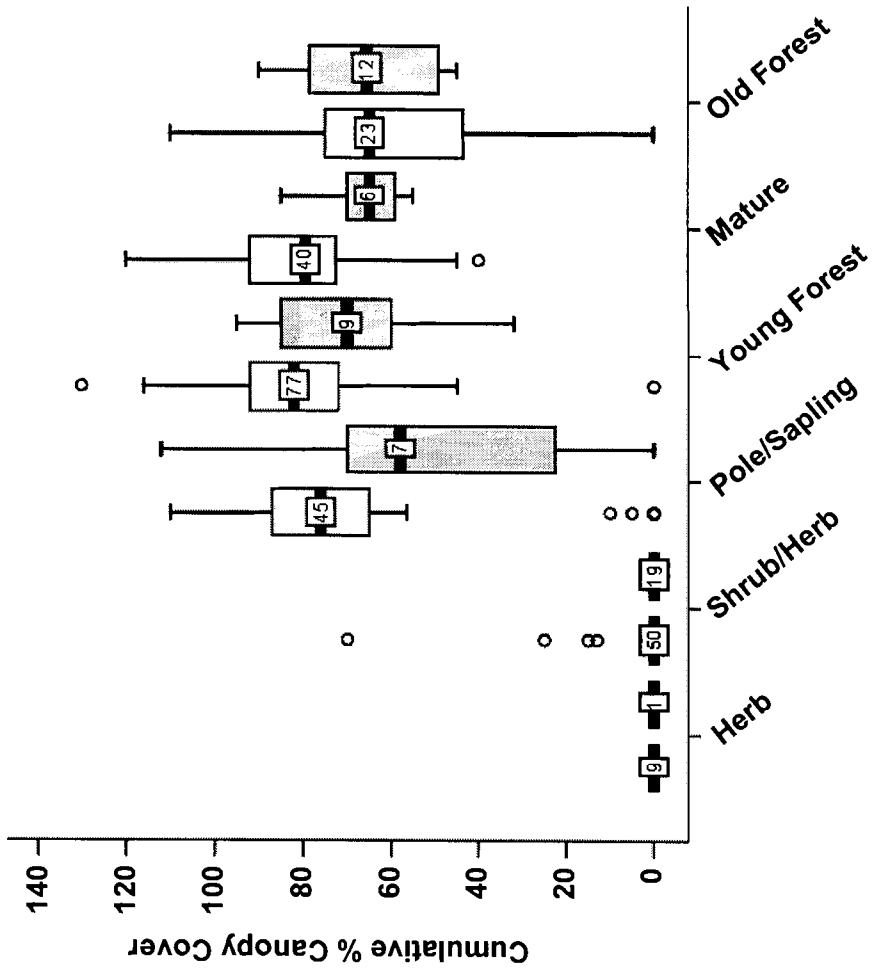
Figure 13: Range of canopy cover for plots with no late-seral species (white bars) and plots with high richness of late-seral species (grey bars), across structural stages. High late-seral richness is defined as plots with late-seral richness greater than 1.5x the inter-quartile range above the upper quartile (i.e., outliers from Figure 3). Numbers on the median line indicate the sample size for each group. Note that each outlier marker may indicate multiple outliers due to overlap.
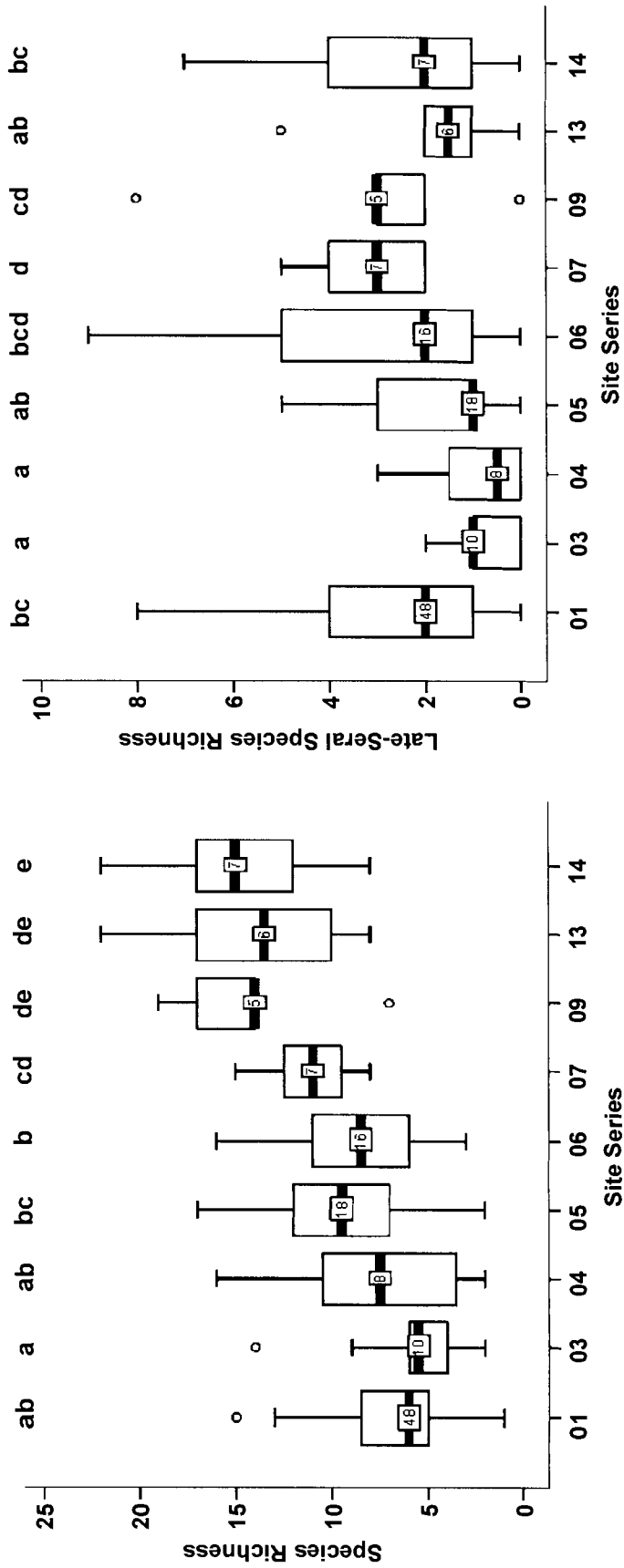
Figure 14: Range of species richness for all species and late-seral species in old forest, by site series. Numbers on the median line indicate the sample size for each group. Different lower case letters indicate site series with significantly different species richness ($P < 0.05$). Note that each outlier marker may indicate multiple outliers due to overlap, and that figures have different scales on the y-axis.
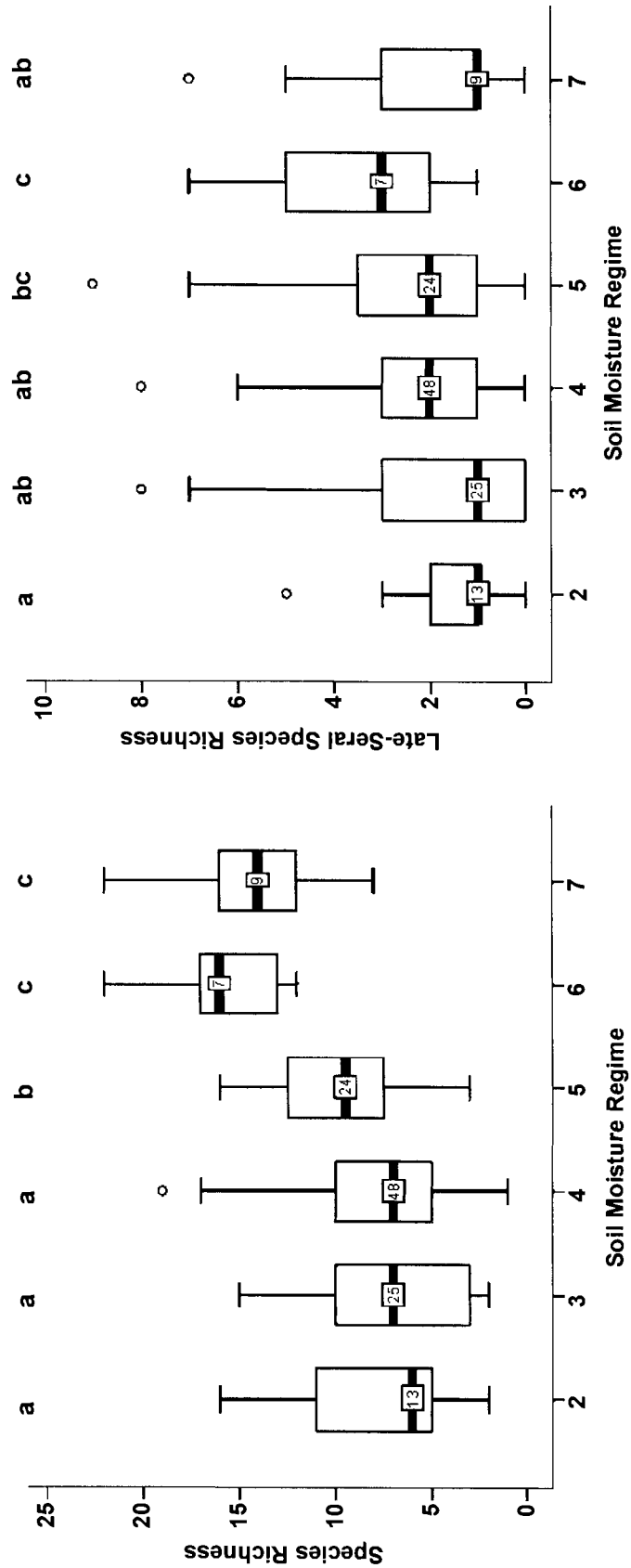
Figure 15: Range of species richness for all species and late-seral species in old forest, by soil moisture regime (SMR). Numbers on the median line indicate the sample size for each group. Different lower case letters indicate moisture levels with significantly different species richness ($P <$ 0.05). Note that each outlier marker may indicate multiple outliers due to overlap, and that figures have different scales on the y-axis.
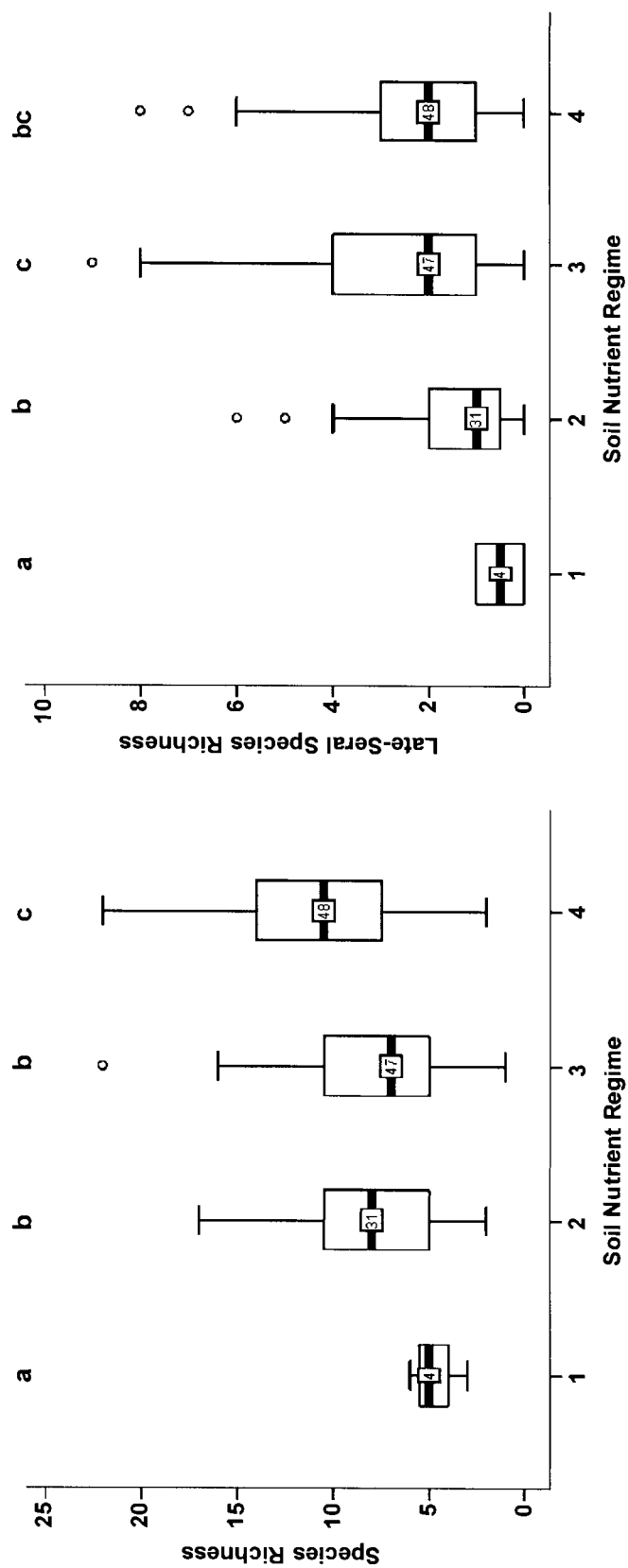
Figure 16: Range of species richness for all species and late-seral species in old forest, by soil nutrient regime (SNR). Numbers on the median line indicate the sample size for each group. Different lower case letters indicate nutrient levels with significantly different species richness ($P < 0.05$). Note that each outlier marker may indicate multiple outliers due to overlap, and that figures have different scales on the y-axis.