AN ABSTRACT OF THE THESIS OF

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Abstract approved:

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Canopy gap formation is a major factor contributing to maintenance of overstory species diversity and stand structure in forests and may be integral to development of understory shrub and herb layers as well. Acknowledgement of gap formation as a fundamental feature of natural forests has led to consideration of gaps as an option in forest management regimes. This study examined understory vegetation communities across canopy gaps created as a part of the Density Management Study (DMS), which investigates the effectiveness of a thinning regime in promoting late-successional habitat development in young Douglas-fir forests of western Oregon. Patterns in understory vegetation community composition in and around 0.1 and 0.4ha gaps created as a part of the DMS treatment were investigated. The primary goal of this research was to investigate the potential role of canopy gap creation in fostering heterogeneity in understory vegetation communities, and to examine the extent of gap influence on the surrounding thinned forest matrix.

Tree species distributions have been shown to partition across gaps in tropical forest systems through differential responses of species to gradients in resource availability, a pattern known as gap partitioning. In temperate forests, understory vegetation communities are much more diverse than the overstories, and display a greater array of habitat requirements. Therefore, understory communities may be more likely than overstories to exhibit gap partitioning in these forests. Patterns in understory community composition across gaps suggest that gap partitioning has occurred. The strength of this partitioning effect appears to differ between gap sizes,

as smaller gaps showed a less powerful effect. Abundance of ruderal species was strongly related to gap partitioning in larger gaps, while smaller gaps were dominated by competitor species. Partitioning may be related to an interactive relationship between harvest-related ground disturbance and resource gradients. Therefore, considerations of gap partitioning processes should take into account intensity and spatial distribution of ground disturbance in relation to resource gradients. In addition, conditions necessary for the expression of gap partitioning in understory vegetation communities may be rare in natural gaps in this region.

The influence of gaps on understory vegetation communities in the surrounding forest appears to be relatively small. This small influence extent may help explain the lack of a stand level response to gap formation in these stands. Larger gaps exhibit a slight influence on the understory plant community in the surrounding forest to the north of the gap. In small gaps, there seemed to be an influence of the surrounding forest on gap interiors, resulting in an area of influence smaller than the physical gap area. This relationship may indicate that the area of gap influence on understory vegetation may not scale linearly with physical gap size.

Species diversity was higher in gap interiors than in surrounding thinned forests. However this effect was partially due to the presence of exotic species, which showed an affinity for gap interiors. Late successional associated species were negatively related to gap interiors, but only in the larger gap size. Gap creation appears to be promoting small scale species diversity in these stands, but creation of large gaps may also promote the establishment of exotic species and may have a negative effect on late successional associated species.

However, any and all of these effects may be transient, as understory communities will be strongly affected by overstory re-establishment, and related changes in resource availability. In general, gap formation may influence small-scale stand heterogeneity as evidenced by understory plant communities, but this effect may rely strongly on the nature of gap formation and intensity of disturbance related to this formation.

Patterns in Understory Vegetation Communities Across Canopy Gaps in Young, Douglas-fir Forests of Western Oregon.

by
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Patterns in Understory Vegetation Communities Across Canopy Gaps in Young, Douglas-fir Forests of Western Oregon.

CHAPTER 1: INTRODUCTION TO THE STUDY

Disturbance is an integral process in the development and maintenance of forest ecosystems (Oliver and Larson 1996). Small scale disturbances dominate the disturbance regime in many forest ecosystems and are important even in regions characterized by large scale disturbances, especially where return intervals between stand replacement events are long (Spies et al. 1990). Canopy gap formation is a common result of small scale disturbance in forests and can be initiated by a number of processes including: wind, disease, ice, senescence of canopy trees, and patchy fire (Watt 1947, Spies and Franklin 1989, Oliver and Larson 1996). Much research has focused on gap formation and vegetation response to gap formation in a variety of forest types (Runkle 1981, Hibbs 1982, Brokaw 1985, Spies et al. 1990).

Some research has focused on the stand and landscape (or patch mosaic) level of gap dynamics (Spies et al. 1990) and has produced a great deal of insight into the function and overall importance of gap formation at these large scales. Gap-phase dynamics are an essential element in understanding forest community change over time (Watt 1947) and can be a vital component in successional development of many forest ecosystems (Oliver and Larson 1996). Gaps are also an integral factor in maintenance of species diversity at multiple scales through creation of a variety of local niches within a landscape (Denslow 1980, Brokaw and Busing 2000). Gaps can also be foci of exotic species establishment within landscapes through creation of invasible niches (Goldblum and Beatty 1999).

Research at large scales has been supplemented by a great deal of study on the effects of gap formation at the patch scale. At smaller scales, gaps can drive resource availability (Canham and Marks 1985, Canham et al. 1990) and species distributions (Runkle 1981, Brokaw 1985, Brokaw 1987, Spies et al. 1990, Gray and Spies 1996, 1997). A number of studies have also focused on the small scale response of growth, flowering, cover, and composition of understory vegetation communities to gap formation (Anderson et al. 1969, Moore and Vankat 1986, Collins and Pickett 1988a, Collins and Pickett 1988b, London 1999, St. Pierre 2000).

The acknowledgement of gap formation as a fundamental feature of natural forest systems has led to consideration of gap creation as an option in forest management regimes. Researchers and forest managers have begun to see the utility of emulating natural disturbance regimes in management (Franklin et al. 2002, Mitchell et al. 2002, Muir et al. 2002), and have thus become interested in mimicking natural gap formation. Gap creation is now a commonly considered option in management treatments in the Pacific Northwest, especially those designed with ecosystem function and development of habitat in mind (Hunter 1993, Cissel 2006, Beggs and Puettmann in review). Effects of gap creation have been studied in a number of silvicultural and experimental settings (Collins and Pickett 1988a, Collins and Pickett 1988b, Gray and Spies 1996, Coates and Burton 1997, Gray and Spies 1997, Coates 2000, St. Pierre 2000, Beggs and Puettmann in review). However, response of forest ecosystems to created gaps has received far less study than have effects of natural gap formation. Studies investigating the consequences of gap creation (vs. natural formation) for understory vegetation communities are few, and most focus on experimental gaps, or on stand scale processes (Collins and Pickett 1988a, Collins and Pickett 1988b, London 1999, St. Pierre 2000, Lindh et al. 2003). Beggs and Puettmann (in review) related that creation of gaps as a component of a thinning regime in western Oregon resulted in high small-scale variability in understory vegetation structure and composition in treatments containing gaps.

Small scale variation in vegetation communities in response to canopy gaps is a topic that has received a great deal of study, although the majority of studies have focused on canopy species. The distribution of tree species in relation to gaps has been shown to be partitioned across gaps in tropical forest systems through differential species responses to resource availability gradients (Ricklefs 1977, Denslow 1980, Brokaw 1985), a phenomenon that is known as gap partitioning (Denslow 1980). Temperate forest systems are less likely to exhibit gap partitioning in the canopy layer because resource partitioning in high latitudes is less extreme and because temperate forests display much lower diversity and specialization of canopy species (Busing and White 1997). Understory vegetation communities in temperate forests generally have higher species diversity than overstories, and display a greater array of habitat requirements among these species (Halpern and Spies 1995, Bailey et al. 1998). Therefore, understory community compositions may be more likely to exhibit gap partitioning in temperate forests. In gaps created as a part of management treatments, responses to localized harvest-related disturbance of vegetation and ground surface may supersede the effects of resource partitioning in structuring the post-disturbance community. Chapter 2 investigates the understory vegetation community in and around gaps to assess the relative contribution of gap partitioning to patterning of the post-harvest community.

Effects of gap formation (or creation) on forest stands and landscapes depend greatly on the extent of gap influence on the surrounding forest (Menard et al. 2002). Gap formation can affect many processes in the surrounding undisturbed forest including tree growth rates (McDonald and Urban 2004), tree mortality or damage (Chen et al. 1992), rates of regeneration (Chen et al. 1992, Lertzman 1992), alterations in tree architecture (Hibbs 1982, Lorimer 1989), availability of a variety of resources (Canham et al. 1990, Canham 1999), expansion and heightened fecundity of understory plants (St. Pierre 2000, Lindh et al. 2003), and invasion of exotic species (Goldblum and Beatty 1999). In assessing the effect of gaps as a component of silvicultural treatments, managers need to know the extent of gap influence into the surrounding forest. Information on small scale gap influence is essential to predicting forest ecosystem responses to gap formation on a stand scale. Extent of gap influence has generally been investigated with a focus on overstory regeneration and resource responses (Dube et al. 2001, Menard et al. 2002). Patterns in understory vegetation composition may also have some efficacy in delineating the extent of gap influence. Chapter 3 examines the extent of gap influence on surrounding forest using understory vegetation community patterns as a metric.

Gap formation has been suggested to play a major role in maintenance of tree species diversity in tropical forests (Denslow 1980, Brokaw 1985, Hubbell et al. 1999, Brokaw and Busing 2000). In temperate forests, small-scale species diversity in understory vegetation communities may increase within gaps following gap formation, especially in harvest-related gaps (Schumann et al. 2003). Harvesting and associated soil disturbances have also been related to establishment of exotic species (Bailey et al. 1998, Thysell and Carey 2000, Battles et al. 2001), as have natural gap openings (Goldblum and Beatty 1999). Late successional associated species may respond negatively to gap openings, as these species are often negatively related to forest harvesting and open conditions (Halpern and Spies 1995). Chapter 4 investigates species diversity and distributions of exotic and late-successional species in relation to gap creation.

In summary, this study investigates whether gap creation in four young, thinned Douglas-fir (*Psuedotsuga meziesii*) dominated stands has enhanced small scale heterogeneity and diversity in vegetation community composition and structure in these stands and focuses on understory vegetation as a measure of this effect. The study sites are part of the Density Management Study (DMS) which is a larger effort focused on characterizing the effects of a thinning regime on many components of forest stands in western Oregon (Cissel 2006). The DMS focuses primarily on the efficacy of thinning treatments in promoting development of late-successional habitat. Within stand heterogeneity has been suggested as an essential feature of late-successional habitat that may be increased in young stands through management (Franklin et al. 2002). In young stands gap creation may be an important tool in promoting horizontal diversity (Beggs and Puettmann in review). Enhancement of heterogeneity in understory vegetation communities in and around gaps may also signal a corresponding small-scale enrichment in heterogeneity of other stand features.

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CHAPTER 2: GAP PARTITIONING IN UNDERSTORY VEGETATION COMMUNITIES IN DOUGLAS-FIR FORESTS OF WESTERN OREGON

Abstract

Canopy gap formation is a common result of small scale disturbance in forests, and may contribute greatly to maintenance of species diversity and stand structure. Differential species responses to gap formation may dominate organization of vegetation community composition in some forests. Patterns in understory vegetation communities were studied on transects across harvested canopy gaps in four young Douglas-fir (*Psuedotsuga menziesii*) dominated forest stands in western Oregon. Variation in ground-layer disturbance and resource gradients in relation to patterns in understory vegetation community composition were addressed. The gap partitioning and gap-size partitioning hypotheses were supported in stands where the understory was not dominated by clonal shrubs. Community composition differed significantly by position relative to gap in 0.4ha gaps ($F_{6,84} = 3.18$, $p = 0.007$) and 0.1ha gaps ($F_{4,56} = 4.82$, $p = 0.002$). Composition of understory communities was strongly related to an interaction between ground-layer disturbance and resource-based gap partitioning. Abundance of ruderal species was related to gap partitioning in larger gaps, while smaller gaps were dominated by competitor species. The concurrent effects of ground-layer disturbance, gap size-related differences in resource partitioning intensity, and pre-gap community composition seem to be influencing the existence of gap partitioning patterns in understory vegetation communities. We conclude that although gap partitioning of understory vegetation communities is possible, conditions necessary for expression of this pattern may be rare in natural forests in western Oregon.

Introduction

Canopy gap formation is a common result of small scale disturbance in forests, and can be an important process regulating species distributions in forest landscapes (Watt 1947, Bormann and Likens 1979, Spies et al. 1990). Many components of forest ecosystems regenerate through formation of small canopy gaps initiated by windthrow, disease, small patchy fires, or senescence of canopy trees (Barnes et al. 1998). Canopy gap formation is a major factor contributing to the maintenance of overstory species diversity and stand structure (Denslow 1980, Hibbs 1982, Brokaw 1985, Spies and Franklin 1989). Gaps may be integral to maintenance of species diversity in shrub and herb layers as well (Collins et al. 1985, Stewart 1988, Spies 1998, Roberts and Gilliam 2003). Availability of many resources increases with gap formation, including light, soil moisture, nutrients, substrates (germination safe sites), and growing space (Canham and Marks 1985). Vegetation community responses to these changes have been studied extensively in a variety of natural systems (Runkle 1981, Brokaw 1985, Moore and Vankat 1986, Stewart 1988). Recently, forest managers have begun to focus on gap creation to promote within-stand diversity (Runkle 1991, Coates and Burton 1997, Franklin et al. 2002). For example, gap creation is of interest in silvicultural prescriptions designed to produce and maintain late-successional habitat features in young forests in the Pacific Northwest region (Hunter 1993, Cissel 2006, Beggs and Puettmann in review). In this study, we investigate patterns in understory vegetation communities in gaps created as part of a thinning regime in western Oregon.

The gap-partitioning hypothesis is a theoretical framework that has been widely utilized to describe variation in vegetation communities in relation to forest canopy gaps. This hypothesis was developed to explain greater diversity in canopy species in tropical forests as compared to temperate forests (Ricklefs 1977). The gap partitioning hypothesis asserts that variation in tree species distributions results from differential responses of species to resource gradients related to canopy gaps, an effect which is suggested to be more extreme in tropical than in temperate regions (Ricklefs

1977, Denslow 1980). The gap partitioning hypothesis has received a great deal of attention in tropical forest ecosystems (Brokaw 1985, Brokaw 1987, Denslow 1987, Schupp et al. 1989, Dalling et al. 1998). The concept has also been investigated in temperate forests, in natural (Runkle 1982, Runkle and Yetter 1987, Lertzman 1992, Sipe and Bazzaz 1994, 1995, Busing and White 1997, Clinton 2003) and harvested gaps (Gray and Spies 1996, 1997, Coates 2000, Coates 2002). Results of these investigations have been mixed, but the majority of studies refute the existence of gap partitioning among canopy species in temperate forests. Reasons cited for this finding include the relatively (compared to tropical forests) low diversity of overstory species in temperate forests, especially coniferous forests compared to tropical forests (Lertzman 1992), as well as lack of adaptation to gap conditions in temperate canopy species (Lertzman 1992, Coates 2002).

The gap-size partitioning hypothesis extends the gap partitioning concept to address the relationship of gap partitioning to gap size (Denslow 1980, Whitmore 1989, Busing and White 1997). This hypothesis suggests that species partitioning is intensified as gap size increases (Busing and White 1997). Most studies do not support gap-size partitioning in overstory species in natural gaps of temperate forest systems (Lertzman 1992, Busing and White 1997). Gap-size partitioning of overstory species however, has been observed in gaps created by harvesting (Gray and Spies 1996, Coates 2002).

Although the gap-partitioning and gap-size partitioning hypotheses have not consistently explained patterns of overstory species in temperate forests, they may be of utility in accounting for patterns in understory vegetation communities. Understories in temperate coniferous forests of the Pacific Northwest generally exhibit higher diversity of species and functional groups than does the overstory (Halpern and Spies 1995, Bailey et al. 1998). Understory species in these forests may exhibit more niche specialization and understory communities would therefore be more likely to exhibit gap partitioning than overstory species (Lertzman 1992). Based on this, we would expect understory community composition to exhibit greater responses to resource gradients associated with gap formation (Roberts 2004). Studies investigating gap partitioning of understory communities in temperate forests have, however, exhibited mixed results. Responses of understory plant growth, abundance, and fecundity to gap formation have been illustrated in deciduous forest systems (Moore and Vankat 1986, Schumann et al. 2003), as well as in coniferous forests of the Pacific Northwest (St. Pierre 2000, Lindh et al. 2003). However, gap partitioning of species composition has not been documented in understory vegetation communities in deciduous (Anderson et al. 1969, Thompson 1980, Moore and Vankat 1986, Schumann et al. 2003), or coniferous forests (London 1999).

We were interested in determining whether gap partitioning can occur in understory vegetation communities. The generally accepted model of vegetation composition in relation to the gap-phase disturbance regime suggests that vegetation composition responds to a combination of the effects of niche partitioning and chance (Brokaw and Busing 2000). In understory vegetation communities, chance is represented by the pre-gap vegetation, seed bank, and dispersed seed available in the location where a gap is formed (Collins et al. 1985). However, the ability of the latter two groups of potential gap species to respond to gap formation may be largely dependant on disturbance of the ground-layer, defined here as the ground surface and existing understory vegetation layer (Collins and Pickett 1988a, 1988b, Roberts 2004). The filling of gaps entirely by pre-gap occupants has been associated with the absence of gap partitioning patterns (Hubbell et al. 1999, Brokaw and Busing 2000). Where present, ground-layer disturbance may allow gap adapted species to colonize areas in which they can respond to gap formation and may therefore promote gap-partitioning patterns. We expected harvest gaps to exhibit a greater propensity for gap partitioning in understory vegetation communities than natural gaps, due to greater disturbance of the ground layer vegetation and soil surface (Collins and Pickett 1988a, Collins and Pickett 1988b, Schumann et al. 2003, Roberts 2004).

The presence of gap partitioning may also depend on gap size and related variation in resource gradients. Studies of understory response to gap formation have generally concentrated on relatively small gap sizes, for example a maximum of $363m^2$ in Moore and Vankat (1986). The lack of gap partitioning in these studies could therefore also be due to a lack of strong resource gradients in small gaps. We investigate patterns in two gap sizes, the larger of which was beyond the upper limit of common natural gap occurrences in our study area (Spies 1990), and was therefore expected to show very strong gradients in resource availability (Canham et al. 1990).

The respective contributions of resource gradients and stochastic disturbances in patterning of post-disturbance community composition may be exhibited through differential responses of individual species or functional groups (Roberts 2004). Different species or species groups have unique capacities for resistance and resilience to disturbance (Grime 1977, Halpern 1988). Patterns of species groupings in relation to location relative to gaps may therefore indicate the relative importance of ground-layer disturbance versus changes in resource availability in patterning the understory vegetation community (Roberts 2004).

Pre-disturbance vegetation distribution can have a strong influence on the post-disturbance community (Hughes and Fahey 1991). The strength of this influence depends strongly on disturbance type and severity (Roberts and Gilliam 2003). The ability of understory communities to respond to gap disturbances may be highly influenced by initial species composition and structure (Brokaw and Scheiner 1989, Halpern 1989). Gap partitioning may be present or detectable in gaps with specific pre-gap vegetation composition (both overstory and understory).

In this study, we investigate variation in understory vegetation communities in and around canopy gaps, which were created as a component of a thinning regime in forest stands in western Oregon. We hypothesize that (1) the potential for gap partitioning exists in understory communities and that the large, highly disturbed gaps in this study system will exhibit this pattern. We also hypothesize that (2) disturbance of the understory vegetation layer and ground surface is an important factor leading to the exhibition of gap partitioning pattern in understory vegetation communities. In testing these hypotheses our objectives are (*i*) to determine whether gap partitioning and/or gap-size partitioning of the understory vegetation community has occurred, (*ii*) to determine whether understory community composition is influenced more strongly by resource gradients or harvest disturbance, and (*iii*) to assess the relative importance of potential environmental factors on understory community composition.

Methods

Site Descriptions

This study is part of the Density Management Study (DMS), which is investigating effectiveness of thinning treatments in fostering development of late successional habitat features. All study stands were even-aged and dominated by 40 to 70 year old Douglas-fir (*Psuedotsuga menziesii*) in a single canopy layer. One site (KM) had a small western hemlock (*Tsuga heterophylla*) component. We focused on four DMS sites located in western Oregon, three in the Coast Range ecoregion (Omernick 1987): Bottomline (BL), OM Hubbard (OMH), and North Soup (NS), and one in the Cascade Foothills ecoregion: Keel Mountain (KM). Sites spanned a variety of elevations, aspects, and stand histories. Site and treatment details are summarized in Table A1.1.

The study stands were treated with a thinning regime which included three sizes of circular gap openings (0.1, 0.2, and 0.4 ha). This study focused on 0.1 and 0.4 ha gaps located in stands thinned to 200 trees per hectare. Gap diameter to tree height ratios for the two gap sizes were approximately 1.0 and 2.0 respectively. Harvest treatments (including gaps) were operational in nature and therefore were not randomly assigned within the sites. Gap location was determined by harvesting constraints and not by condition of overstory or understory vegetation. Gaps that were used as landings for timber extraction were avoided in this study, but all gaps contained some ground-layer disturbance from logging operations.

Study design and data collection

Gap transects along which understory vegetation, substrates and environmental factors were sampled were established between July 1 and August 31 of 2004. We sampled eight gaps (four each of 0.1 and 0.4 ha sizes) at three sites (KM, OMH, NS) and six gaps (three of each size) at the fourth site (BL), resulting in a total of 15 gaps of each size. Transects originated at the gap center and extended on both a north/northeast and south/southwest bearing beyond the gap edge (defined as the line extending between the boles of the nearest surrounding canopy trees) and 23 meters into the surrounding thinned forest matrix (Figure A2.1). Gaps were selected according to suitability for the transect layout, with the stipulation that transects avoid other gaps, leave islands (unthinned patches), or the treatment or site boundaries Understory vegetation (< 6 m in height) was sampled in plots (transect positions) made up of sets of five contiguous 4m^2 square sampling quadrates (subplots) established along the transect. Our sampling design attempted to balance investigation of pattern at two scales, a small (10m) scale and a larger, transect level scale. This study focused on analysis at the transect scale. Transect positions included: South Forest Matrix (SM; centered ~54m from gap center in 0.4ha gaps and ~36m in 0.1ha gaps), South Edge (SE; ~36m, ~18m), South Gap Interior (SG; only in 0.4 ha gaps, ~18m), Gap Center (C), North Gap Interior (NG, only in 0.4 ha gaps), North Edge (NE), and North Forest Matrix (NM) (Figure A2.1).

Ocular estimates of percent cover were made for all vascular plant species (with cover < 6m in height) in each subplot. Taxonomic nomenclature follows the USDA Plants Database (USDA-NRCS 2005). Maximum cover for a species was 100 percent, but cumulative cover of all plants could exceed 100 percent due to multiple vegetation layers. Percent cover was also estimated for substrate types: litter, exposed mineral soil, coarse woody debris, stump/tree bole, and exposed rock, and for growth form classes: ground-dwelling lichen, ground-dwelling bryophyte, fern, forb, grass, sedge/rush, low shrub, tall shrub, hardwood, and conifer. Data were averaged to the plot level to account for lack of spatial independence of subplots.

Hemispherical canopy photographs were taken at subplot centers to characterize the understory light environment. The camera was positioned at 1.5 m height. We used a Nikon Coolpix 4500 digital camera with FC-E8 Fisheye Converter Lens Attachment. Photographs were captured in black and white or on “high contrast” setting to increase the distinction between sky and foliage and to reduce effects of chromatic aberration associated with digital photography (Frazer et al. 2001).

Photographs were taken at dawn, dusk, or on days with uniform cloud cover to further reduce effects of chromatic aberration and increase contrast between foliage and sky.

Photos were analyzed using Gap Light Analyzer 2.0 (Frazer et al. 1999). We used an alternative projection function described by Frazer et al. (2001) to minimize lens projection distortion. A third order polynomial was used to describe the projection:

[1] $Y = 6.6380X - 0.0025X^2 - 2.4014E - 0.5X^3$

$0^\circ \leq X \leq 90^\circ$

where, Y is the radial position of a projected point measured in pixels from the optical center of a full-resolution (1600 × 1200 pixels) digital image, and X is the angular distance (◦) from the lens' optical axis to a point located in the hemispherical object region. Photos were analyzed using GLA and estimates of percent canopy openness; leaf area index integrated over the zenith angles 0-60º; transmitted direct, diffuse, and total solar radiation ($mol/m^2/d$); and percent transmitted direct, diffuse, and total solar radiation were obtained using this program.

Data Analysis

Gap partitioning of community composition

Tests of gap partitioning and gap-size partitioning in understory plant species were made using multivariate techniques. To investigate species composition patterns, non-metric multi-dimensional scaling ordination (NMS; Kruskal 1964, Mather 1976) was employed using PC-ORD v 4.0 (McCune and Medford 1995). All ordinations were run using the "slow and thorough" autopilot setting. Sørensen distance was used in all multivariate analyses (McCune and Grace 2002). Plots were ordinated in species space for the full dataset. Sites were then investigated individually to account for overwhelming differences in species communities among sites. Ordinations for each individual site were rotated to maximize separation of transect positions along axis 1 to facilitate interpretation of correlations with environmental variables. In addition, we investigated the relative contributions of species composition and abundance (cover) by converting the datasets to presence/absence, and re-running each NMS ordination to compare the effect of this change on results for each site.

We used the multi-response permutation procedure (MRPP; Mielke 1979) to test for differences in species composition among transect positions. Gap sizes were analyzed separately. This procedure is a non-parametric test of differences between two or more predefined groups (McCune and Grace 2002). The A statistic derived from this analysis measures the chance-corrected within-group agreement and in this analysis is a measure of the homogeneity of vegetation community composition within transect positions.

We also tested for differences in community composition among transect positions, which could demonstrate the pattern and intensity of partitioning along the gap transects. Each site level NMS ordination was rotated to maximize the amount of total community variation explained by the first axis and scores for each plot on this axis were used as a univariate community composition variable (hereafter NMS community composition variable). Differences in these scores between positions were examined using analysis of variance (ANOVA) with repeated measures in space (along each transect), and blocked by site, using the MIXED procedure in SAS v 9.1 (SAS-Institute-Inc. 2005) with the model:

$$[6] \qquad Y_{ijk} = \mu + \beta_i + \lambda_{ijk} + P_l + \varepsilon_{ijkl}$$

where:

μ = the overall mean value of Y

β_i = the random effect of site that adds variability to the value of Y, i = 1,2,3,4.

λ_{ijk} = the random effect of transect k within site i, k = 1,2,3,4,5,6,7,8

P_l = the fixed effect of the lth level of position, l = 1,2,3,4,5,6,7 for large gaps and 1,2,3,4,5 for small gaps

ε_{ijkl} = the random effect among positions within transects, and $\varepsilon_{ijkl} \sim MVN(0,\Sigma)$ and $\Sigma =$

$$\begin{array}{|c|c|c|c|c|}\hline \sigma^2_{11} & \sigma^2_{12} & \sigma^2_{13} & \sigma^2_{14} & \sigma^2_{15} \\ \hline \sigma^2_{12} & \sigma^2_{22} & \sigma^2_{23} & \sigma^2_{24} & \sigma^2_{25} \\ \hline \sigma^2_{13} & \sigma^2_{23} & \sigma^2_{33} & \sigma^2_{34} & \sigma^2_{35} \\ \hline \sigma^2_{14} & \sigma^2_{24} & \sigma^2_{34} & \sigma^2_{44} & \sigma^2_{54} \\ \hline \sigma^2_{15} & \sigma^2_{25} & \sigma^2_{35} & \sigma^2_{45} & \sigma^2_{55} \\ \hline \end{array}$$

represents an unstructured covariance among positions along a transect across the small gap size.

The Akaike Information Criteria (AIC; Gotelli and Ellison 2004) statistic was used to select the most appropriate covariance structure for the models used to analyze each of the response variables. The covariance structure for both models was Banded Toeplitz, with two positions correlated in the large gaps, and one position correlated in the small gaps (SAS-Institute-Inc. 2005). All comparisons of means were adjusted using the Tukey-Kramer procedure (Gotelli and Ellison 2004).

We used multivariate ANOVA techniques to corroborate findings of the NMS community composition variable ANOVA, and to determine whether the NMS community composition variable was representative of the full community response and appropriate for use in other analyses. For this purpose we employed permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to test for differences in the NMS community composition variable among transect positions. This method was applied to both the combined and individual site datasets using the PERMANOVA program (Anderson 2005). While it does not adjust for repeated measures, this test accounts for nesting in the sampling design (each transect position was nested within a transect and transects were nested within sites). Also, this test is not suitable for unbalanced designs, and we tested only the sites for which there were four transect replicates of each size (KM, NS, and OMH).

Gap partitioning versus disturbance

We examined which plant species were most strongly related to community composition patterns as a means of assessing the relative importance of gap partitioning and harvest-related disturbance. For this question we used indicator species analysis (ISA; Dufrene and Legendre 1997, McCune and Grace 2002) and Spearman rank correlation coefficients (Gotelli and Ellison 2004) comparing species functional groups with the NMS community composition variable. ISA, implemented using PC-ORD v4.1 (McCune and Medford 1995), evaluated the faithfulness of species to transect positions based on relative species frequencies and abundances. Spearman rank correlation coefficients between the NMS community composition variable and growth-form groups, habitat preference groups (Halpern et al. 1999), and disturbance response strategy groups (Grime 1977) were calculated using PROC CORR in SAS v9.1 (SAS-Institute-Inc. 2005). Growth form groups are those described above in methods. Disturbance strategy groups followed Grime (1977) and were classified as: ruderals, competitors, and stress tolerators. Habitat preference groups (Halpern et al. 1999) were: open site species (early seral species), forest understory species (includes late seral species), and intermediate species (tolerant of a variety of conditions). Species were assigned to groups based on life-history and growth form attributes based on Hitchcock and Cronquist (1973). Classifications for all species can be found in Table A4.1. In addition, in order to evaluate the strength of these attributes in influencing the full community composition, we plotted overlays of these variables on the NMS ordinations and evaluated their correlations with the ordination axes.

Environmental variables and gap partitioning

We also directly investigated which environmental variables were most strongly associated with gap partitioning patterns and related them to community composition. For this purpose we examined overlays of environmental variables on NMS ordinations, Spearman rank correlations between the NMS community composition variable and environmental variables, and performed a regression of the

NMS community composition variable on environmental variables. Environmental variables included in these overlays and in the Spearman correlation analysis were: canopy openness (percent open sky), estimated percent transmitted radiation (total, direct, and diffuse), leaf area index (over the zenith angles 0-60°), percent exposed mineral soil, percent litter, percent slash and coarse woody debris cover (included all woody debris greater than 1in or ~2.5cm in diameter), predicted soil moisture, slope, elevation, heat load index, predicted above canopy radiation, and distance to nearest road or skid trail. Soil moisture response to gap formation was predicted based on information about temporal soil moisture response to gap creation in western Oregon forests as described by Gray et al. (2002), whose gaps were similar but not equivalent in size to our gaps. This variable is a coarse estimate of the effect of gap creation on soil moisture over the time since gap creation. Soil moisture values of edge and gap interior positions relative to interior forest were based on 6 year mean response values for north-south transects as presented in Gray et al. (2002). Heat load index and above canopy radiation represent above canopy solar radiation levels predicted from aspect, latitude, elevation, and slope (McCune and Keon 2002). We selected a subset of these environmental variables for inclusion in a regression model that best allowed us to investigate the relationship between disturbance and resource related variables. Variables selected included; canopy openness, leaf area index, estimated percent total transmitted radiation, percent exposed mineral soil, predicted soil moisture, elevation, heat load index, and distance to nearest road or skid trail. Canopy openness, leaf area index, and transmitted radiation were not allowed to enter into the same models because of high correlation between these variables. Potential models were evaluated using the Bayesian Information Criteria (BIC; Gotelli and Ellison 2004), with the MIXED procedure in SAS v. 9.1 (SAS-Institute-Inc. 2005). The model selected for the NMS community composition variable in the large gap size was:

[7] $Y_i = \beta_0 + \beta_C C + \beta_M M + \beta_E E + \varepsilon_i$

where the β's are the regression coefficients and:

Y_i = the NMS axis score for the ith plot

C_i = the percent canopy openness for the ith plot

M_i = the log percent cover of mineral soil substrate for the ith plot
E_i = the elevation (m) for the ith plot
ε_i = the random effect for each vegetation plot and $\varepsilon \sim N(0, \sigma_\varepsilon^2)$ and all ε_i are independent of each other

The model selected for the NMS community composition variable in the small gap size was:

[8] $$Y_i = \beta_0 + \beta_L L + \beta_M M + \beta_D D + \varepsilon_i$$

where the β's are the regression coefficients and:

Y_i = the NMS axis score for the ith plot
L_i = the leaf area index for the ith plot
M_i = the log percent cover of mineral soil substrate for the ith plot
D_i = the distance (m) to the nearest road/skid trail for the ith plot
ε_i = the random effect for each vegetation plot and $\varepsilon \sim N(0, \sigma_\varepsilon^2)$ and all ε_i are independent of each other

Models selected for each gap size were tested using the MIXED procedure, and met all assumptions of regression analysis.

Results

Gap partitioning of community composition

The range of stand histories and ecoregions represented in this study was evident as NMS ordination of plots in the full dataset revealed separation primarily among sites. MRPP of all sites combined supported this conclusion, as the A statistic, an indicator of within-group homogeneity, was quite small (Table 2.1). It is important to note that the MRPP could not account for site differences as we were unable to block by site in this analysis due to the unbalanced sampling design. After eliminating influences of site differences on vegetation communities by ordinating each site individually, community composition separated among gap transect positions (Figures 2.1 – 2.4).

Table 2.1. MRPP results (A statistic and associated p-value) for all sites combined and each site individually. * denotes $p < 0.05$.

	Species	
	A	p
All Sites	0.01221	0.003*
Bottomline	0.01071	0.333
Keel Mountain	0.04268	0.020*
North Soup	0.03282	0.078
OM Hubbard	0.05006	0.001*

All individual site ordinations had three dimensional solutions (see Table 2.2 for specifics of ordination solutions); Axis 1 and the stronger of the other two axes are shown (Figures 2.1 – 2.4). At each of the four sites, Axis 1, along which there was separation among transect positions, was most strongly correlated with estimated percent transmitted radiation, although the strength of this correlation differed among sites. For each site, environmental variables and species groups that were strongly ($r > 0.4$) correlated with axis 1 are presented in Figures 2.1 – 2.4. At all sites, a substantial portion of the residual variation, relative to that explained by Axis 1, was explained by a non-partitioning related axis.

Table 2.2. Results of NMS ordinations. P values were obtained from Monte Carlo tests of stress versus 50 randomized runs of the data. “Cover” is results with species represented by their percent cover, “P/A” is data transformed to presence/absence.

	Bottomline		*Keel Mountain*		*North Soup*		*OM Hubbard*	
	Cover	P/A	Cover	P/A	Cover	P/A	Cover	P/A
Stress	14.84	18.22	14.96	17.50	15.04	17.59	14.53	17.70
p	0.0196	0.0196	0.0196	0.0196	0.0196	0.0196	0.0196	0.0196
Total R^2	81.8	69.9	80.3	72.0	81.7	76.4	82.7	80.9
Axis 1 R^2	8.6	19.1	41.5	33.2	28.1	24.9	32.5	38.2
Axis 2 R^2	21.3	12.0	15.8	11.3	16.1	22.5	30.0	30.8
Axis 3 R^2	51.9	38.8	23.0	27.6	37.5	29.0	20.2	11.9

Community patterns at the BL site were not strongly influenced by gap partitioning and were dominated by clonal species that were likely present before gap creation (Figure 2.1). The NMS ordination of vegetation communities at BL explained 81.8% of the total variation in the original data in a three dimensional solution. Separation among transect positions on Axis 1, representing the impact of gap partitioning, explained only 8.6% of the variation (Table 2.2). The majority of variation at BL was explained by Axis 3 (51.9%), which was not strongly correlated with any of the measured environmental variables. The lack of a strong gap partitioning pattern at this site was supported by the non-significance of the MRPP test (Table 2.1). Instead, the dominance of Axis 3 points to the influences of clonally spreading, rhizomatous species such as *Symphoricarpos* (r = 0.686), *Vancouveria hexandra* (r = 0.583), *Whipplea modesta* (r = -0.571), *Gaultheria shallon* (r = -0.509), *Linnea borealis* (r = -0.506), and *Vicia Americana* (r = 0.523).

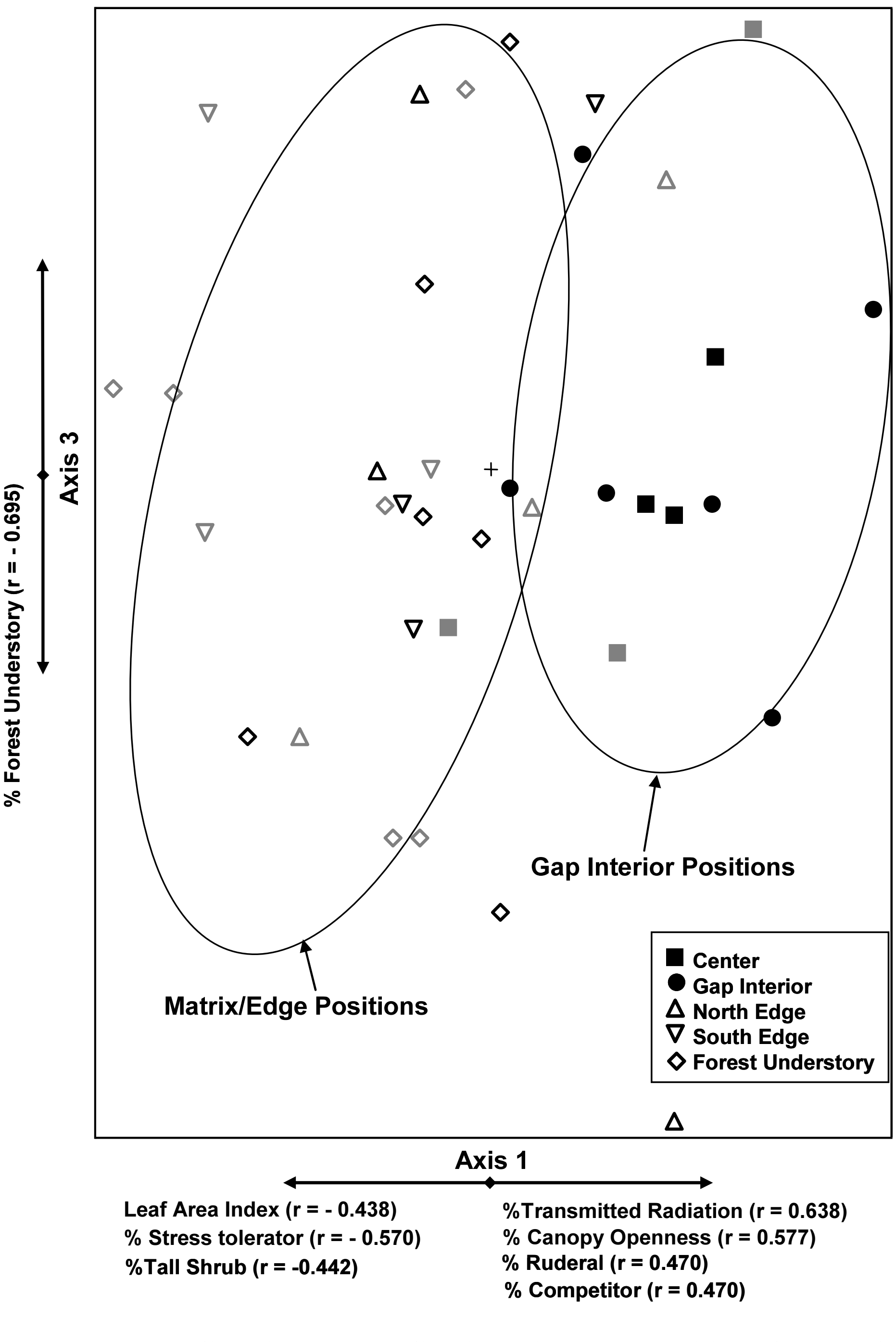

Figure 2.1**.** Bottomline site NMS ordination of transect position plots on abundance of species. (Axis 1 and 3; Axis 2 is not shown). Overlain ovals encompass the majority of gap interior and edge/matrix plots. Black symbols represent 0.4ha gaps, and gray symbols represent 0.1ha gaps. Species groups and environmental variables and their correlations with axes are included along both axes.

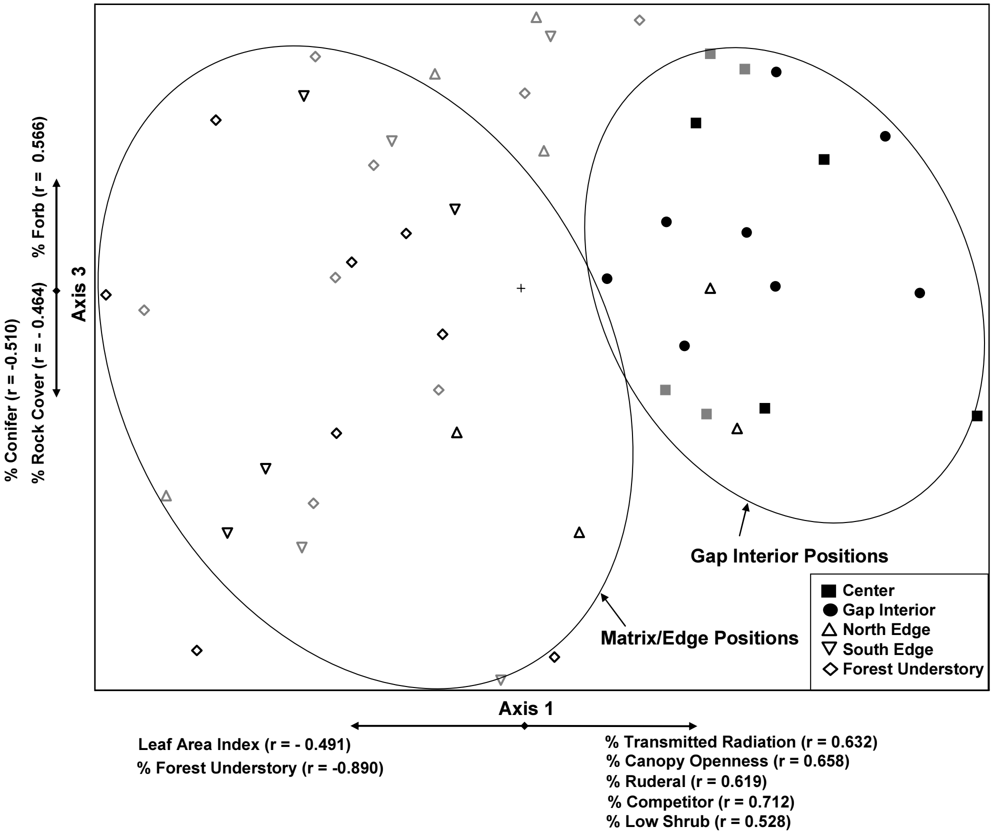

Figure 2.2. Keel Mountain site NMS ordination of transect position plots on abundance of species. (Axis 1 and 3; Axis 2 is not shown). Overlain ovals encompass the majority of gap interior and edge/matrix plots. Black symbols represent 0.4ha gaps, and gray symbols represent 0.1ha gaps. Species groups and environmental variables and their correlations with axes are included along both axes.

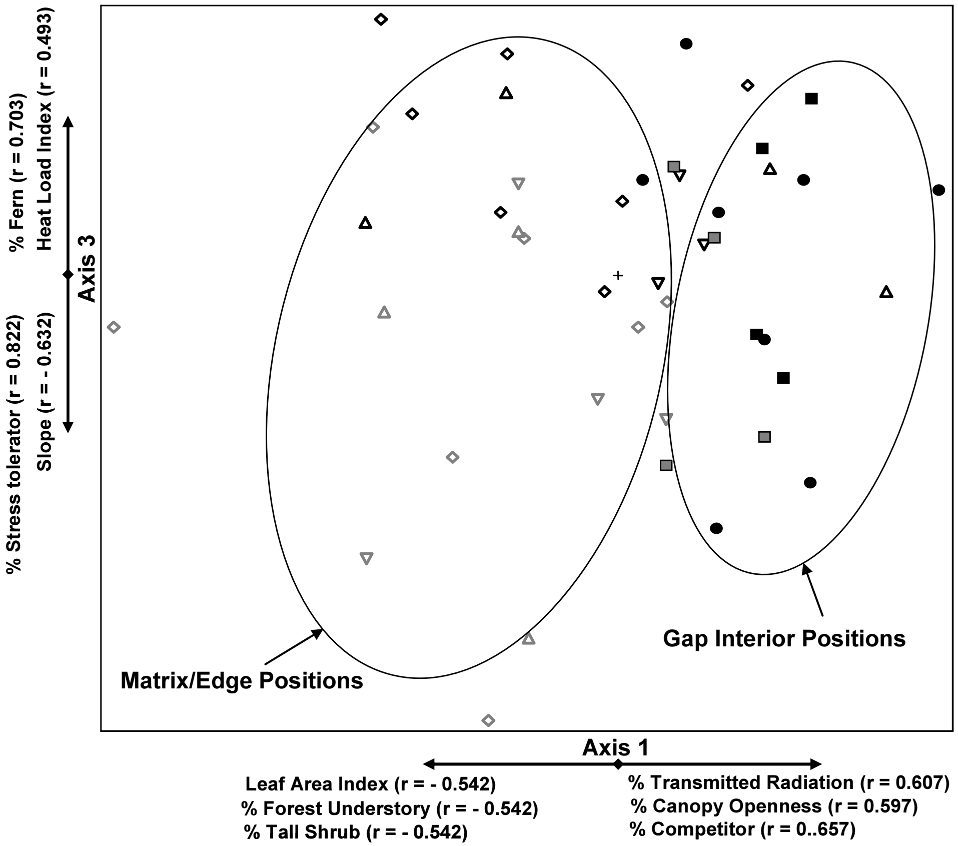

Figure 2.3. North Soup site NMS ordination of transect position plots on abundance of species. (Axis 1 and 3; Axis 2 is not shown). Overlain ovals encompass the majority of gap interior and edge/matrix plots. Black symbols represent 0.4ha gaps, and gray symbols represent 0.1ha gaps. Species groups and environmental variables and their correlations with axes are included along both axes.

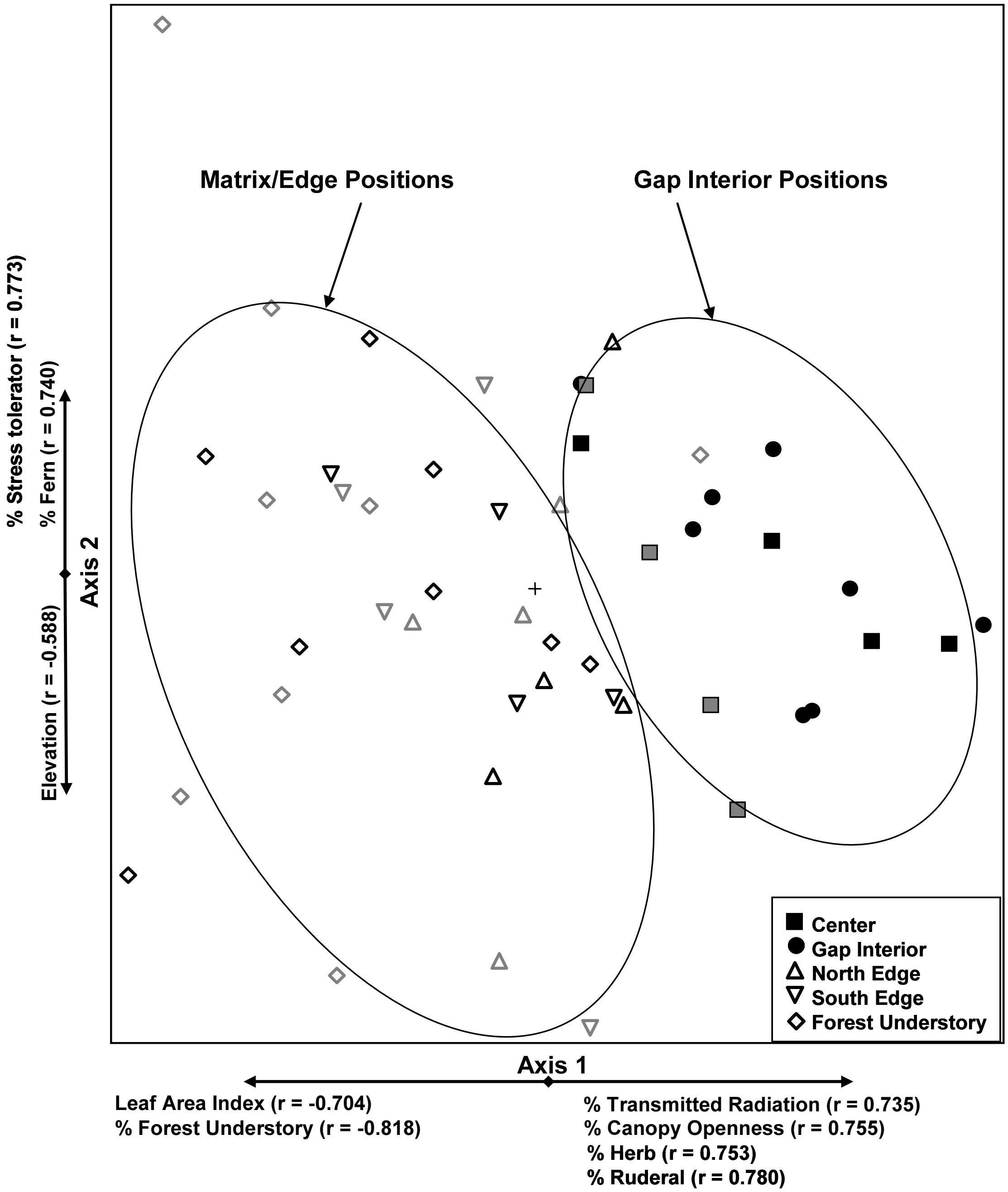

Figure 2.4. OM Hubbard site NMS ordination of transect position plots on abundance of species. (Axis 1 and 2; Axis 3 is not shown). Overlain ovals encompass the majority of gap interior and edge/matrix plots. Black symbols represent 0.4ha gaps, and gray symbols represent 0.1ha gaps. Species groups and environmental variables and their correlations with axes are included along both axes.

At KM, gap partitioning exhibited the strongest influence on patterns in species composition (Figure 2.2). The ordination for KM explained 80.3% of the variation in the original dataset in a three dimensional solution (Table 2.2). Axis 1 explained the majority (41.5%) of the variation in the original data, compared with axes 2 and 3 (23.0% and 15.8% respectively). Axis 1 was most strongly correlated with a number of early seral species (both native and exotic), such as *Rubus luecodermis* (r = 0.690), *Digitalis purpurea* (0.632), *Chamerion angustifolium* (0.614), and *Veronica officinalis* (0.594). The MRPP test at this site was highly significant and suggested relatively strong homogeneity within transect positions (Table 2.1).

At the NS site, gap partitioning was responsible for a large part of the overall pattern but a within-site gradient in heat loading related to slope and aspect differences also contributed to this pattern (Figure 2.3). Ordination of the vegetation community resulted in a three dimensional solution which explained 81.7% of the variation in the original data (Table 2.2). Axis 3 explained the most variation from the original vegetation community dataset (37.5% compared with 28.1% for Axis 1) and was highly correlated with heat load index (r = 0.493) and slope (r = -0.632) as well as cover of *W. modesta* (r = -0.824), *Asynuema prenanthoides* (r = -0.699), and *Rhododendron macrophyllum* (-0.528), all of which are dry site associated species (Hitchcock and Cronquist 1973). Axis 1 on the other hand was associated with species such as *Rubus leucodermis* (r = 0.678), *Epilobium ciliatum* (r = 0.582), *Cirsium vulgare* (r = 0.575), and *Rubus parviflorus* (r = 0.565). The MRPP test for differences between vegetation communities by transect position was not significant (Table 2.1).

At the OMH site, gap partitioning was responsible for the largest part of the overall pattern but a within-site elevation gradient also contributed to the pattern (Figure 2.4). The ordination for the OMH site explained 82.7% of the variation in the original dataset in a three dimensional solution (Table 2.2). Axis 1 explained the most variation at this site, but a substantial portion of the variation in the original data was explained by Axis 2 (30.0% compared with 32.5% for Axis 1). Axis 1 was correlated most strongly with early seral species such as *Elymus glaucus* (r = 0.710), *Aira* *caryophyllea* (r = 0.680), *Hypochaeris radicata* (r = 0.626), and *Cirsium vulgare* (r = 0.580). Axis 2 was most strongly correlated with elevation (r = -0.588) and cover of two common understory species, *G. shallon* (r = 0.617) and *Polystichum munitum* (r = 0.601). The MRPP test for difference among vegetation communities by transect position at this site was highly significant (Table 2.1).

Conversion of data into presence/absence form had little effect on the conclusions of the ordination analyses at the three sites that exhibited gap partitioning (Table 2.2). Therefore, abundance data were taken to be indicative of composition, and not merely differences in species cover between plots. The BL site showed more gap-related pattern when the data were converted to presence/absence, suggesting that the slight compositional partitioning effect seen at this site was effectively masked by changes in cover.

We found significant differences in community composition among position groups within both large ($F_{6,84}$ = 3.18, p = 0.007) and small gaps ($F_{4,56}$ = 4.82, p = 0.002). However, patterns and strengths of pairwise differences among positions varied between the gap sizes (Figures 2.5 and 2.6). The positions with the most gap-influenced communities (i.e., community that most strongly differed from the forest matrix, as expressed in the NMS community composition variable) were generally located on the north side of the gap openings (Figures 2.5 and 2.6). As expected, gap interior positions differed in both gap sizes from forest understory positions. In the large gaps, mean values of the NMS community composition variable were lowest (most gap associated) in the north gap position and gap center positions and were highest (most forest associated) in the north matrix position (Figure 2.5). The north gap and gap center positions were significantly different from the north matrix position, but only the north gap position was significantly different from the south matrix position (Figure 2.5). In small gaps, the mean value of the NMS community composition variable was lowest (i.e., most gap influenced) in the north edge position, which differed significantly from all other positions, and highest in the south matrix position (Figure 2.6).

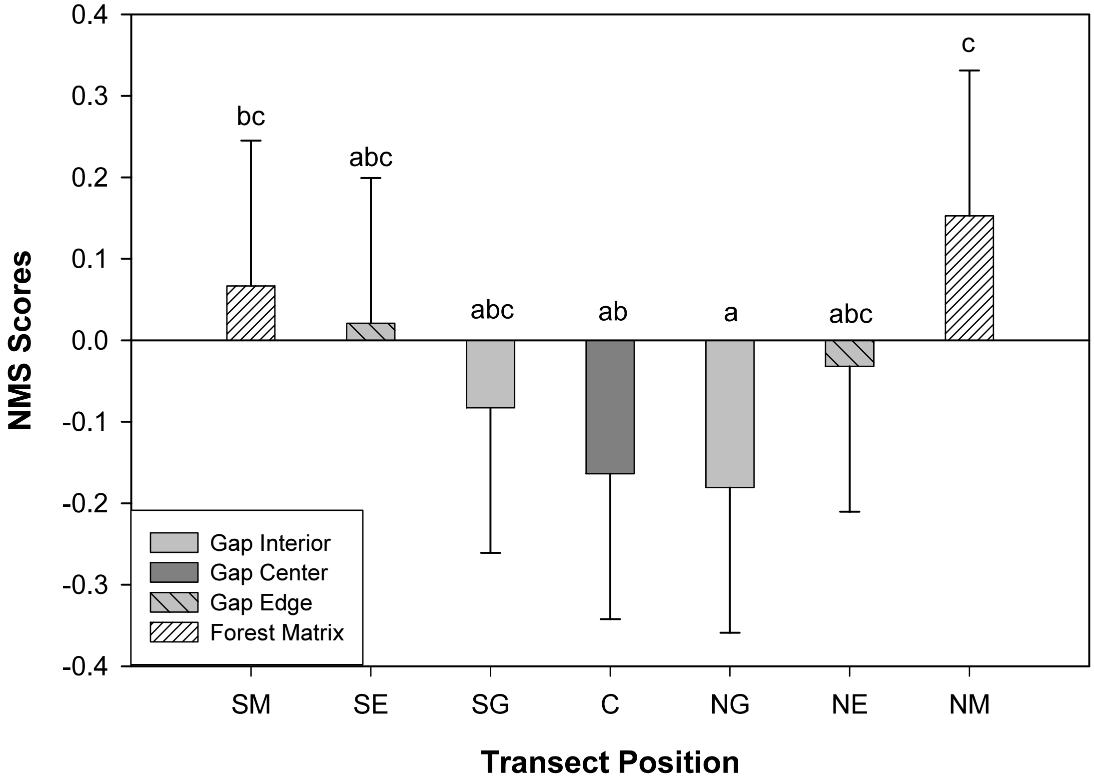

Figure 2.5. Least squares mean values of Whittaker's beta diversity, Sorensen's distance, and the NMS community composition variable for each transect position in the 0.4ha gaps. Results of position comparisons are indicated by letters above bars, positions sharing letters are not significantly different from each other at the $p < 0.05$ level. Error bars represent standard errors for each position.

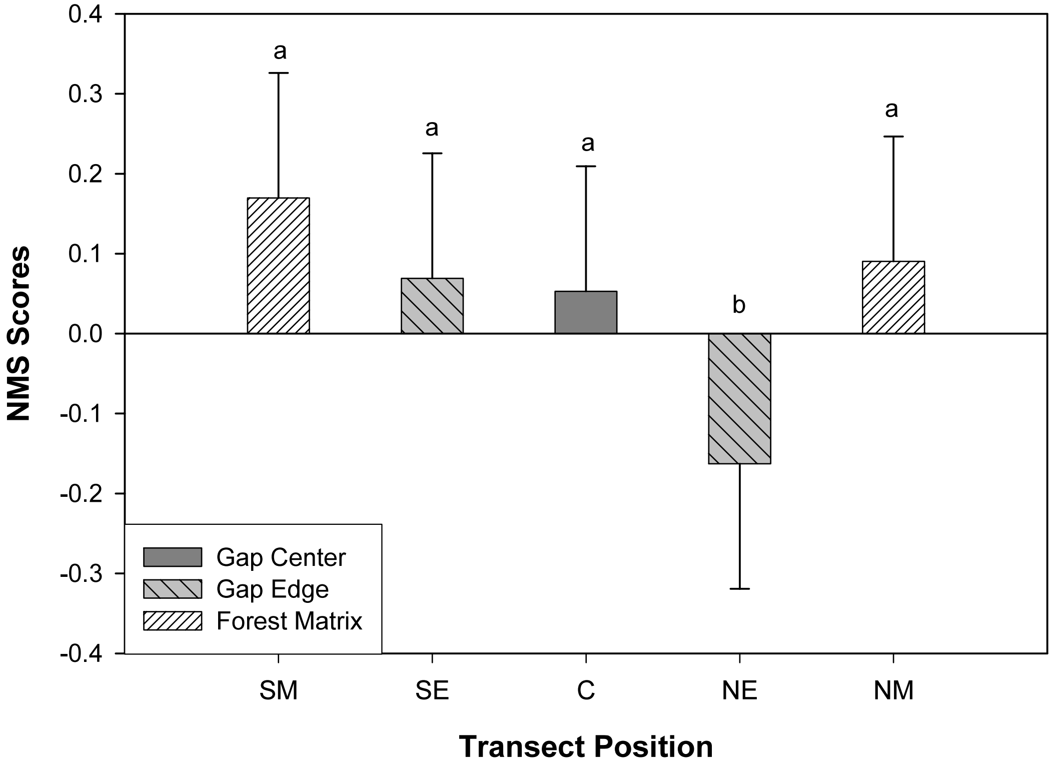

Figure 2.6. Least squares mean values of species richness, Sorensen's distance, and the NMS community composition variable for each transect position in the 0.1ha gaps. Results of position comparisons are indicated by letters above bars, positions sharing letters are not significantly different from each other at the $p < 0.05$ level. Error bars represent standard errors for each position.

Patterns in understory species composition in the full community (multivariate with each species considered), as opposed to the reduced NMS community composition variable, were similar to those presented above, except that impacts of gap sizes were more evident. Small gaps generally showed less obvious partitioning effects. Community composition differed by transect position (nested within site) for the three sites that contained eight gap transects (which were also the sites that exhibited the strongest gap partitioning effect) in the large gaps ($F_{18,63} = 1.41$, $p = 0.0001$). Transect positions were not strongly significantly different in the small gaps ($F_{12,45} = 1.15$, $p = 0.1064$). Comparisons between transect positions were similar to those displayed in the ANOVA of the NMS community composition variable in the large gap size, but not in the small which displayed very few significant differences between positions (results of pairwise comparisons are included in Table A3.1).

In summary, individual sites exhibited gap partitioning patterns, but these patterns were generally limited to distinctions between gap interior and gap edge/forest matrix plots. This result was apparent at all but one site, where species patterns were dominated by the presence of a dominant clonal layer. In addition, large gaps displayed stronger partitioning patterns than the smaller ones in the analysis that considered the full community response.

Gap partitioning versus disturbance

Correlations among species groups and the NMS community composition variable showed that groups commonly associated with disturbance also had the strongest influence on community composition. Spearman rank correlations of the NMS community composition variable for many species groupings showed strong relationships (Table 2.3). Competitor species cover was highest and stress tolerator cover was lowest in gap interiors in both gap sizes. Cover of ruderal species, an indicator of recent disturbance, made up a minor proportion in all positions, except the center and north gap positions in the large gaps (Figures 2.7 and 2.8). However, in both gap sizes, the NMS community composition variable was correlated strongly and positively with the ruderal group, negatively with the stress tolerator group, and not strongly correlated with the competitor group.

Among growth form groups, the NMS community composition variable was most strongly and positively correlated with the grass group, and negatively correlated with the fern and bryophyte groups. Low shrubs and ferns were the most abundant growth forms at all transect positions in both gap sizes (Figures 2.9 and 2.10). Grass and forb covers were consistently higher, and tall shrub cover was consistently lower in gap interiors. Among habitat preference groups there were no strong correlations in either gap size, although a few of the relationships were significant (Table 2.3). At least one of the growth form, life-history strategy, and habitat preference groups exhibited strong correlations with ordination axes at each site (Figures 2.1 - 2.4).

Gap interior positions generally had the most and strongest (based on ISA indicator values) indicator species, compared to edge or forest matrix positions. As expected, patterns of individual species as indicators of transect positions differed between sites and gaps sizes (Figure 2.11), but gap interior positions in both gap sizes were generally characterized by early seral species, both native and exotic. Indicator species were generally more strongly indicative of positions in small versus large gaps. The presence of the two additional gap interior positions in the large gaps may have been quite influential. These additional positions may have made the gap center position less “unique” in those transects, lessening the statistical power of these tests to identify indicators for any of the gap interior positions.

In summary, the ruderal species group seemed most responsible for the gap partitioning patterns exhibited in these gaps. A variety of species were flagged as indicators of gap interior positions most of which were early seral species, and all of which were either competitor or ruderal species. Indicators of the gap interior were stronger in the small gap size, either because these species were more strongly limited to these positions in this gap size as compared to the large gaps or because the large gaps included extra transect positions located in the gap interior.

Table 2.3. Spearman rank correlations of species groups with NMS community composition variable. Strongest correlations among life history categories and growth forms are bolded.

	NMS 0.4 ha		NMS 0.1 ha	
	r	p	r	p
Species groups				
Late Seral	0.3280	0.001	0.3155	0.006
Exotic	-0.4109	<0.001	-0.3458	0.002
Ruderal	-0.4336	<0.001	-0.4651	<0.001
Competitor	-0.2214	0.023	-0.1627	0.163
Stress-tolerator	0.2376	0.015	0.4401	<0.001
Disturbed	-0.2368	0.015	0.0049	0.967
Forest	0.3127	0.001	0.3454	0.002
Intermediate	-0.2079	0.033	-0.1480	0.205
Growth forms				
Forb	-0.4168	<0.001	-0.1189	0.310
Grass	-0.6205	<0.001	-0.6170	<0.001
Sedge/Rush	0.0834	0.398	-0.0391	0.739
Fern	0.3676	<0.001	0.4904	<0.001
Bryophyte	0.2260	0.020	0.2198	0.058
Lichen	0.2192	0.025	0.0543	0.644
Low Shrub	-0.1683	0.086	-0.0769	0.512
Tall Shrub	0.0992	0.314	0.1526	0.191
Hardwood	-0.1785	0.068	-0.2095	0.071
Conifer	0.3639	<0.001	0.3804	0.001

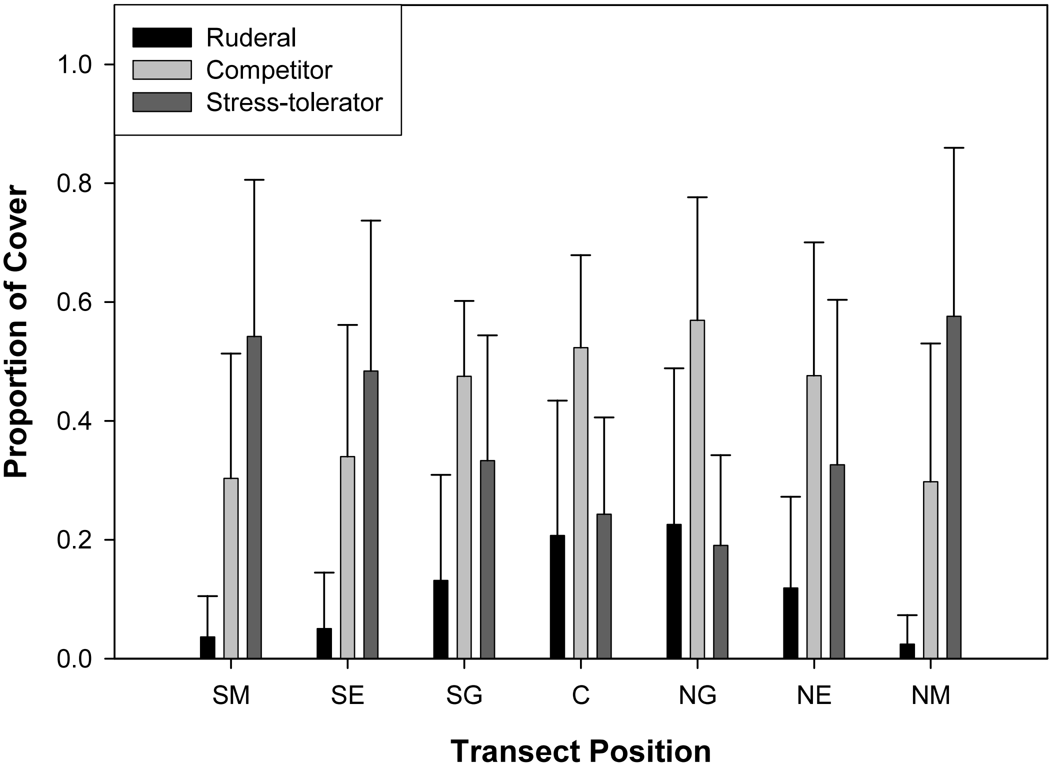

Figure 2.7. Mean proportion of total cover in Grime's (1977) life history strategy groups by transect position in the 0.4ha gaps. Error bars represent standard errors.

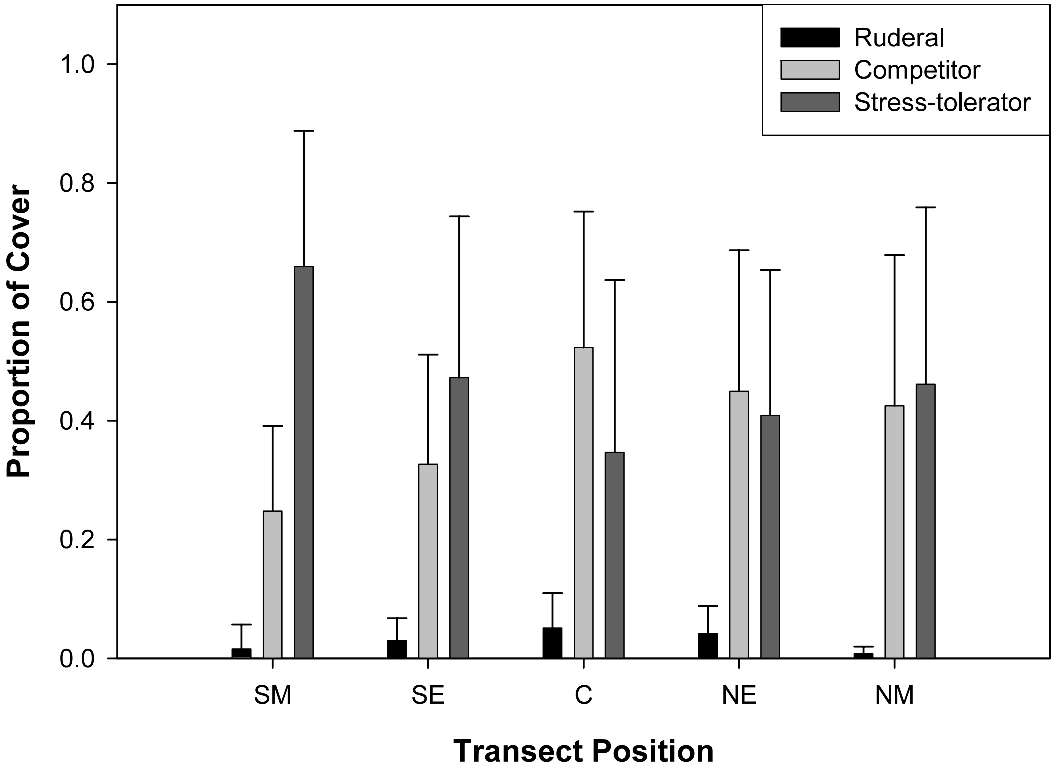

Figure 2.8. Mean proportion of total cover in Grime's (1977) life history strategy groups by transect position in the 0.1ha gaps. Error bars represent standard errors.

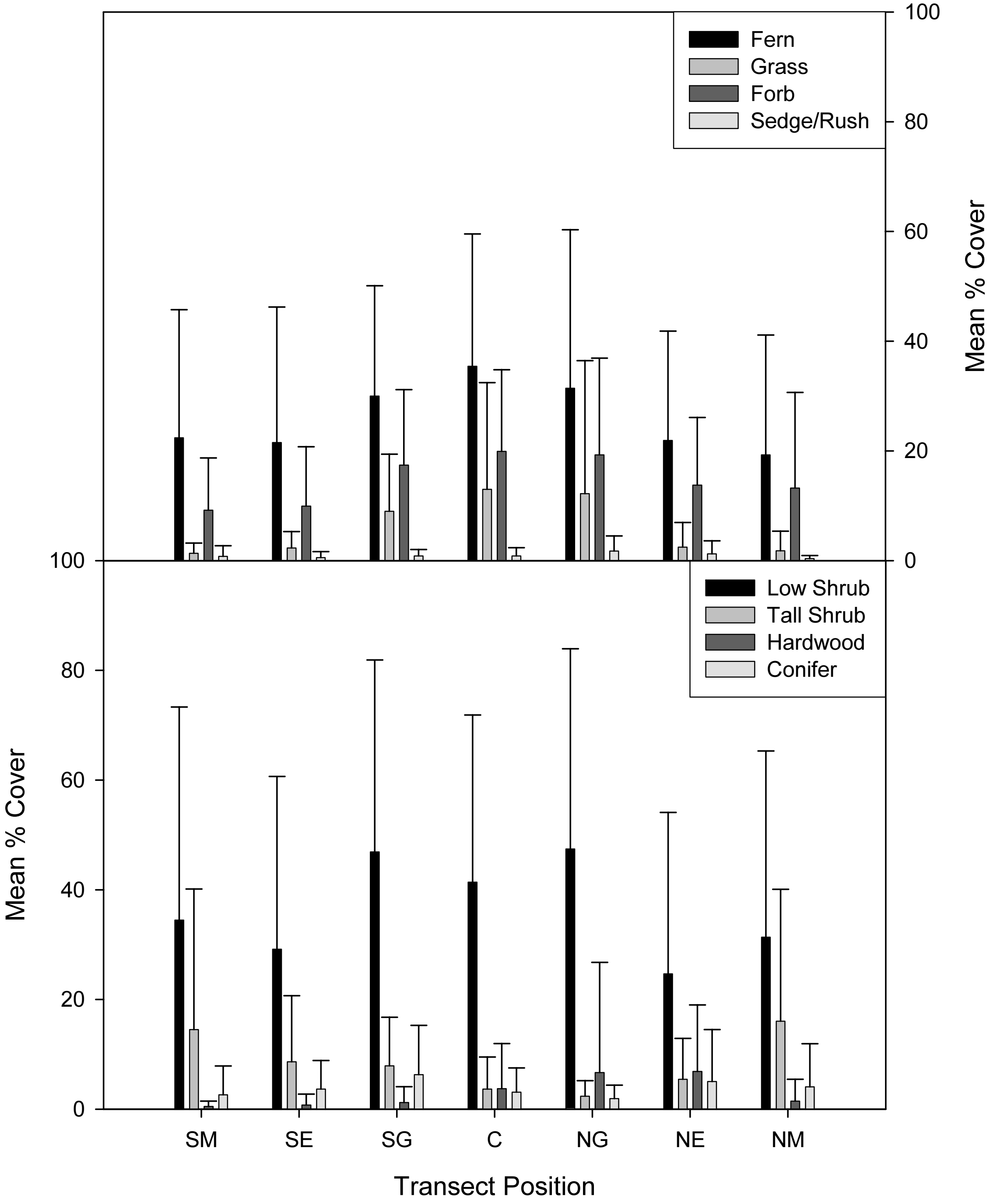

Figure 2.9. Mean percent cover of growth form groups by transect position in the 0.4ha gaps. Error bars represent standard errors.

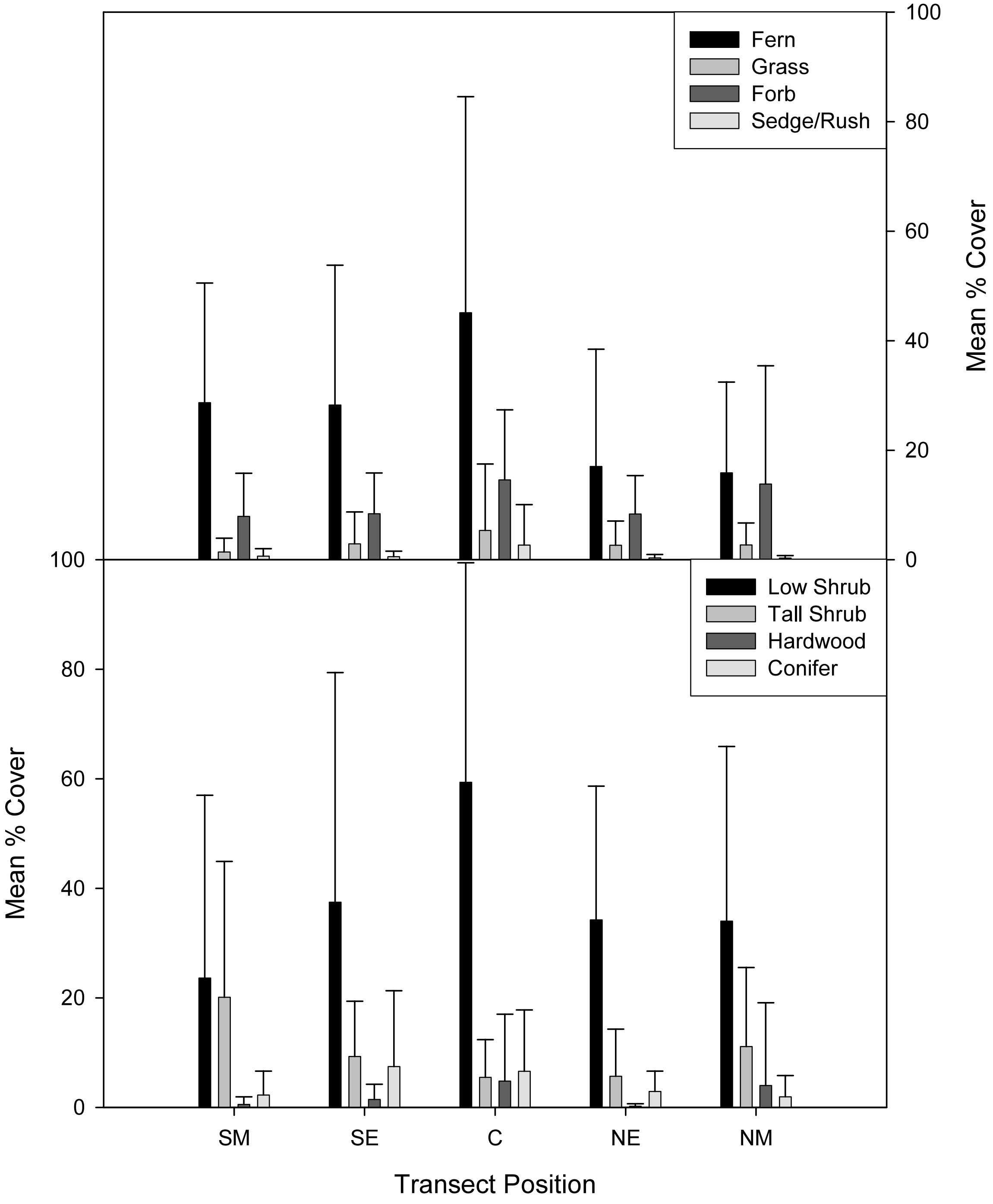

Figure 2.10. Mean percent cover of growth form groups by transect position in the 0.1ha gaps. Error bars represent standard errors.

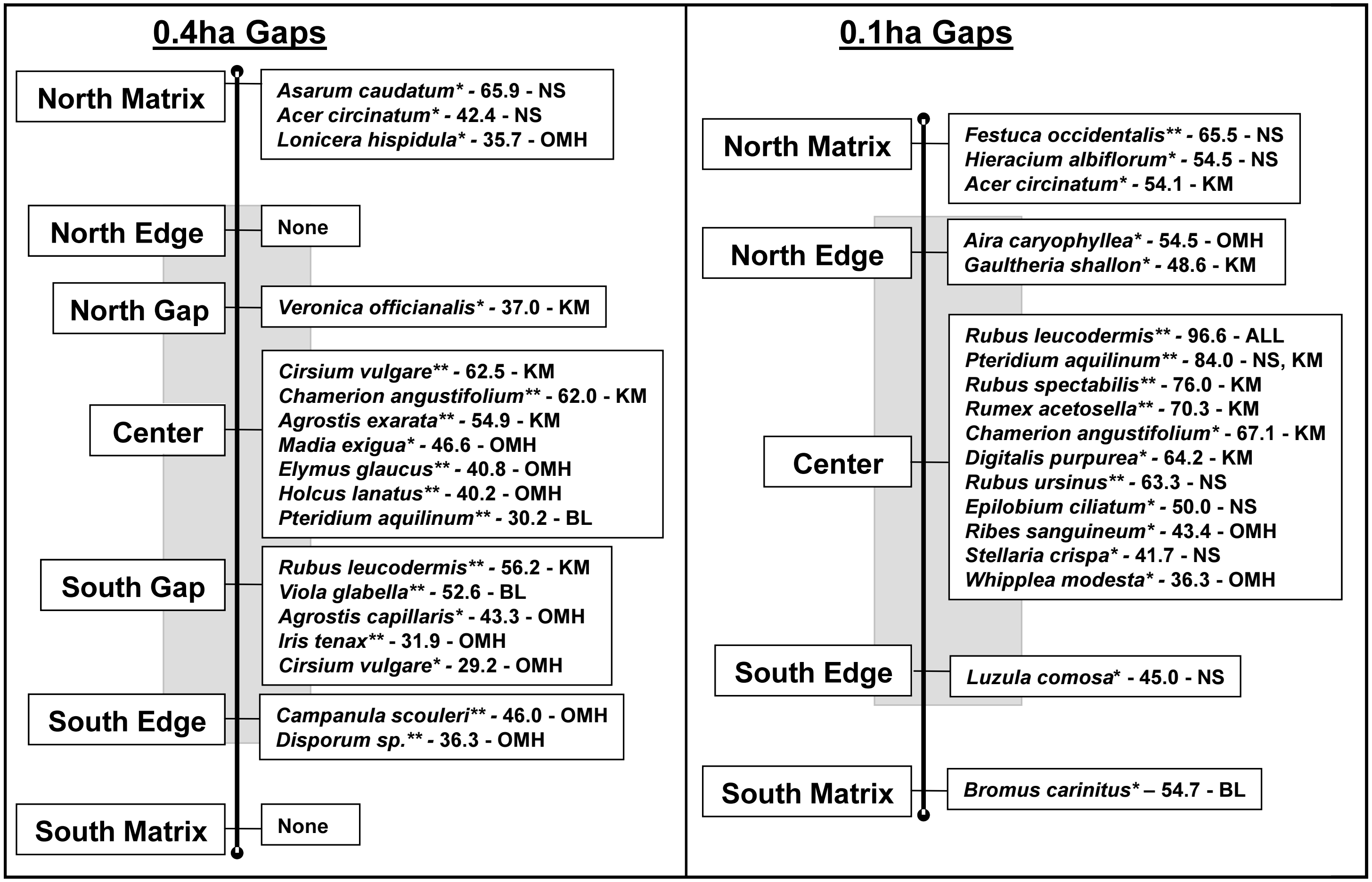

Figure 2.11. Indicator species by transect position for both gap sizes. Indicator values and site at which the species was an indicator are included after each species name. * indicates $p < 0.1$, and ** indicates $p < 0.05$.

Environmental variables and gap partitioning

Patterns in understory community composition were correlated most strongly with disturbance-related variables, but these relationships differed between gap sizes. At each site, ordination Axis 1, which reflects separation among transect positions, was strongly correlated with percent canopy openness, percent total transmitted radiation, and (negatively) leaf area index (Figures 2.1 - 2.4). Spearman correlation analyses also illustrated the influence of environmental variables as predictors of community response (Table 2.4). Mineral soil cover had the strongest correlation with the NMS community composition variable in large gaps, while leaf area index displayed the strongest correlation in small gaps. The general interactive relationship between light resource availability, percent cover of mineral soil, and the NMS community composition variable is illustrated in Figure 2.12.

Table 2.4. Spearman rank correlations of environmental variables with NMS community composition variable, bolded values represent highest correlations.

	NMS 0.4 ha		NMS 0.1 ha	
	r	p	r	p
Environmental Variables				
% Canopy Openness	-0.4715	<0.001	-0.4707	<0.001
% Transmitted Direct	-0.4050	<0.001	-0.2722	0.018
% Transmitted Total	-0.4264	<0.001	-0.3887	<0.001
% Transmitted Diffuse	-0.4024	<0.001	-0.3141	0.006
Leaf Area Index	0.4710	<0.001	0.5391	<0.001
Elevation	0.3464	<0.001	0.1829	0.116
Slope	-0.1141	0.247	-0.1422	0.224
Above Canopy Radiation	-0.0412	0.677	0.2239	0.054
Heat Load Index	0.2912	0.003	0.3162	0.006
Predicted Soil Moisture	-0.0942	0.339	0.0999	0.394
% Exposed Mineral Soil	-0.6136	<0.001	-0.4548	<0.001
Distance to Road/Skid	0.3883	<0.001	0.3212	0.005

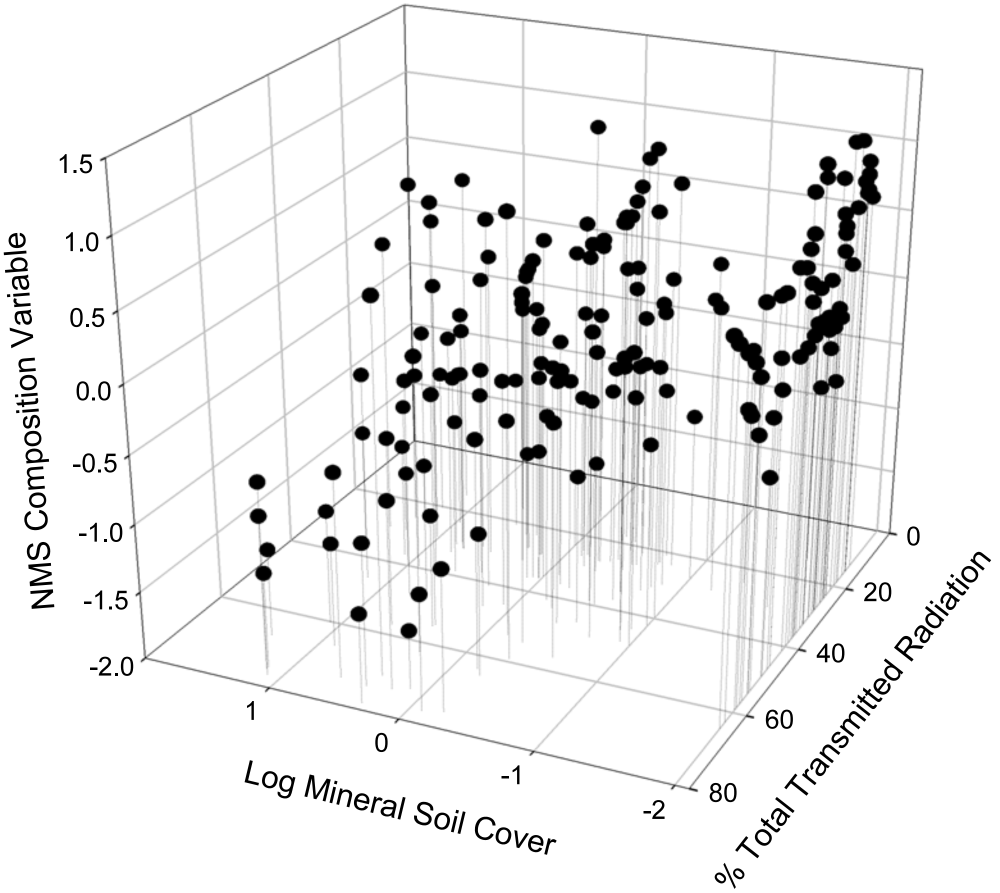

Figure 2.12. NMS Composition variable plotted against percent total transmitted radiation and Log of mineral soil cover, showing interactive relationship between disturbance and resource gradients. Lower values of the NMS variable are more "gap associated".

The regression model explaining variation in the NMS community composition variable in the large gaps had an adjusted R^2 value of 0.58. Log of mineral soil cover ($F_{1,\,101} = 49.24$, $p < 0.0001$) was the strongest predictor in the model, followed by elevation ($F_{1,101} = 29.51$, $p < 0.0001$), and canopy openness ($F_{1,101} = 21.77$, $p < 0.0001$). The final model was $Y = -0.1542 + -0.1892$ Log Min $+ -0.0184$ Canopy Open $+ 0.0004$ Elevation (SE $\beta_0 = 0.1693$, SE $\beta_M = 0.0270$, SE $\beta_C = 0.0040$, SE $\beta_E = 0.0001$). The regression model for the small gap size had an adjusted R^2

value of 0.54. The strongest predictor in this model was leaf area index ($F_{1,71}$ = 41.16, $p < 0.0001$), followed by log of mineral soil cover ($F_{1,71}$ = 34.22, $p < 0.0001$), and distance to road/skid trail ($F_{1,71}$ = 14.31, $p = 0.0003$). The final model was Y = -1.8207 + -0.0775 Log Min + 0.8136 Leaf Area Index + 0.0050 Dist (SE β_0 = 0.2432, SE β_M = 0.0133, SE β_C = 0.1268, SE β_D = 0.0013).

Cover of exposed mineral soil, indicative of the intensity of harvesting-related ground-layer disturbance, was the most powerful predictor of species composition in the large gaps. Leaf area index was the strongest predictor in small gaps. Both regression models were successful in explaining a significant portion of the variation in the NMS community composition variable.

Discussion

In the presence of harvest-related ground-layer disturbance, gap partitioning of understory species composition has apparently occurred. Conditions necessary for gap partitioning among understory plant species were met in harvested gaps, but may be rare in natural gaps in this region. Gap partitioning patterns are likely transient and their effect on the long-term species composition of these understory communities is not certain.

Gap partitioning of understory community composition

Gap partitioning seems to be an important factor in patterns of understory vegetation community composition 5 to 7 years after gap creation in large, harvest related gaps lacking a dominant clonal shrub layer. Gap partitioning appears to be a potential response of understory vegetation communities to gap formation. In harvest gaps the influence of ground-layer disturbance may promote species compositional differences, but these differences may be largely driven by resource partitioning after disturbance. Understory vegetation community composition differed by location relative to gap openings, suggesting that the species making up these communities have partitioned resources in relation to these openings (Denslow 1980, Brokaw and Busing 2000). In contrast, previous studies of understory plant responses to gap formation found little variation in community composition (Brewer 1980, Thompson 1980, Moore and Vankat 1986, Collins and Pickett 1988a, Schumann et al. 2003). In these studies understory responses were generally related to increased cover of remnant species, rather than invasion by ruderal species. However, even species cover responses were minimal in deciduous forests of Ohio (Moore and Vankat 1986), Pennsylvania (Collins and Pickett 1988a, Collins and Pickett 1988b), Ontario (Reader and Bricker 1992), and New York (Goldblum 1997). In deciduous forests, light demanding understory species with a spring ephemeral growth form can persist under an undisturbed forest canopy (Collins et al. 1985, Moore and Vankat 1986). This pattern promotes pre-disturbance communities in these forests that are well adapted to post-disturbance gap conditions, making them better able to persist in gap interiors (Collins et al. 1985). In contrast, coniferous canopy cover is persistent throughout the year, and ruderal and other light demanding species are more likely to be limited to gaps and edges (Nelson and Halpern 2005). Therefore, overstory condition prior to gap creation may be an important variable in determining the impact of gaps on understory vegetation communities. Research in coniferous forests of the Pacific Northwest has typically illustrated strong responses in understory vegetation cover related to gap creation (St. Pierre 2000, Lindh et al. 2003). In one study of understory responses to gap creation, a gap-related pattern was expressed in species cover responses that was similar to that seen in community composition in our study (London 1999). However, all of these studies investigated gaps that were both smaller and less disturbed than those in this study and none illustrated a gap partitioning response in understory vegetation communities.

Gap size partitioning also appears to occur in communities that exhibit some gap partitioning. Previous studies had found little evidence that gap-size influences understory community composition in gaps in deciduous forests (Collins and Pickett 1988a, Collins and Pickett 1988b). However, the influence of gap size has been documented on growth and fecundity of understory plants in Douglas-fir forests (St. Pierre 2000). Since these attributes affect community dynamics, one would expect that they influence vegetation composition in the long term. Compared to other experiments (e.g. (Gray and Spies 1996, 1997, Coates 2000), our study had a limited range of gap sizes and both sizes lie at the high end of the range investigated in other studies. Coates (2002) found partitioning of recruitment in large (>300m^2), but not small (<300m^2) gaps. Gray and Spies (1996) also found differences in partitioning patterns between gap sizes, in 0.2, 0.4 and 1.0 diameter to height ratio gaps, in western Oregon. However despite the lack of a wide range of gap sizes, we illustrated distinctly different patterns in compositional partitioning between gap sizes. Gap size appears to influence partitioning patterns in understory vegetation communities. Small gaps, such as those investigated in other studies, may not create strong enough gradients in resource differentiation to elicit a response in some gap associated species. We propose that gap partitioning of understory vegetation communities is limited to certain gap sizes, which would likely vary between systems, but may be somewhat consistent in the relative strength of resource gradients they exhibit.

Another factor that may influence the vegetation community and presence of gap partitioning is the age of a gap. Time since gap formation affects the strength of its influence on the environment and the understory community (Runkle 1982, Moore and Vankat 1986, Dirzo et al. 1992). Cover of understory species may vary with gap age (Moore and Vankat 1986), and it is likely that species composition would change over time in a gap environment as well (Schumann et al. 2003), especially as resource availability changes and competition results in replacement of ruderal species (Runkle 1982, Brokaw 1985, Brokaw 1987). Under open, clearcut conditions, the importance of invader species has been shown to peak around year seven post-disturbance (Halpern 1989). Gaps in our study (6-7 years post-harvest) may therefore also be near peak abundances of these species. As regeneration of canopy species fills the gaps and reduces resource availability to the understory layer, importance of light-demanding species is likely to be reduced (Halpern 1989, Lindh and Muir 2004). Therefore, gap effects on understory communities may be transient (Halpern 1989). The gap partitioning response observed here may be short lived, as is common with understory responses as stands regenerate after disturbances (Dyrness 1973, Halpern 1989).

Overall, the patterns exhibited in this study system support the hypothesis that gap partitioning may result in understory vegetation communities. This hypothesis was supported across two gap sizes, although the strength of partitioning was greater in larger gaps. This disparity suggests that gap size, and related differences in the strength of resource gradients, may be an important factor in determining whether partitioning will occur in understory communities.

Gap partitioning versus disturbance

The expression of gap partitioning in understory vegetation communities may depend greatly on physical disturbance of the ground surface and understory vegetation layers. Gap partitioning was seemingly related to an interactive effect of resource partitioning and harvesting disturbance of the ground surface and understory vegetation layers. Ruderal species, which are commonly associated with disturbance effects (Halpern 1989), were strongly related to differentiation in community composition. Many of these species are common in seed banks in Pacific Northwest forests (Halpern et al. 1999), and others are efficient colonizers (Hitchcock and Cronquist 1973). Physical harvesting impacts, such as exposure of mineral soil beds and destruction of existing vegetation, are at least partially responsible for initiating gap partitioning. This "initial disturbance effect" (sensu Roberts 2004) leads to increased availability of invasible niches. Thus gap partitioning may not be found in gaps lacking high levels of ground-layer disturbance (Moore and Vankat 1986, Collins and Pickett 1988a, Collins and Pickett 1988b). Most studies that showed no evidence of gap partitioning in tree species investigated gaps with low levels of disturbance (e.g. Runkle 1981, Brokaw 1987, Lertzman 1992, Gray and Spies 1996, 1997). However, in a study of tree regeneration in harvest gaps, Coates (2002) found evidence for partitioning of growth niches, but not regeneration niches in different gap positions. All tree species were able to germinate across a range of gap positions, but persistence of these germinants differed among gap positions and among species. A similar effect may be driving gap patterning of understory communities in this study system. Invasible niches were likely available across all gap interior positions due in part to ground-layer disturbance, however gap partitioning will have affected resource availability and micro-climatic conditions at these sites (Gray and Spies 1997, Wright et al. 1998). The survival, growth, and fecundity of species that colonize gap locations are additionally influenced by patterns in above and below-ground resource availability (Hughes et al. 1988, St. Pierre 2000). The ability of understory species to persist (and reproduce) in invasible niches may be one of the main factors affecting partitioning across these gaps over the long term.

The relationship between gap partitioning and ground-layer disturbance in influencing understory vegetation community patterns appears to depend highly on gap size. Gradients in resource availability in smaller gaps may not be powerful enough to result in gap partitioning even in the presence of significant disturbance. Bazzaz and Pickett (1980) suggest that small gaps favor established species and large gaps opportunistic, shade-intolerant species. Our results support this conclusion as ruderal, exotic, and early seral species were less prevalent in small gaps. The distributions of species groups in our study suggested either that disturbance may have had a lesser role in partitioning in the small gap size, or that resource availability was not high enough in gap locations to create the interactive effect described above. There was no evidence that large gaps contained greater harvest disturbance than small gaps, as mineral soil exposure was actually slightly higher in the small gaps (2.6%) than in the large (2.4%). Therefore, it seems likely that a lack of strong resource gradients in small gaps could be playing a role in gap-size partitioning on our sites (Collins and Pickett 1988a, Collins and Pickett 1988b).

Variation in gap partitioning between sites suggests that there is likely a strong influence of disturbance intensity and/or pre-disturbance vegetation community composition on gap partitioning effects. Portions of the OMH site were tractor logged (as opposed to cable yarding primarily employed at the other three sites), which likely resulted in more intense, widespread disturbance of ground surface and understory vegetation at this site, as was still evident in mineral soil exposure (Table A1.1). At the same time ruderal species were most abundant at this site, suggesting that interactions between seed availability and harvest disturbance resulted in vegetation composition largely patterned by disturbance (Grime 1977, Halpern et al. 1999). The community at BL was either more resistant and/or resilient to disturbance than communities at the other sites (Halpern 1988), or the disturbance intensity related to gap creation was lower. The dominance of clonal shrubs at this site suggests that the former may be true. Further support for the influence of resistance to disturbance comes from the fact that gap transects at BL did not exhibit decidedly lower levels of harvest-related ground-layer disturbance than those of the other three sites.

In summary, our results support the view that understory responses to gaps combine the effects of gap partitioning and disturbance of understory vegetation layers and ground surface. In understory vegetation communities, gap partitioning may be contingent on the occurrence of ground-layer disturbance, and although this factor falls outside of the definition of the gap partitioning mechanism, it should be included in further investigations into gap effects on understory communities.

Environmental variables and gap partitioning

The influence of an interactive relationship between ground-layer disturbance and resource gradients on understory vegetation community patterns was supported in analysis of the relationship between environmental variables and these patterns. Disturbance associated variables were strongly related to patterns in understory community composition, especially exposed mineral soil which resulted largely from harvesting related ground surface disturbance, and to a lesser extent from animal burrows (R. Fahey pers. obs.). The relationship of understory species distributions to ground disturbance in natural settings has been documented in other forest systems (Thompson 1980, Beatty 1984). For example, increased abundance of a ruderal herb was attributed to canopy gap creation, but only in the presence of animal burrow associated soil disturbance (Collins and Pickett 1988a). Another indicator of the importance of ground-layer disturbance was the association between community composition and distance to nearest road or skid trail, which was relatively strong in our study. Roads and skid trails are extreme disturbances of all vertical stand layers (Roberts 2004). These features of harvesting operations have been shown to be invasion pathways for early seral species (Berger et al. 2004). Cover of slash, which is also a component of harvest disturbance, was related to change in community composition in a study of responses of understory species to green tree retention harvests in the Pacific Northwest (Nelson and Halpern 2005). Slash cover was not strongly related to vegetation distributions in this study system, but lack of a response to this disturbance related variable is likely due to slash management (piled and burned outside the gaps) at our sites.

Resource related variables were less important in explaining patterns in species composition, however they did seem to have a strong effect on within gap patterns. Canopy openness and leaf area index were stronger predictors of community composition than light variables in our regression models, suggesting that the physical opening of the canopy and associated disturbance were more influential on species composition than increases in direct radiation availability. The physical canopy opening could be indicative of the influence of a number of resources, including nutrients, water, and diffuse radiation. Heightened levels of diffuse radiation are largely confined to the physical gap area (see Chapter 3) however this variable was not a strong predictor of understory vegetation composition in either gap size. The Mediterranean climate regime of the Pacific Northwest is characterized by seasonal drought, therefore availability of soil moisture may be important in this region (Lindh et al. 2003). Partitioning of growth and fecundity of herbaceous understory species has been related to availability of soil moisture in experimental canopy gaps (St. Pierre 2000). Lindh et al. (2003) also observed that response in understory cover to canopy gap formation was more strongly related to belowground resource availability than light availability in this region. Even in eastern deciduous forests where no pattern of seasonal drought exists, soil moisture was a major factor affecting understory cover in relation to gaps (Anderson et al. 1969, Moore and Vankat 1986). However, a study specifically investigating the influence of soil moisture on regeneration of canopy species in experimental gaps in mature forests in the Pacific Northwest did not support a dominant soil moisture effect (Gray and Spies 1997, Gray et al. 2002). These authors suggested that microsite variation superseded the larger scale effect of enhanced soil moisture availability. As discussed earlier, the limited number of canopy species in this region may provide only a crude measure of partitioning, compared to the variety of understory species (Halpern and Spies 1995, Bailey et al. 1998). However, we also did not find a strong relationship between predicted soil moisture response and community composition.

We support the notion that vegetation responses to gap-phase disturbance are determined by a combination of the effects of niche partitioning and chance. However, we also suggest that ground surface and understory vegetation layer disturbance may be an integral component in this model. The influence of ground-layer disturbance appears to allow gap partitioning patterns to be expressed in the understory vegetation community by enabling germination and growth of gap adapted species in areas affected by gap formation.

Limitations

Although the data we present strongly suggest that the understory communities at three of our study sites have been partitioned by gap formation, pre-disturbance species composition can have a profound influence on the makeup of the post-disturbance community (Hughes and Fahey 1991, Nelson and Halpern 2005). We lack specific knowledge of the pre-treatment vegetation communities at these sites. This shortcoming makes it difficult to draw conclusions about effects of gap creation on performances of individual species (Nelson and Halpern 2005). We have attempted to base our conclusions therefore on species groups, rather than individual species, as these groups may be less affected by residual bias from pre-treatment conditions.

It is also important to note that we do not have specific information on variation in soil moisture or nutrient dynamics, which could strongly influence understory vegetation communities (Canham and Marks 1985, Muller 2003). Although we estimated the influence of gap creation on soil moisture (based on Gray et al. 2002) we have no actual data from the time directly following gap creation when, conceivably, initial partitioning of the vegetation community was occurring. A complete temporal record of soil moisture response to gap formation might have exhibited a more powerful relationship (Gray et al. 2002). Also, all the data we present are merely a snapshot of the system, and we cannot account for variation in environmental factors over the life of a gap.

Conclusions

Gap partitioning in understory vegetation communities was evident in harvest gaps created in young Douglas-fir forests of western Oregon. Both resource gradients and ground-layer disturbance may be necessary for expression of gap partitioning patterns in understory communities. Gap-size partitioning was also evident and may be in part due to variation in the strength of resource gradients between gap sizes. The presence of a dominant clonal shrub layer, which can quickly expand following gap creation, may prevent the occurrence of gap partitioning, indicating that the effects of gap partitioning in understory vegetation communities may be dependent on species composition and structure. The presence of gap partitioning in understory vegetation communities may be largely dependent on the concurrent influence of gap size, ground-layer disturbance, and pre-disturbance vegetation composition. We conclude that gap partitioning of understory vegetation communities may occur in natural gaps, but only in relatively large gaps containing high levels of ground-layer disturbance. These conditions may be rare in natural forest stands of western Oregon and therefore gap partitioning might be a relatively rare occurrence in this region.

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CHAPTER 3: DETERMINATION OF GAP INFLUENCE EXTENT USING UNDERSTORY VEGETATION DISTRIBUTIONS

Abstract

Gap formation in forests can result in impacts on the forest ecosystem that extend beyond the physical boundary of the canopy opening. The extent of gap influence may affect the response of many components of forests to gap formation on a stand and landscape scale. In this study, depth of gap influence on surrounding forest was investigated using patterns in understory vegetation communities in and around 0.1 and 0.4 ha harvested canopy gaps in four young Douglas-fir (*Psuedotsuga menziesii*) dominated stands in western Oregon. Understory vegetation community composition was correlated most strongly with a "light" gap definition, based on percent transmitted direct radiation, in both gap sizes. Areas deemed to have been influenced by gap formation differed between species groups and individual gap-associated species. Gap influence on the surrounding forest matrix in this study system was minimal in terms of distributions of understory plants. Estimates of depth of gap influence on understory community composition in 0.4ha gaps were between 0 and 2m beyond the gap edge on the north side and 2 and 4m from the gap edge inside the gap on the south side. In 0.1ha gaps depth of influence was between 4 and 14m inside the gap on the north side and between 0 and 2m inside the gap on the south side. In the smaller gap size an influence of the surrounding forest extending into the gap openings was apparent. Area of gap influence on understory vegetation communities may not scale linearly with gap size as suggested by differing patterns seen between gap sizes in this study. Edge influence related to gaps was low suggesting that patch contrast between gaps and surrounding forest was low where understory communities were concerned. We hypothesize that low depth of influence levels were related in part to thinning in the surrounding forest, which opened the canopy around the gaps and resulted in less contrast between gap and forest understories.

Introduction

Canopy gaps have long been seen as an important component of forested ecosystems (Watt 1947, Bormann and Likens 1979, Spies et al. 1990). More recently creation of gaps has become a focus of managers striving to emulate natural systems (Runkle 1991, Coates and Burton 1997, Franklin et al. 2002). Canopy gaps are often considered in silvicultural prescriptions designed to produce and maintain late-successional habitat features in young forests (Hunter 1993, Cissel 2006, Beggs and Puettmann in review). As a management tool, gap creation is aimed at increasing habitat heterogeneity and diversity in stand structure (Runkle 1991, Coates and Burton 1997, Beggs and Puettmann in review), both of which can promote development of late-successional habitat conditions (Franklin et al. 2002, Muir et al. 2002).

The effects of gap creation on forest processes within the gap area, such as tree regeneration, stand structural development, and dynamics of the understory layer have been documented (Canham and Marks 1985, Collins and Pickett 1988b, Spies et al. 1990). However, gap influence is not always limited to the physical opening (Canham et al. 1990, Van Pelt 2000, Gray et al. 2002), and the extent of gap influence on the surrounding forest is less well understood (Coates et al. 1997, Menard et al. 2002). A measure of the extent of gap influence would be useful in efforts to characterize the impact of gap creation on a stand or landscape scale (Menard et al. 2002). Delineation of gap influence can be approached from three general perspectives, based around 1) physical, 2) resource, and 3) biotic measures of extent. These three methods of expressing gap influence represent increasing complexity and abstraction in the variables used to define gap influence extent. In this study, we explore the magnitude of gap influence from each of these perspectives using two different methodologies.

One approach to defining the extent of a canopy gap is as a physical area of bole or canopy removal (Runkle 1982). The classic physical definitions of gap extent are the “canopy gap”, which encompasses the land surface area within the gap projecting to the edge of the canopy of the surrounding trees, and the “extended gap” which is defined as the area extending to the bases of surrounding trees (Runkle 1982). Physical disturbance of ground and understory layers will be largely confined to this gap area, in both natural and harvest-related gaps (Coates and Burton 1997).

Another method of illustrating gap extent is utilizing definitions related to resource levels. The “light gap”, the area influenced by higher light levels related to gap formation, is one example of a resource-defined gap delineation. Although Runkle (1982) suggested that the extended gap would suffice in describing elevated light levels, we define the light gap according to measured levels of direct beam solar radiation at ground level. In the northern hemisphere, this gap delineation is centered toward the north edge of the physical canopy opening and extends into the forest matrix on the north side of the gap (Canham et al. 1990). Another possible gap definition is the “root gap”, which is the area within a gap from which neighboring tree roots are excluded following gap formation (Gray et al. 2002). Availability of a number of belowground resources is likely temporarily heightened in this area. Another resource driven gap definition is the “moisture” gap, this is the area characterized by a positive response in sub-surface soil moisture availability. Soil moisture is highest on the south side of a gap in the northern hemisphere due to the interaction between solar radiation levels and decreased root competition at that location (Wright et al. 1998, Gray et al. 2002).

Finally, it may be advantageous to define gap influence extent by investigating responses in the biota, which integrate the effects of multiple resource gradients as well as the effects of disturbance. Research approaches used to quantify gap influence extent have investigated this influence using overstory tree responses (Payette et al. 1990), regeneration responses (Kobe 1999), and modeling of tree growth and regeneration (Dube et al. 2001, Menard et al. 2002). The “release extended gap” (Menard et al. 2002) and “species extended gap” (Dube et al. 2001) concepts are examples of gap definitions produced by modeling approaches that used overstory species distributions and growth responses to delineate gap influence. Understory vegetation distributions may be another useful tool in quantifying gap influence extent. Gap definitions stemming from this metric may differ greatly from those based on overstory species responses because understory communities are generally more diverse and members of these communities are more highly specialized than those of the overstory in temperate forests (Gilliam and Roberts 1995, Halpern and Spies 1995). Therefore, small scale responses of species composition to gap formation are more likely to be quantifiable in the understory than the overstory. The use of understory species as a metric for delineating gap influence has a number of additional advantages: the response is easily measurable, can be used as indicator of wildlife habitat (Carey 2003), and can also be an indicator of general ecosystem response (Nilsson and Wardle 2005). Disadvantages in relying on understory vegetation communities to illustrate gap influence include the effects of stand history and initial condition on vegetation response (Palik and Murphy 1990, Hughes and Fahey 1991), the high degree of variability in the response (Halpern et al. 2005), and the temporally dynamic nature of the response (Halpern 1989, Roberts and Gilliam 1995).

Treating gap influence as an edge effect emanating from the gap edge into the surrounding forest is one approach to quantifying gap influence extent based on biotic responses. Determination of depth of edge influence (DEI) in forests has received a great deal of attention (Chen et al. 1992, 1995, Cadenasso et al. 2003, Harper et al. 2005), and has a strong associated methodology (Harper and Macdonald 2001, Toms and Lesperance 2003). Although these studies have generally focused on edges resulting from large natural or anthropogenic disturbances (such as clearcuts), the methods are also applicable to edges related to smaller forest canopy gaps. DEI is highly reliant on the contrast in environmental conditions between the areas separated by an edge, or patch contrast, at the edge in question. Patch contrast has been found to vary by forest type, edge orientation, disturbance agent, magnitude of disturbance, edge age, climate regime, primary disturbance regime, regional flora, and landscape heterogeneity (Cadenasso et al. 2003, Harper et al. 2005). Edge orientation has a particularly strong influence on both patch contrast and DEI (Wales 1972, Fraver 1994). In the northern hemisphere, south facing edges exhibit greater DEI than north facing ones (Palik and Murphy 1990, Burton 2002). Different local floras may also affect DEI on understory vegetation distributions (Harper et al. 2005). Magnitude of the disturbance (i.e. gap size) that resulted in edge formation can also affect edge characteristics, and thus DEI (York et al. 2003). Response parameters included in DEI studies have included: microclimate (Chen et al. 1995), tree mortality (Chen et al. 1992), tree growth (Chen et al. 1992, Laurance et al. 1998, McDonald and Urban 2004), tree species distributions (Wales 1972), tree regeneration (Chen et al. 1992), and understory vegetation (Fraver 1994, Euskirchen et al. 2001, Harper and Macdonald 2002b).

The objective of this study was to quantify extent of gap influence in a managed forest using understory vegetation communities as a metric. We assessed gap influence extent by (1) comparing the relationship of understory community parameters to the four physical and resource gap definitions presented above, the: “canopy gap”, “light gap”, “soil moisture gap”, and “root gap”, and (2) evaluating depth of edge influence emanating from gap edges on the same understory variables. Both analyses compared results between south and north facing gap edges and between gap sizes.

Methods

Site Descriptions

This study is part of the Density Management Study (DMS), which is investigating effectiveness of thinning treatments in fostering development of late successional habitat features. All study stands were even-aged and dominated by 40 to 70 year old Douglas-fir (*Psuedotsuga menziesii*) in a single canopy layer. One site (KM) had a small western hemlock (*Tsuga heterophylla*) component. We focused on four DMS sites located in western Oregon, three in the Coast Range ecoregion (Omernick 1987): Bottomline (BL), OM Hubbard (OMH), and North Soup (NS), and one in the Cascade Foothills ecoregion: Keel Mountain (KM). Sites spanned a variety of elevations, aspects, and stand histories. Site and treatment details are summarized in Table A1.1.

The study stands were treated with a thinning regime which included three sizes of circular gap openings (0.1, 0.2, and 0.4 ha). This study focused on 0.1 and 0.4 ha gaps located in stands thinned to 200 trees per hectare. Gap diameter to tree height ratios for the two gap sizes were approximately 1.0 and 2.0 respectively. Harvest treatments (including gaps) were operational in nature and therefore were not randomly assigned within the sites. Gap location was determined by harvesting constraints and not by condition of overstory or understory vegetation. Gaps that were used as landings for timber extraction were avoided in this study, but all gaps contained some ground-layer disturbance from logging operations.

Study design and data collection

Gap transects along which understory vegetation, substrates and environmental factors were sampled were established and sampled between July 1 and August 31, 2004. We sampled eight gaps (four each of 0.1 and 0.4 ha sizes) at three sites (KM, OMH, NS) and six gaps (three of each size) at the fourth site (BL), resulting in a total of 15 gaps of each size. Transects originated at the gap center and extended on both a north/northeast and south/southwest bearing beyond the gap edge (defined as the line extending between the boles of the nearest surrounding canopy trees) and 23 meters into the surrounding thinned forest matrix (Figure A2.1). Gaps were selected according to suitability for the transect layout, with the stipulation that transects avoid other gaps, leave islands (unthinned patches), or the treatment or site boundaries Understory vegetation (< 6 m in height) was sampled in plots (transect positions) made up of sets of five contiguous 4m^2 square sampling quadrates (subplots) established along the transect. Transect positions included: South Forest Matrix (SM), South Edge (SE), South Gap Interior (SG, only in 0.4 ha gaps), Gap Center (C), North Gap Interior (NG, only in 0.4 ha gaps), North Edge (NE), and North Forest Matrix (NM) (Figure A2.1). In addition, interior forest plots, defined as having no gap influence, were obtained from a stand scale study of vegetation response to thinning treatments (Cissel 2006). Plots in this survey were randomly located within the DMS thinning treatments and contained four 18.55m^2 circular vegetation sampling subplots within a 0.1ha plot area. Plots used in this capacity were limited to those that were 30 meters or more from any natural or management related gap greater than or equal to 0.1 hectares in size.

Ocular estimates of percent cover were made for all vascular plant species (with cover < 6m in height) in each subplot in both the transect survey and the stand scale survey. Taxonomic nomenclature follows the USDA Plants Database (USDA-NRCS 2005). Maximum cover for each species was 100 percent while the cumulative cover of all plants could exceed 100 percent due to multiple vegetation layers. Percent cover was also estimated for growth form classes: ground-dwelling lichen, ground-dwelling bryophyte, fern, forb, graminoid, shrub, hardwood, and conifer.

Hemispherical canopy photographs were taken at subplot centers in order to characterize the understory light environment. To avoid influence of ground vegetation, the camera was positioned at 1.5 m height. We used a Nikon Coolpix 4500 digital camera with FC-E8 Fisheye Converter Lens Attachment. Photographs were captured in black and white or on "high contrast" setting to increase the distinction between sky and foliage and to reduce effects of chromatic aberration associated with digital photography (Frazer et al. 2001). Photographs were taken at dawn, dusk, or on days with uniform cloud cover to further reduce effects of chromatic aberration and increase contrast between foliage and background sky.

Data analysis

Light availability

Photos were analyzed using Gap Light Analyzer 2.0 (GLA; Frazer et al. 1999). We used an alternative projection function described by Frazer et al. (2001) to minimize lens projection distortion. A third order polynomial was used to describe the projection:

$$[1] \qquad Y = 6.6380X - 0.0025X^2 - 2.4014E - 0.5X^3$$

$$0^\circ \leq X \leq 90^\circ$$

where, Y is the radial position of a projected point measured in pixels from the optical center of a full-resolution (1600 × 1200 pixels) digital image, and X is the angular distance (◦) from the lens' optical axis to a point located in the hemispherical object region. Photos were analyzed using GLA and estimates of percent canopy openness, leaf area index integrated over the zenith angles 0-60º, transmitted direct, diffuse, and total solar radiation (mol/m^2/d), and percent transmitted direct, diffuse, and total solar radiation were obtained using this program.

Correlation analysis

To assess the fit of our data to the four physical and resource gap extent definitions described above (Canopy, Light, Root, and Moisture), we used a correlation analysis approach. We used Spearman Rank correlations (Gotelli and Ellison 2004) to compare variables based on the four gap definitions with a set of understory community variables which related community composition and diversity. Each of the four gap definition variables was defined using either a measured or estimated resource parameter. The canopy gap variable was defined using values of percent transmitted diffuse radiation (Figures 3.1 and 3.2). The light gap variable was defined using the values of percent transmitted direct radiation (Figures 3.1 and 3.2). The root gap was defined as extending 15m from the gap edge into the gap on both sides of the gap. For the root gap variable, plots in the area beyond 15m (in the gap center) were assigned a value of 0, and all other plots were assigned values based on their distance from this central "rootless" area. Root gap extent was based on upper estimates of root extent derived from the literature (Brockway and Outcalt 1998). However, lower values for root extent are common in the literature and may be more similar to our canopy gap definition (Wilczynski and Pickett 1993, Taskinen et al. 2003). The moisture gap was defined using predicted soil moisture values based on the results of Gray et al. (2002). We used Spearman Rank correlations (Gotelli and Ellison 2004) to compare these resource-based gap definition variables with the set of understory community variables described below.

Critical values analysis

To directly assess depth of gap influence we employed the Critical Values Approach of Harper and MacDonald (2001, 2002a). This approach uses randomization tests to compare mean values of response variables at different distances along transects to values obtained from reference (interior) forest plots. Critical values of response variables were the 2.5 and 97.5 percentiles of 5000 permuted means, and a significance level of $\alpha = 0.01$ was used to evaluate our results. Mean values of response variables on transects were considered significantly different from reference forest levels if they lay outside these critical values (Harper and Macdonald 2001). Depth of edge influence is defined as the location where two or more consecutive values fall outside the critical values threshold (Harper and Macdonald 2001). This analysis was performed on the same set of community variables examined in the correlation analysis (outlined below).

Vegetation community variables

The first vegetation community variable that was analyzed was a univariate community composition variable, obtained from Non-metric Multidimensional Scaling (NMS; Kruskal 1964, McCune and Grace 2002) ordination of the full set of transect plots, at all sites, and for both gap sizes, in species space. All ordinations were run using the "slow and thorough" autopilot setting in PC-ORD v4.1 (McCune and Medford 1995) with "random" starting configurations using Sorensen's distance measure. Each ordination was rotated to maximize the amount of community variation explained by the first axis, scores from this axis were then used as a univariate community response variable, known hereafter as the NMS community composition variable. In order to obtain scores for reference forest interior plots in the ordination space defined by the transect data, we used the NMS Scores procedure in PC-ORD v4.1 (McCune and Medford 1995). This procedure fits new plots into an existing ordination space using an iterative approach to finding the best fit position for each new plot individually (McCune and Grace 2002). Use of this procedure allowed us to define the ordination space based on the data of interest (transects), while utilizing plots from the larger stand survey as reference plots.

We also investigated species diversity using patterns in Simpson's diversity index (Simpson 1949), which was calculated as

$$[2]\ D = 1 - \sum_{i=1}^{s} p_i^{\ 2}$$

where p_i is the proportion of total cover in species i and s is the total number of species (Magurran 2004). In this form, this measure represents the likelihood that two randomly chosen units of cover will belong to different species (McCune and Grace 2002). For the reference plots, values of Simpson's diversity measure were adjusted to the mean of the forest matrix transect plots to account for difference between the plot sizes in the two surveys. For each site, the mean of D for the reference plots was divided by the mean of D for the forest matrix position transect plots. The value of D for each reference plot was multiplied by the number obtained above to create a scaled value of D for each reference plot. We also examined distributions of disturbance response strategy groups, defined as: competitor, ruderal, and stress tolerator (Grime 1977). Species were assigned to groups based on life history characteristics, shade tolerance, and disturbance response strategies (full species list and classifications are found in Table A4.1). In addition, we investigated the response of some individual species that were flagged as indicators of the gap interior using Indicator Species Analysis (see Chapter 2).

Results

Light availability and canopy openness

Light availability in canopy gaps varied as a function of gap size and gap edge orientation. Estimated percent transmitted radiation was consistently higher at north edge positions than south edges in the large gap size. The extent of heightened radiation in the adjacent forest was also greater in larger gaps (Figures 3.1 and 3.2). Percent transmitted direct radiation was responsible for this pattern, as diffuse light exhibited a symmetrical distribution (Figures 3.1 and 3.2). As expected, canopy openness exhibited much greater gap related enhancement in large gaps. The pattern of greater canopy openness was symmetrical between edge orientations in both gap sizes (Figures 3.1 and 3.2).

Correlation analysis

In the correlation analysis, variation in species composition was related to the light gap (defined by availability of direct radiation) in both gap sizes, but individual species and species groups were generally correlated with the canopy and root gaps. In both gap sizes, the light gap definition was most strongly correlated with the NMS community composition variable (Tables 3.1 and 3.2). The stress-tolerator group was also most highly correlated with the light gap definition in both gap sizes. None of the gap indicator species were correlated strongly with the light gap definition though.

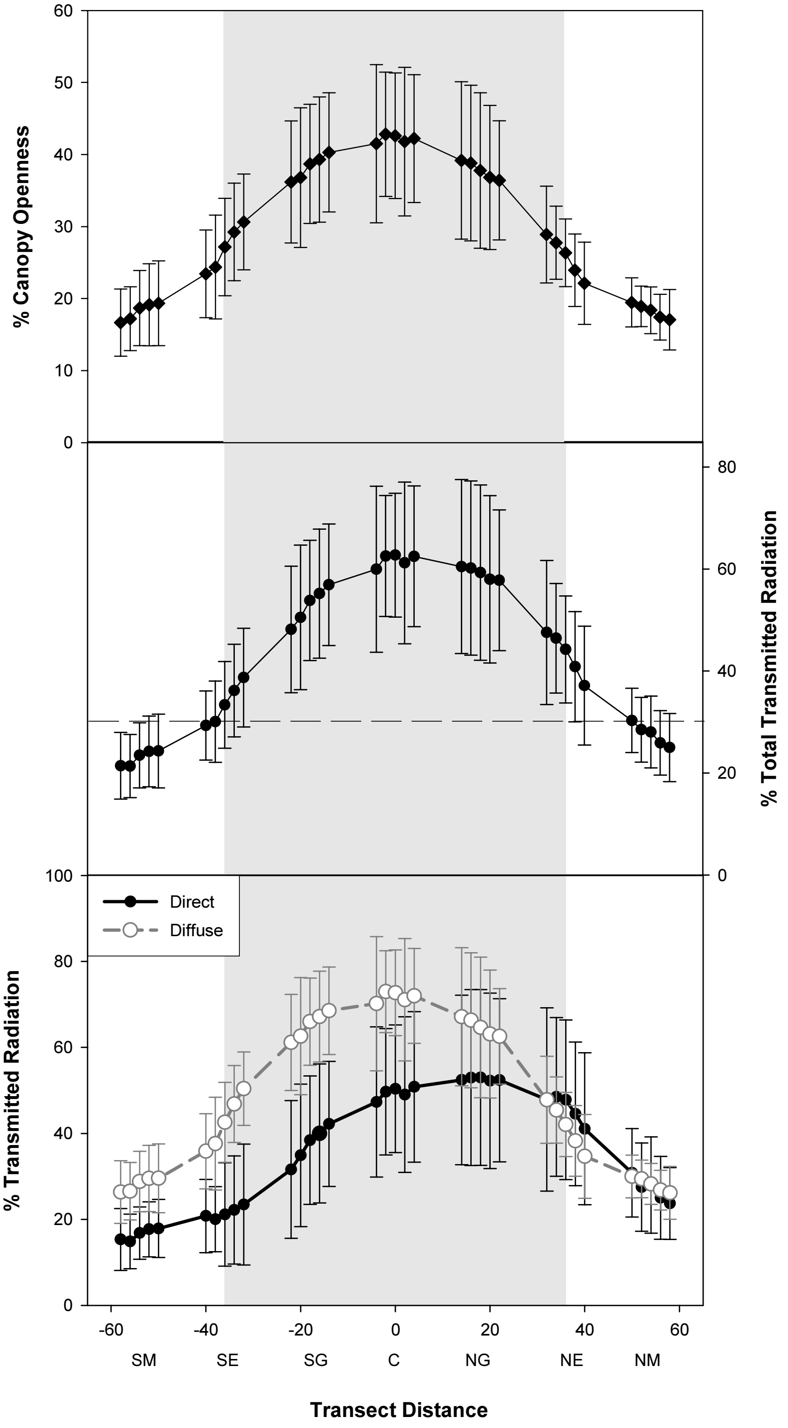

Figure 3.1. Light analysis results for 0.4ha gap size. Dotted line represents cutoff used to determine northward extent of “light gap” definition. Gray shaded areas represent gap interior. Transect distance in meters on the X axis for all.

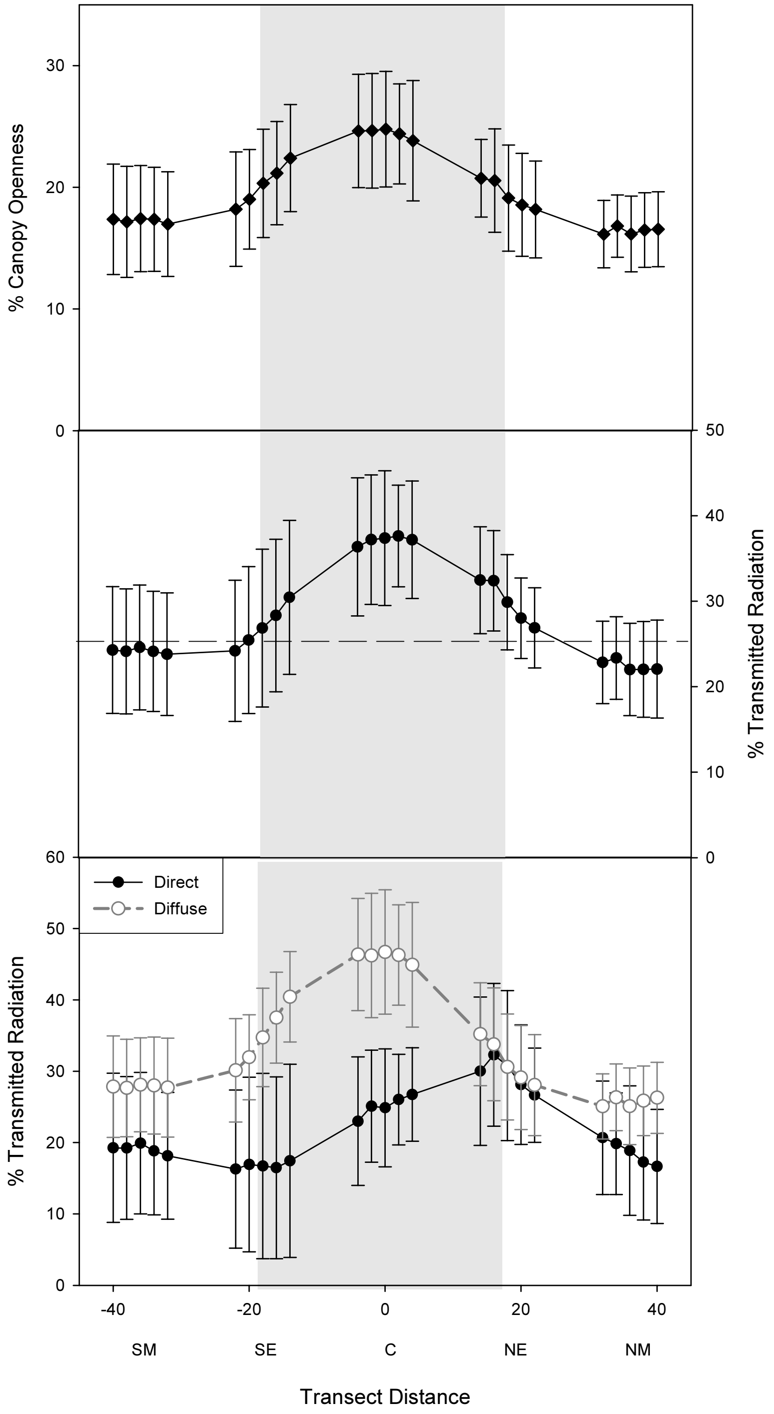

Figure 3.2. Light analysis results for 0.1ha gap size. Dotted line represents cutoff used to determine northward extent of "light gap" definition. Gray shaded areas represent gap interior.

Table 3.1. Spearman rank correlations of understory community variables, species groups and indicator species with gap definition variables in large (0.4ha) gaps. Bolded values represent strongest correlation for each community variable. All correlations except those with * were significant at $p < 0.05$.

	Light	*Canopy*	*Moisture*	*Root*
NMS Scores	-0.3245	-0.3171	-0.0389*	0.0740*
Simpson Diversity	0.1647	0.2806	0.2495	-0.2807
Ruderal	0.4519	0.5714	0.3241	-0.5363
Competitor	0.2209	0.4253	0.2875	-0.4630
Stress-tolerator	-0.3296	-0.1995	0.0195*	0.1228
Aira caryophyllea	0.4483	0.4829	0.2382	-0.3457
Chamerion angustifolium	0.0989	0.1998	0.2329	-0.3010
Crepis capillaris	0.1922	0.2438	0.1446	-0.2256
Digitalis purpurea	0.0406*	0.1344	0.1479	-0.2699
Elymus glaucus	0.3545	0.4204	0.2642	-0.3466
Epilobium ciliatum	0.0798*	0.2748	0.3097	-0.3225
Holcus lanatus	0.2117	0.3382	0.2857	-0.3312
Pteridium aquilinum	0.0825*	0.1972	0.1256	-0.2764
Rubus luecodermis	0.2426	0.3739	0.2974	-0.4147
Rubus ursinus	0.0997	0.3122	0.2763	-0.3407

Table 3.2. Spearman rank correlations of understory community variables, species groups and indicator species with gap definition variables in small (0.1ha) gaps. Bolded values represent strongest correlation for each community variable. All correlations except those with * were significant at $p < 0.05$.

	Light	*Canopy*	*Moisture*	*Root*
NMS Scores	-0.2790	-0.2478	0.0932*	0.0278*
Simpson Diversity	0.1672	0.2008	0.0860*	-0.1646
Ruderal	0.1827	0.5048	0.2681	-0.4914
Competitor	0.1520	0.4281	0.2477	-0.3912
Stress-tolerator	-0.1469	-0.0815*	0.1357	-0.0204*
Chamerion angustifolium	0.0051*	0.1748	0.1714	-0.2701
Epilobium ciliatum	-0.0276*	0.2033	0.1917	-0.2308
Pteridium aquilinum	-0.0107*	0.1052	0.1655	-0.1773
Rubus luecodermis	0.0397*	0.3435	0.3336	-0.4602
Rubus ursinus	0.1754	0.2472	0.1402	-0.2800
Anaphalis margaritacea	0.0974*	0.2928	0.1897	-0.3187
Claytonia siberica	-0.0371*	0.1625	0.2287	-0.1868
Rumex acetosella	0.1376	0.1708	0.0389*	-0.1976
Rubus spectabilis	-0.1037	0.1522	0.2265	-0.1594

The strongest correlations seen in this analysis were between the ruderal group and the canopy gap (defined by diffuse radiation availability) in both gap sizes (Tables 3.1 and 3.2). In the large gaps, a number of the gap indicator species, three of which were grasses (*Elymus glaucus, Holcus lanatus,* and *Aira caryophyllea*) and the other of which was a ruderal forb (*Crepis capillaris*), were also highly correlated with this definition. In the small gaps, the competitor group was most strongly correlated with the canopy gap definition, but none of the gap indicator species exhibited this correlation.

The root gap and moisture gap exhibited the highest correlations with the majority of the gap indicator species that we investigated in this analysis. Few of the correlations were very strong, with the strongest being the correlation between *Rubus luecodermis* and the moisture gap in both gap sizes (Tables 3.1 and 3.2).

Critical values analysis

Gap influence on the composition of the understory vegetation community was largely limited to the extended gap, according to critical values analysis of the NMS scores variable. The extent of gap influence, as defined by the location where NMS scores reached the critical values threshold for no difference from the reference forest condition, differed between gap sizes and edge orientations (Figures 3.3 – 3.6). In large gaps (0.4 ha), depth of gap influence was limited to between 0 and 2m beyond the edge into the forest matrix on the north edge transects, and between 2 and 4m from the gap edge inside the gap on the south edge transects (Figures 3.3 and 3.5). The extent of influence was reversed by edge orientation in the 0.1ha gaps, where depth of gap influence was between 4 and 14m inside the gap edge on the north edge and between 0 and 2m inside the edge on the south edge (Figures 3.4 and 3.6).

Actual depth of gap influence on the NMS community composition variable differed between sites, but the general pattern of differentiation between gap and non-gap locations was evident in both gap sizes and at all sites (Figures 3.7 and 3.8). However, differentiation of gap plots from reference forest conditions was more common and more extreme at some sites than at others. Patterns of understory community composition across transects at the four sites are presented in Figures 3.7 and 3.8.

Edge effects as evident in understory plant diversity showed more complex patterns. Simpson's diversity index was lower than reference levels at edge locations in both gap sizes, and higher than reference in the center and south gap locations in 0.4ha gaps (Figures 3.3 – 3.6). As with the NMS variable, gap influence on species diversity was skewed south in the 0.4ha gaps (Figures 3.3 and 3.5) and north in the 0.1ha gaps (Figure 3.4 and 3.6). Gap interior influence on species diversity was obvious only in the larger gap size and was limited to the gap center and south gap positions (Figures 3.3 and 3.4).

Depth of gap influence differed among life history groups and responses of these groups varied between gap sizes and edge orientations (Figures 3.9 and 3.10). The ruderal and competitor species groups showed strong gap influence in both gap sizes, but this effect extended into the forest understory only in the large gaps (Figures 3.3 and 3.9). In both gap sizes, the stress tolerator group was below reference forest levels on the north side of transects, but not on the south side (Figures 3.9 and 3.10).

Patterns in depth of gap influence for indicator species differed between species, although broad patterns were discernable. In general, in both gap sizes, higher than reference abundance of gap indicator species extended farther from gap center on the north side of the transect than on the south side. Also, competitor species such as *Pteridium aquilinum* and *Rubus ursinus* (Figures 3.11 and 3.13) occurred at higher levels than in the forest matrix farther from gap center than did ruderal species such as *Aira caryophyllea* and *Anaphalis margaritacea* (Figures 3.12 and 3.14).

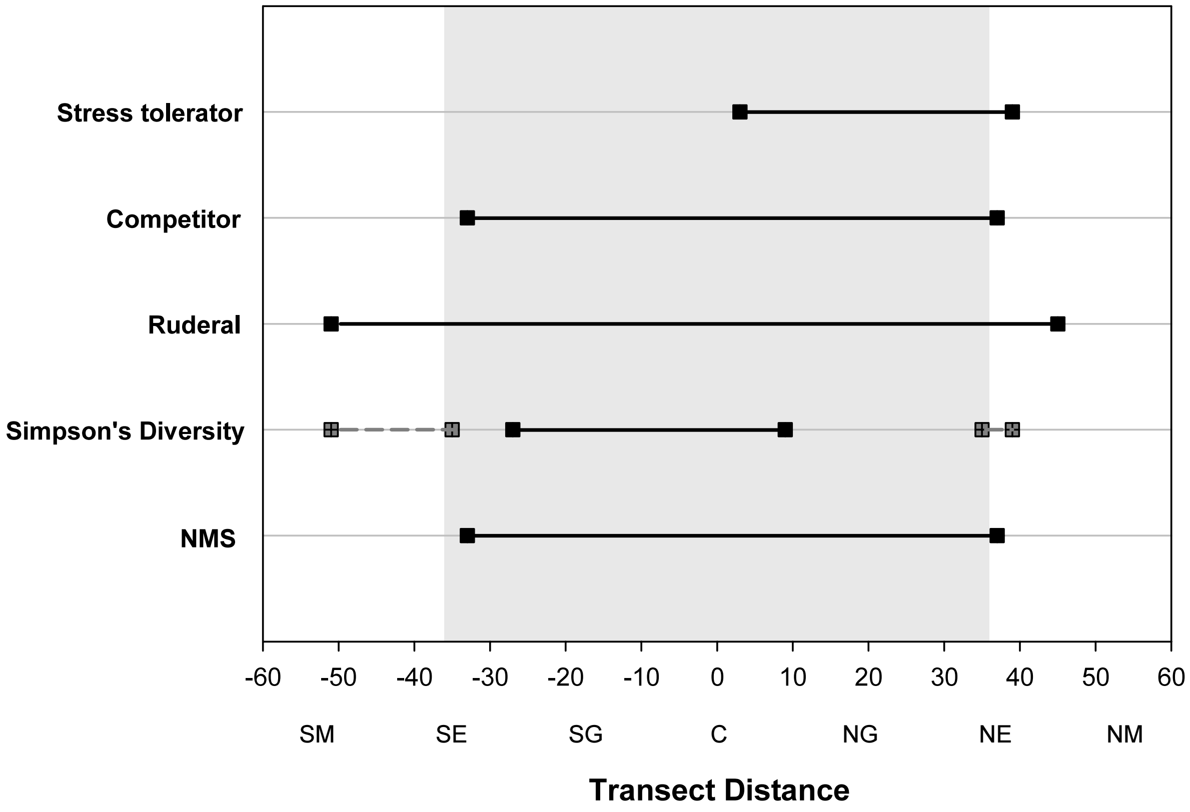

Figure 3.3. Depth of edge influence for NMS community composition variable, diversity, and Grime (1977) strategy groups in 0.4ha gaps. Gray area represents physical gap opening (extended gap). Black lines represent areas along transects at which each variable lay outside critical values for reference forest plots. Gray dotted lines represent non gap interior related departures from reference forest levels.

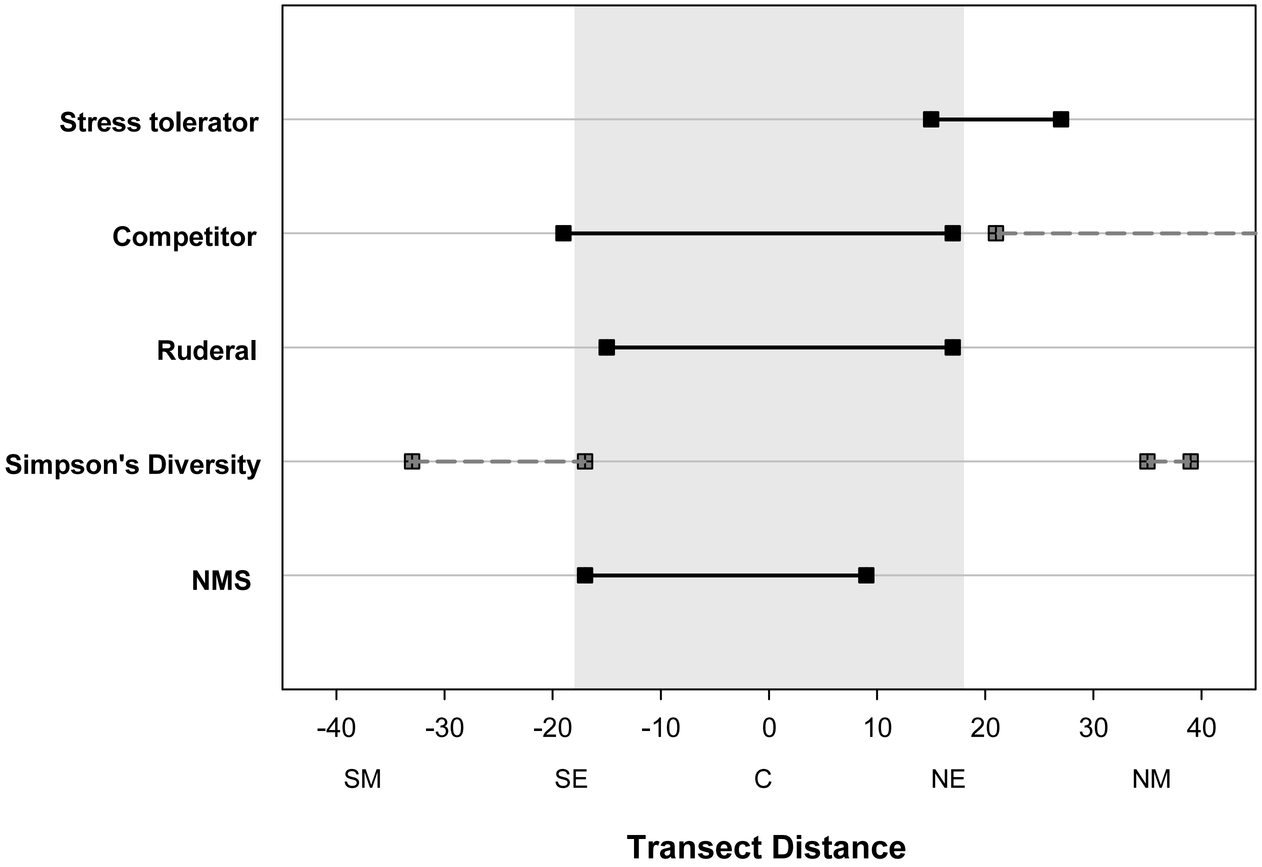

Figure 3.4. Depth of edge influence for NMS community composition variable, diversity, and Grime (1977) strategy groups in 0.1ha gaps. Gray area represents physical gap opening (extended gap). Black lines represent areas along transects at which each variable lay outside critical values for reference forest plots. Gray dotted lines represent non gap interior related departures from reference forest levels.

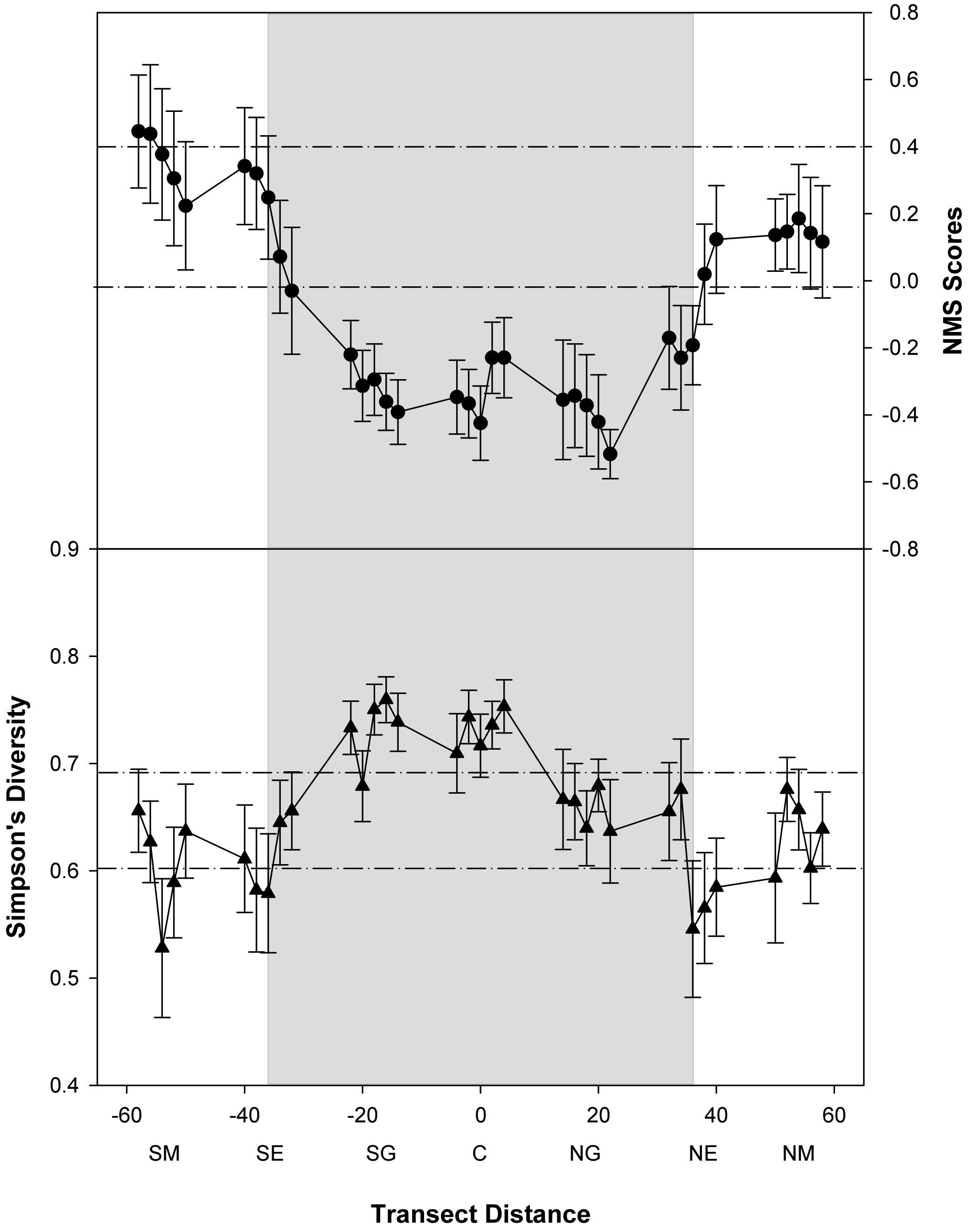

Figure 3.5. Mean values of NMS community composition variable and Simpson's diversity index across 0.4ha gaps. Bars represent standard errors. Gray shaded areas represent gap interior. Dotted lines represent critical values for each variable.

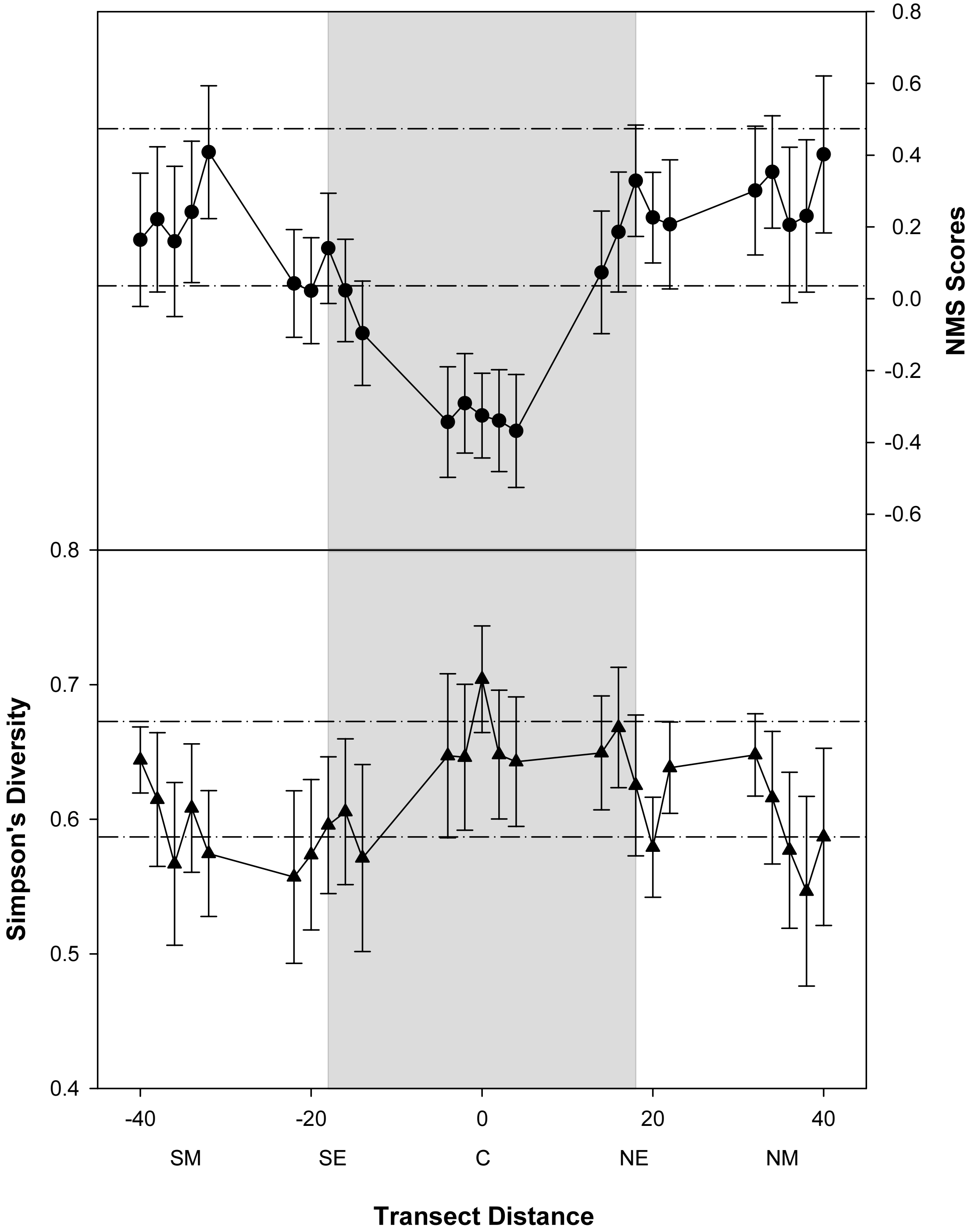

Figure 3.6. Mean values of NMS community composition variable and Simpson's diversity index across 0.1ha gaps. Bars represent standard errors. Gray shaded areas represent gap interior. Dotted lines represent critical values for each variable.

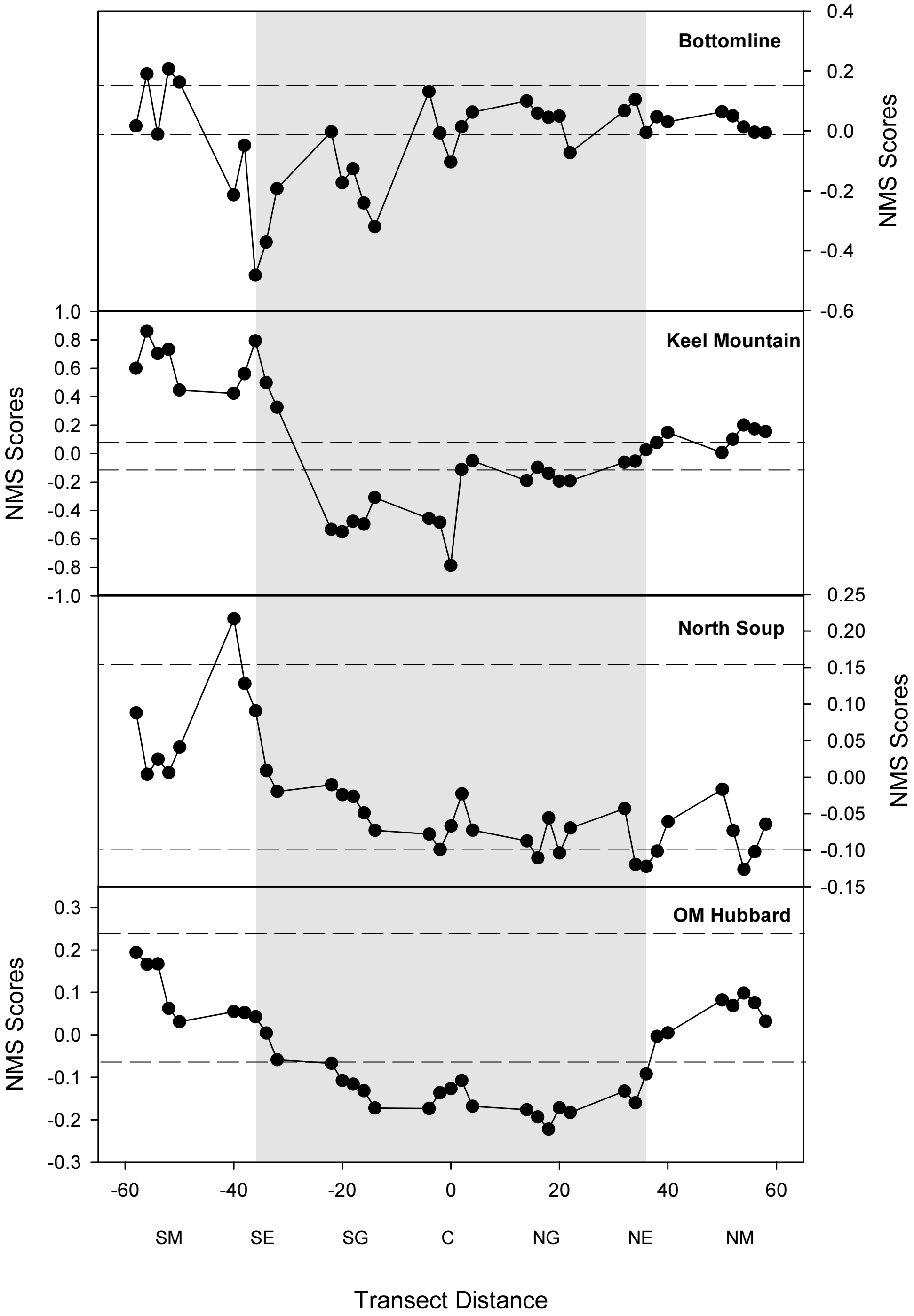

Figure 3.7. Mean values of NMS community composition variable across 0.4ha gaps for each site. Gray shaded areas represent gap interior. Dotted lines represent critical values for community composition variable.

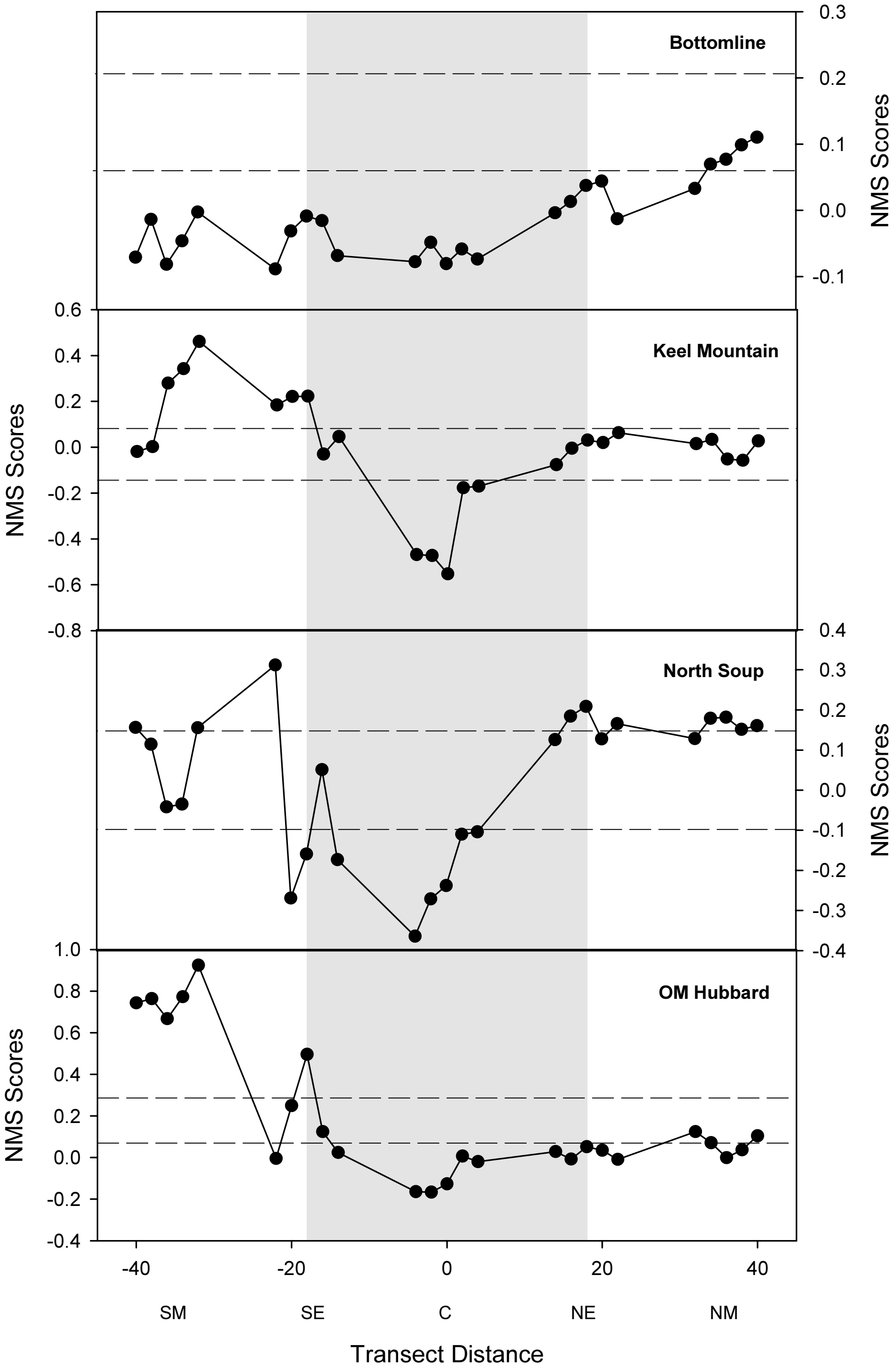

Figure 3.8. Mean values of NMS community composition variable across 0.1ha gaps for each site. Gray shaded areas represent gap interior. Dotted lines represent critical values for community composition variable.

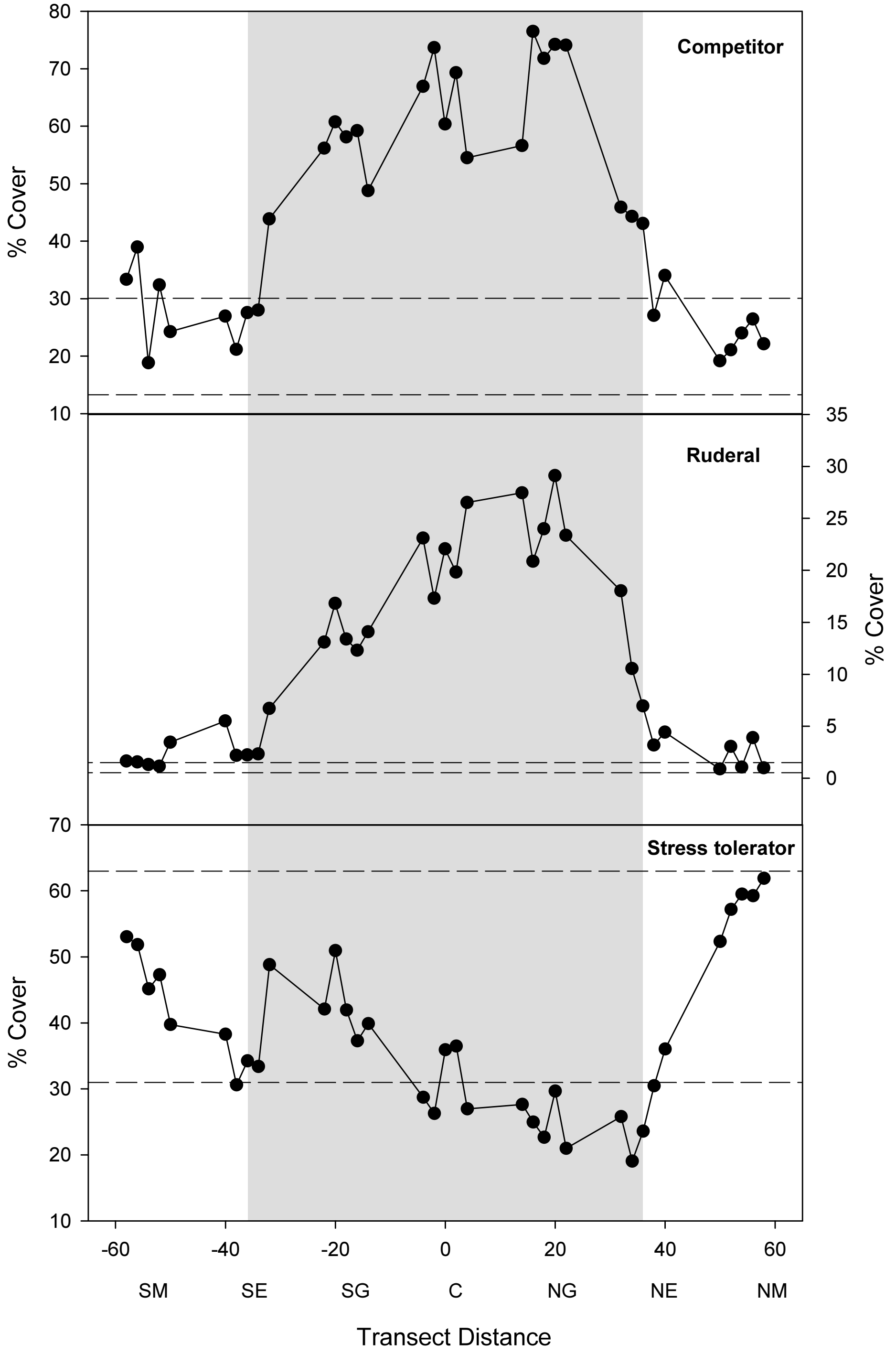

Figure 3.9. Mean cover of Grime (1977) strategy groups by transect position in 0.4ha gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for each group.

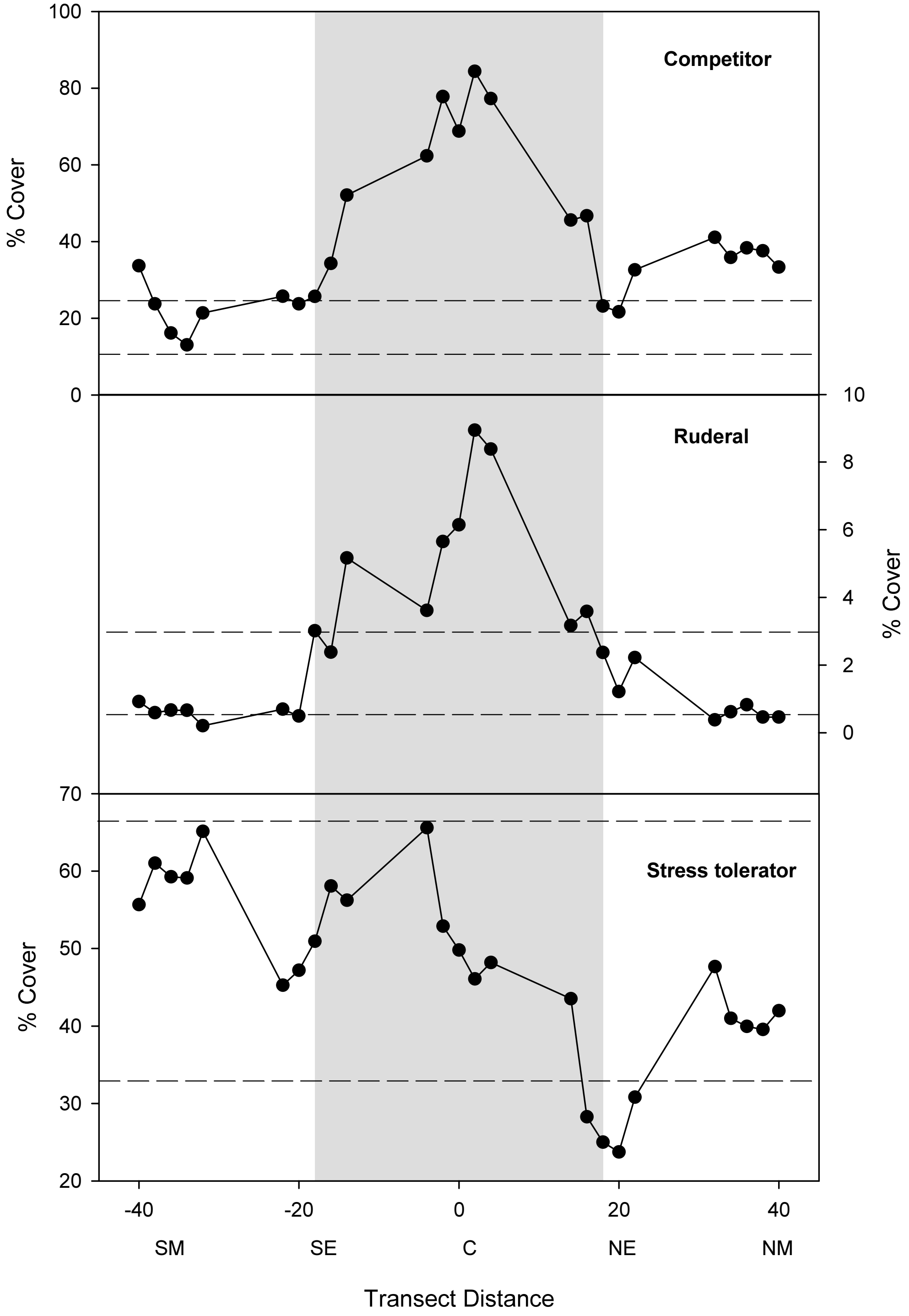

Figure 3.10. Mean cover of Grime (1977) strategy groups by transect position in 0.1ha gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for each group.

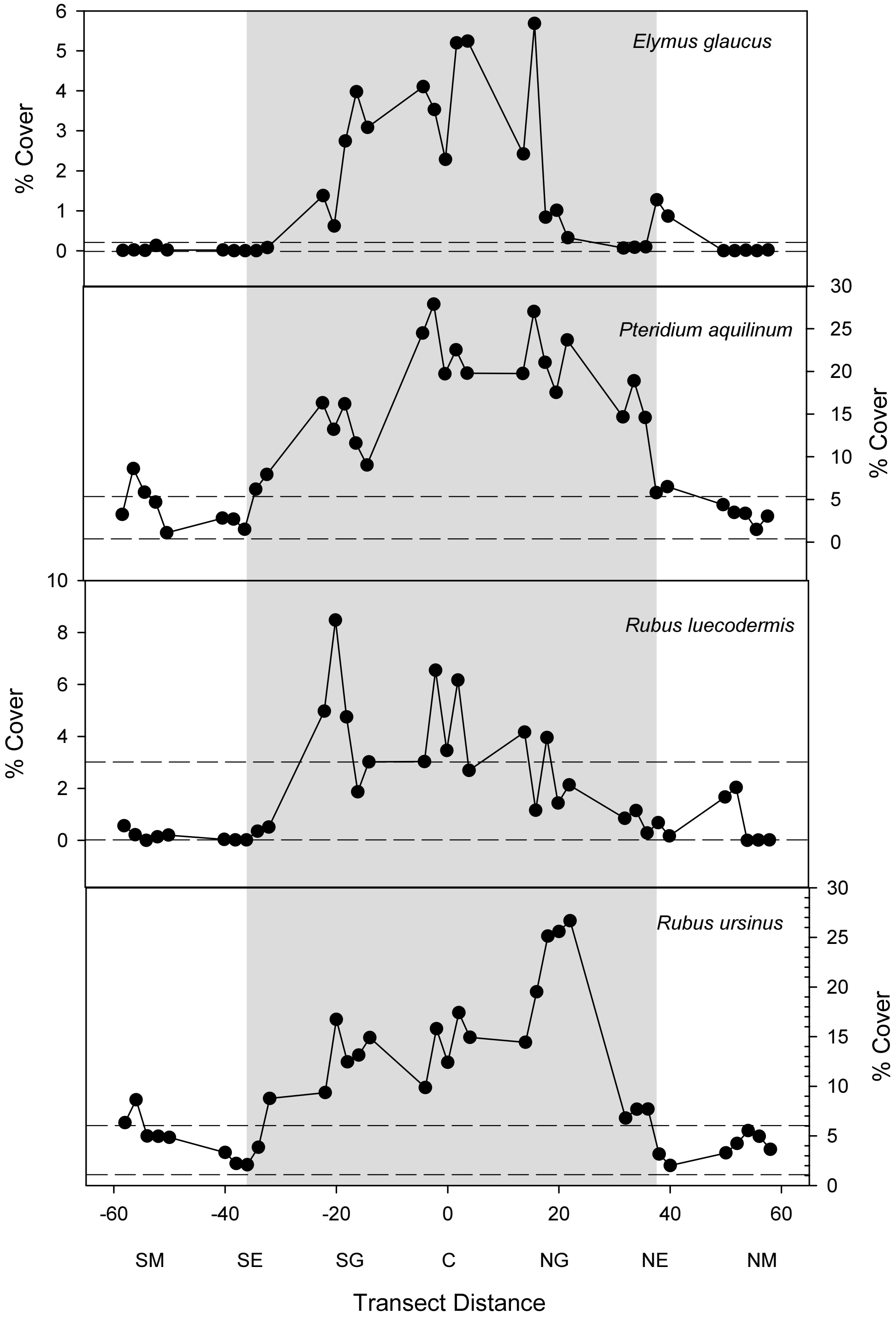

Figure 3.11. Mean cover of gap indicator species by transect position in 0.4ha gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for each species.

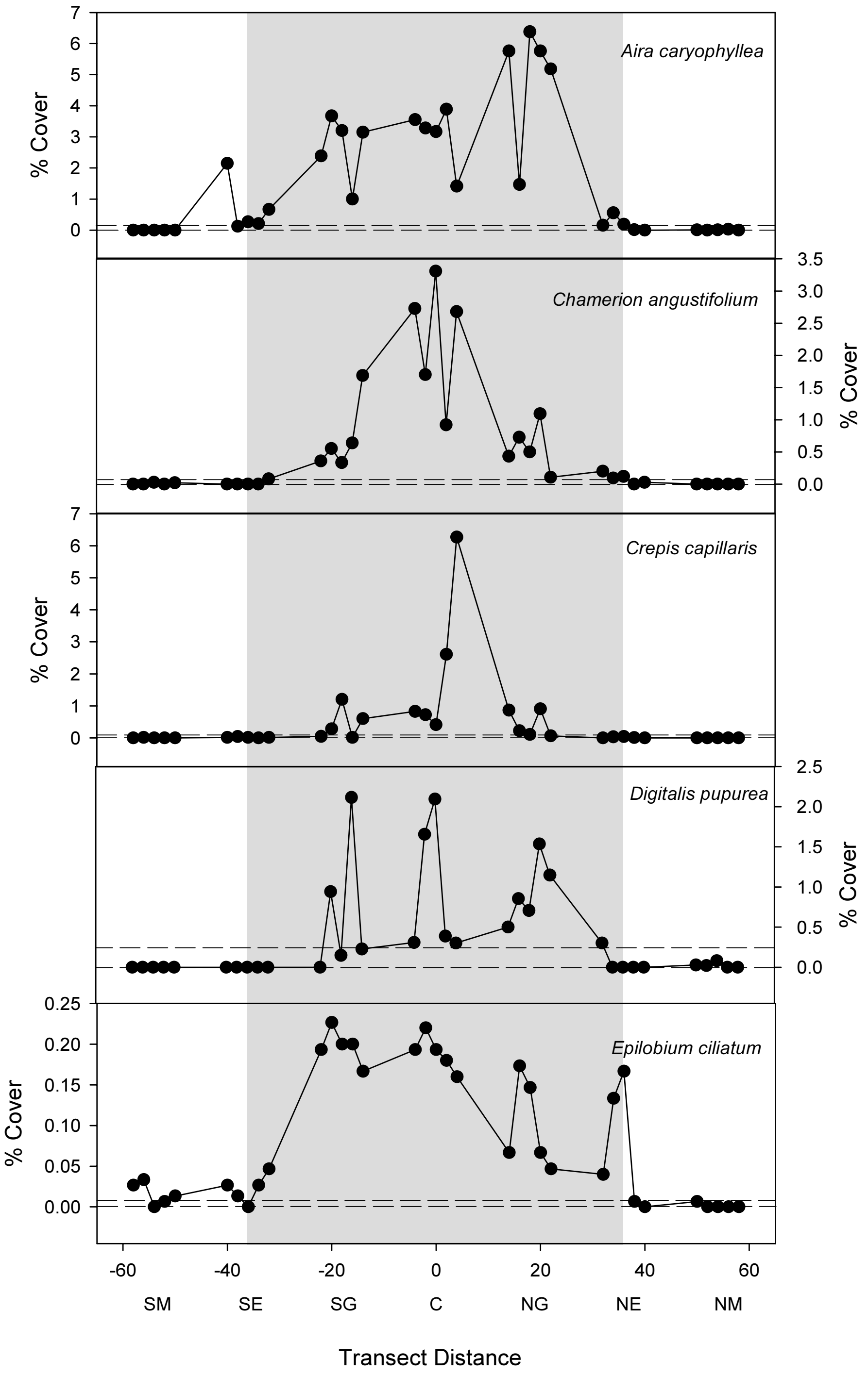

Figure 3.12**.** Mean cover of gap indicator species by transect position in 0.4ha gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for each species.

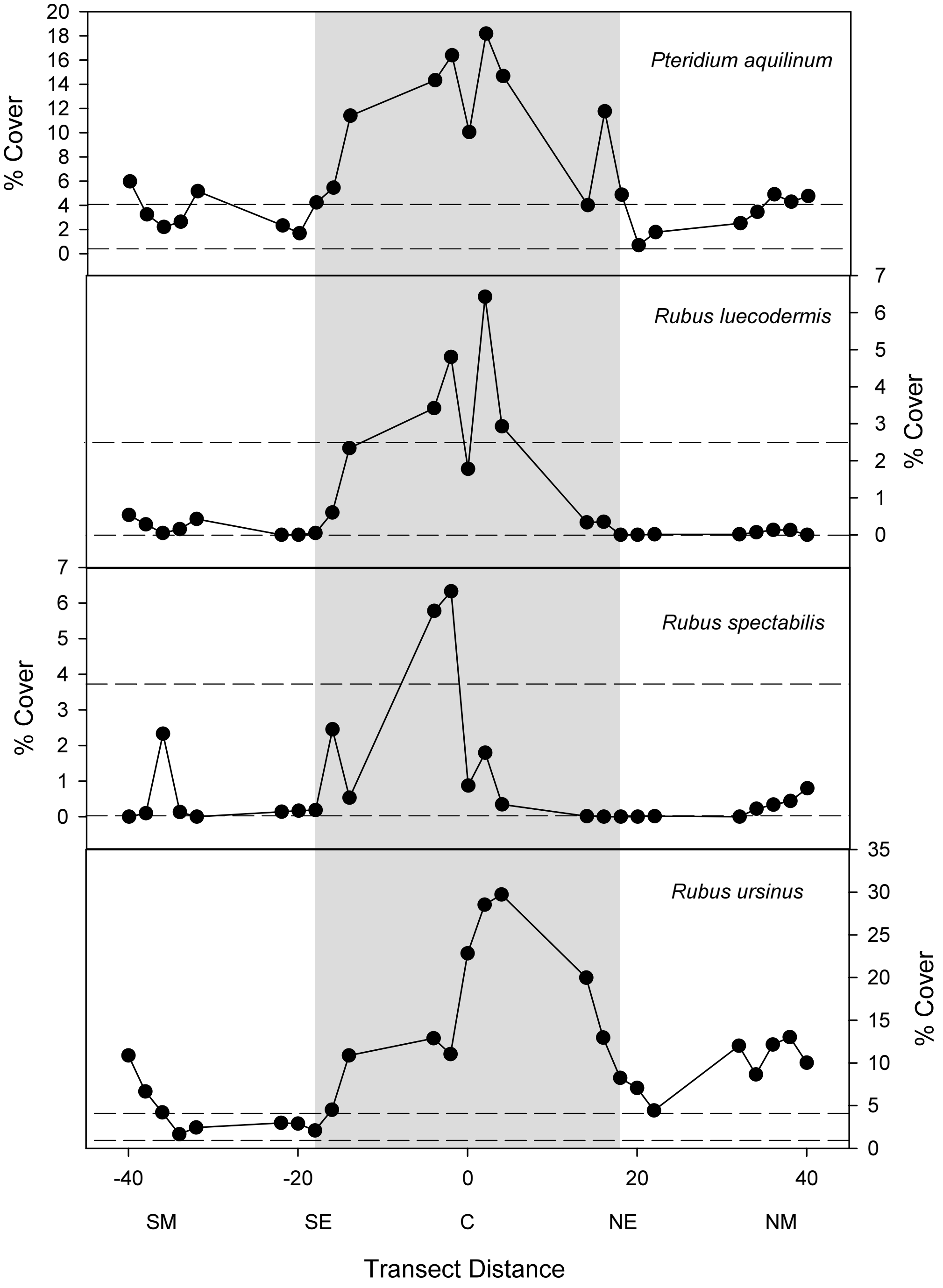

Figure 3.13. Mean cover of gap indicator species by transect position in 0.1ha gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for each species.

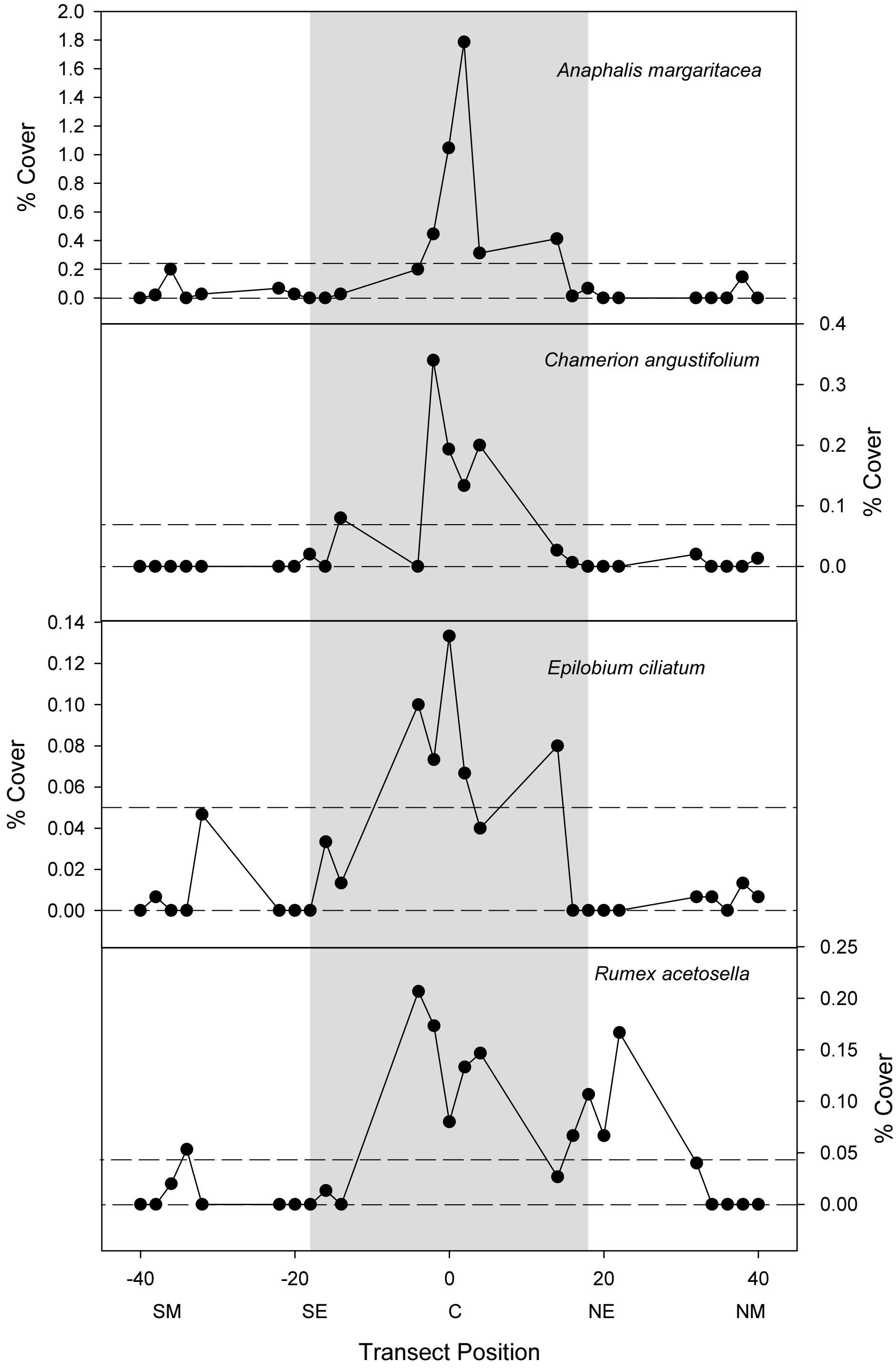

Figure 3.14. Mean cover of gap indicator species by transect position in 0.1ha gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for each species.

Discussion

The influence of gap creation on understory vegetation communities in the forest surrounding gaps may be low in young, thinned Douglas-fir forests of western Oregon. Stand and landscape level responses to gap formation could be affected by this low influence. Area of gap influence on understory vegetation seems to be highly dependent on gap size, and may not scale linearly with variation in gap size. Extent of gap influence on understory vegetation appears to be a useful metric for delineating gap influence. However, the high degree of variability in the response of understory vegetation distributions to gap formation may limit the functionality of this measure.

Gap influence extent

We suggest that gap definitions based around a single resource may be misleading, and that definitions based around biotic responses are more useful in delineating gap influence. Extent of gap influence as determined by understory vegetation community composition generally exhibited low correlation with resource-based gap definitions. This lack of correlation could be related to the fact that interactions among multiple resources often influence understory plant species distributions (Collins et al. 1985, Roberts and Gilliam 2003). In addition, factors not directly related to resource gradients such as physical disturbance and propagule availability may have had a significant influence on understory species composition (Beatty 1984, Collins and Pickett 1988a, Collins and Pickett 1988b). The distribution of plant species may be strongly influenced by ground-layer disturbance which can open growing space and create safe-sites and invasion niches inside the “physical” gap (Coates and Burton 1997, Gray and Spies 1997, also see Chapter 2). In similar forest ecosystems, Nelson and Halpern (2005) also found a relationship between harvest disturbance and edge effects. The “release extended gap” concept of Menard et al. (2002), which is roughly equivalent to our light gap definition, may be somewhat appropriate for describing understory community composition. This conception of gap influence would encompass an area as much as four times that of the extended gap (Menard et al. 2002), but may be valid only in certain gap sizes. No single gap definition appears to be appropriate in describing gap influence on understory vegetation communities across a range of gap sizes and environmental conditions.

In general, gap influence on understory vegetation communities may not extend greatly beyond the physical canopy area. DEI emanating from harvested gaps in our study was similar to that found at other temperate forest edges when cover or composition of understory species was measured (Euskirchen et al. 2001, Harper and Macdonald 2002b). In large gaps, only a very small area beyond the north edge exhibited understory community composition similar to that found inside the gaps. The small skew to the north suggests a light driven response, a result that is backed by the finding that community composition was most correlated with the light gap definition. Our results suggest that Runkle's (1982) "extended gap" definition is not entirely appropriate for assessing light availability influence on understory species composition. A modified version of the extended gap, offset slightly to the north, may best describe gap influence on understory vegetation in large gaps.

In smaller gaps, there appears to be an effect of the intact forest extending into the gap interior rather than a gap effect on the surrounding forest. Other investigators have found similar results and have related a negative gap effect to small opening sizes (Hughes and Bechtel 1997, York et al. 2003). We support the notion that small gaps are more prone to be influenced by the surrounding forest rather than have an influence extending beyond their boundaries. Soil moisture availability appears to be somewhat related to gap influence on understory vegetation communities in smaller gaps. Soil moisture availability is generally skewed to the south side of gap openings, as was the area of gap-associated species composition in the small gaps, as a consequence of high levels of solar radiation and soil surface drying on the north side of the gaps (Gray et al. 2002). However, the influence of soil moisture on community composition was not supported by the correlation analysis.

Increases in gap size may have greater impact on gap influence than expected from the increase in physical size alone. The much greater DEI seen in interfaces between clearcuts and intact forest (Chen et al. 1992) suggests that this effect may continue to increase with increasing gap size beyond the range studied in our experiment.

Depth of gap influence on understory species diversity does not seem to follow a simple pattern. Edge locations appear to support lower understory species diversity than the surrounding forest matrix or the gap interior. Gap influence on diversity exhibited both an interior (high diversity) component and an edge (low diversity) component. While many other studies have found that edges support higher species diversity (Brothers and Spingarn 1992, Fraver 1994, Euskirchen et al. 2001), Harper and MacDonald (2002) found mixed results, i.e., both higher and lower levels of diversity in edge locations, and Matlack (1994) found no increase in diversity at edge locations. These other DEI studies generally concentrated on established edges between highly dissimilar systems (such as an old field-forest edge) where two distinct vegetation communities intersected. In small forest canopy gaps the distinction between the gap community and the forest understory community is not likely as great as that seen at an old field edge.

The “species extended gap” concept of Dube et al. (2001) may be appropriate for describing patterns in individual indicator species and life history groups. This concept suggested that individual tree species would exhibit different areas of gap influence. Understory species and species groups generally displayed individualistic patterns in relation to gap openings, suggesting that gap influence on the understory layer may also vary greatly among species and groups.

DEI and Patch contrast

Overall, DEI between gaps and interior forest appears to be low, suggesting that patch contrast between these environments is also low. We hypothesize that the presence of a thinned matrix around the gap openings may be important in the lack of strong edge influence found in this study. Thinning results in a relatively open canopy condition creating an environment that is more similar in many ways to a gap than to a closed canopy forest.

Many factors have been shown to influence the magnitude of patch contrast in forest systems including: climate, aspect, latitude, edge age, canopy height, canopy cover, vegetation community composition, dominant disturbance regime, magnitude of disturbance, and landscape heterogeneity (Cadenasso et al. 2003, Harper et al. 2005). The presence of open canopy conditions near a gap can have a negative influence on patch contrast (Harper et al. 2005). Opening of the canopy in the surrounding forest by thinning may have contributed to the low DEI exhibited in our study system. Gap size may also have affected the strength of patch contrast in this system, as gap sizes exhibited different understory responses (York et al. 2003). The gap sizes in our study may have shown low levels of patch contrast because of their relatively small size, as compared to the clearcuts or old-fields investigated in other studies of edge influence (e.g. Chen et al. 1992, Harper and MacDonald 2002b). Aspect of edge may also have affected patch contrast, because in the northern hemisphere north facing edges generally have lower depth of gap influence than south facing ones (Wales 1972, Palik and Murphy 1990, Chen et al. 1992, Fraver 1994, Burton 2002). Depth of gap influence also differed between sites, suggesting that pre-disturbance vegetation composition may have a significant effect on patch contrast (Harper and Macdonald 2002b, Harper et al. 2005). The abruptness of the edge in gaps may also increase over time through "self-armoring" of gap edges related to tree and shrub responses (Cadenasso and Pickett 2001, Nelson and Halpern 2005), or it may decrease over time as gaps are filled by overstory regeneration.

Measurement of gap influence using understory vegetation

In this study, understory vegetation communities were useful measures of gap influence extent. However, because of the dominant influence of initial vegetation distributions on post-disturbance communities in the absence of ground-layer disturbance, these variables may not be as useful in non-harvest related gaps (Moore and Vankat 1986, Hughes and Fahey 1991). Patterns in understory species composition appear to be strongly related to understory and ground-layer disturbance associated with harvesting (see Chapter 2). In the absence of harvest disturbance to the area surrounding the gap there may be an even lower effect of gap creation on understory species distributions. However, a gap effect on growth and flowering of existing vegetation would likely occur (St. Pierre 2000, Lindh 2005). Therefore, it seems likely that understory vegetation may be a useful measure of gap extent only in large gaps with relatively high levels of ground-layer disturbance.

Scaling implications

The lack of a large gap influence on the surrounding thinned forest matrix may have strong implications for many components of forest ecosystems on the stand and landscape level (Coates and Burton 1997). This lack of influence also could play a role in the absence of a response in understory diversity or composition to gap formation on a stand scale (Berryman et al. 2005, Beggs and Puettmann in review). With a greater gap influence extent, gap creation may be more likely to have an effect on stand scale comparisons. Gap influence extent on the order of that exhibited in this study, though limited to the physical gap area, may nonetheless have implications on both stand and landscape scales (Menard et al. 2002), and effects on some organisms or processes could be substantial (Carey 2003).

Limitations

This study is limited by its short temporal scope, because edge effects (Matlack 1994, Harper et al. 2005) and species distributions in disturbed systems (Halpern 1989) are temporally variable. Changes in species composition are a secondary process in relation to edge creation, and DEI on composition is therefore hypothesized to increase over time in systems in which forest redevelopment does not occur (Harper et al. 2005). Therefore, temporal changes in forest structure associated with gap closure will have strong implications for gap influence in the long term. Our research also suffers from a lack of pre-treatment data which limit our use of causal inference about treatment effects on understory variation, especially where individual species distributions are concerned (Nelson and Halpern 2005).

Conclusions

Extent of gap influence appears to be highly variable, and may depend greatly on the measure used to delineate this influence and the nature of the gaps investigated. Gap influence on composition of understory vegetation communities is apparently limited primarily to the physical gap area in young forests in western Oregon. In large gaps a minor influence of gaps on the surrounding forest was apparent, while in smaller gaps the influence of the intact forest extended into the gap interior. Depth of gap influence on the surrounding forest was minimal suggesting that patch contrast between gaps and the surrounding forest was also low. Thinning in the forest matrix surrounding the gap openings may be partly responsible for low levels of gap influence and patch contrast. Understory vegetation distributions may be a useful measure of gap extent influence in harvested gaps, but may be less useful in natural systems with low levels of disturbance related to gap creation. The small area of gap influence on understory vegetation communities may help explain a lack of stand level responses to gap creation. In addition, area of gap influence and influence of gaps on stand level processes, does not appear to scale linearly with gap size. Gap influence on understory vegetation communities may depend greatly on gap size and intensity of ground-layer disturbance related to gap formation.

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CHAPTER 4: PATTERNS IN UNDERSTORY VEGETATION COMMUNITY DIVERSITY AND SPECIES GROUPS ACROSS CANOPY GAPS

Abstract

The distribution of individual plant species in forests has been linked to the occurrence of canopy gaps. Broad scale species diversity patterns in forest landscapes have also been related to gap formation and responses of species to gaps. In this study, patterns of understory plant species diversity, and distributions of late-successional and exotic species were investigated in relation to harvest-related gaps in Douglas-fir (*Psuedotsuga menziesii*) dominated forest stands in western Oregon. Understory vegetation community diversity was related to position along transects across two sizes of circular gap opening (0.1 and 0.4ha). Species richness differed among positions (along transects) relative to the gap in both 0.1ha gaps ($F_{4,56} = 4.65$, $p = 0.003$) and 0.4ha gaps ($F_{6,84} = 4.29$, $p = 0.001$). The Simpson (D) and Shannon-Wiener (H’) diversity indices differed among positions only in the 0.4ha gaps (D - $F_{6,84} = 4.89$, $p < 0.001$, H’ - $F_{6,84} = 3.49$, $p = 0.004$). All three measures, when they differed by position, were greater in gap interior positions than in the surrounding forest understory. Rare, ruderal species were largely responsible for differences in diversity among positions. Species turnover (beta-diversity) at a small scale (10m) was lower in gap interior positions than in gap edge or non-gap positions. Abundance of late-successional species was low across all positions, but was lowest in the interior of the 0.4ha gaps. Abundance of exotic species was positively associated with gaps, but was lower than that of native early seral species in all positions. Harvest gaps appear to increase understory plant species diversity at the gap scale in the short term, but this effect may be transient based on the life history characteristics of the species that are driving these differences.

Introduction

Canopy gap formation is a major factor contributing to overstory species diversity and stand structure in many forest ecosystems (Denslow 1980, Hibbs 1982, Brokaw 1985, Spies and Franklin 1989). Gaps play a key role in controlling patterns of tree species occurrence and distribution in forest stands (Brokaw and Busing 2000). Gaps may be integral for species diversity in the shrub and herb layers as well (Collins et al. 1985, Stewart 1988, Spies 1998, Roberts and Gilliam 2003). A variety of resources are affected by gap formation, such as light, soil moisture, nutrients, substrate (germination safe sites) and growing space, and variation in these factors may contribute to maintenance of species diversity (Ricklefs 1977, Denslow 1980, Canham and Marks 1985). Vegetation community response, in the overstory and understory, to gap-related variation in these resources has been studied extensively in a variety of natural systems (Runkle 1981, Brokaw 1985, Moore and Vankat 1986, Stewart 1988).

Recently, forest managers have begun to focus on gap creation in efforts to increase within-stand diversity (Runkle 1991, Coates and Burton 1997, Franklin et al. 2002). Inclusion of gaps in thinning treatments can introduce important spatial variability in stand structure (Franklin et al. 2002, Beggs and Puettmann in review). Creation of canopy gaps is often considered in silvicultural prescriptions designed to produce and maintain late-successional habitat features in young forests, especially in the Pacific Northwest region (Hunter 1993, Cissel et al. 2006). Gap creation, especially when used in concert with thinning, is seen as a method for increasing habitat heterogeneity, biodiversity, and stand structural heterogeneity, all of which can be indicative of, and help foster, the development of late-successional habitat conditions (Franklin et al. 2002). In this study, we investigate understory vegetation communities in harvest gaps created as part of a thinning regime in western Oregon.

Gap-related influences on understory plant species diversity and turnover, and distributions of certain components of understory vegetation communities are of interest in forests of the Pacific Northwest (Halpern and Spies 1995, Bailey et al.

1998). One goal of forest management on many public lands in this region is maintenance of understory plant species diversity at stand and landscape scales (Bailey et al. 1998, Franklin et al. 2002, Muir et al. 2002). Gaps have been shown to be related to small scale enhancement of understory species diversity (London 1999). Gap edge areas may exhibit high species turnover, and function as small scale ecotones (Eysenrode et al. 2002) between the gap interior and the surrounding forest (also see Chapter 3). Enhanced species diversity and turnover at the gap scale may prove to be important at stand and landscape scales. Both species diversity and turnover may also be indicators of general habitat heterogeneity, and gaps may help foster this heterogeneity on a stand scale.

Also of special interest in forests of the Pacific Northwest are distributional patterns of understory plant species associated with late-successional habitat. These species generally exhibit low level abundance in intensively managed forests in this region (Spies 1991) and are indicators of habitat used by many wildlife species (Carey 2003). Abundance of late successional plant species is often reduced by harvest activities and stand conditions following harvesting (Halpern 1989, Halpern and Spies 1995, Battles et al. 2001, Lindh and Muir 2004) and we hypothesize that they may display a negative response to gaps as well.

Additionally, concerns related to the distribution and spread of exotic species exist in the Pacific Northwest region. We have a limited understanding of the role of gap creation in facilitating the expansion of these species (Goldblum and Beatty 1999, Beggs and Puettmann in review). These species may be positively related to gap creation, as harvest gaps exhibit high levels of ground-layer disturbance, a factor that is often related to exotic species establishment. However, this relationship could be strongly dependant on the existence of local seed sources and vectors for dispersal (Mack et al. 2000, Parendes and Jones 2000, Beggs and Puettmann in review), and may therefore differ among stands. Comparison of exotic cover with that of native early seral species cover may help illustrate the overall impact of exotics on the gap associated vegetation community.

In this study, we investigated variation in understory vegetation communities in and around canopy gaps, which were created as a component of a thinning regime in forest stands in western Oregon. We hypothesized that: (1) gap interiors would exhibit higher plant species diversity than the surrounding thinned forest, (2) gap edge areas would exhibit higher small scale species turnover than gap interiors or the surrounding forest, (3) abundance of exotic species would be higher in the gap interior, and (4) abundance of late-successional species would be lower gap interiors.

Methods

Site Descriptions

This study is part of the Density Management Study (DMS), which is investigating effectiveness of thinning treatments in fostering development of late successional habitat features. All study stands were even-aged and dominated by 40 to 70 year old Douglas-fir (*Psuedotsuga menziesii*) in a single canopy layer. One site (KM) had a small western hemlock (*Tsuga heterophylla*) component. We focused on four DMS sites located in western Oregon, three in the Coast Range ecoregion (Omernick 1987): Bottomline (BL), OM Hubbard (OMH), and North Soup (NS), and one in the Cascade Foothills ecoregion: Keel Mountain (KM). Sites spanned a variety of elevations, aspects, and stand histories. Site and treatment details are summarized in Table A1.1.

The study stands were treated with a thinning regime which included three sizes of circular gap openings (0.1, 0.2, and 0.4 ha). This study focused on 0.1 and 0.4 ha gaps located in stands thinned to 200 trees per hectare. Gap diameter to tree height ratios for the two gap sizes were approximately 1.0 and 2.0 respectively. Harvest treatments (including gaps) were operational in nature and therefore were not randomly assigned within the sites. Gap location was determined by harvesting constraints and not by condition of overstory or understory vegetation. Gaps that were used as landings for timber extraction were avoided in this study, but all gaps contained some ground-layer disturbance from logging operations.

Study design and data collection

Gap transects along which understory vegetation, substrates and environmental factors were sampled were established and sampled between July 1 and August 31, 2004. We sampled eight gaps (four each of 0.1 and 0.4 ha sizes) at three sites (KM, OMH, NS) and six gaps (three of each size) at the fourth site (BL), resulting in a total of 15 gaps of each size. Transects originated at the gap center and extended on both a north/northeast and south/southwest bearing beyond the gap edge (defined as the line extending between the boles of the nearest surrounding canopy trees) and 23 meters into the surrounding thinned forest matrix (Figure A2.1). Gaps were selected according to suitability for the transect layout, with the stipulation that transects avoid other gaps, leave islands (unthinned patches), or the treatment or site boundaries Understory vegetation (< 6 m in height) was sampled in plots (transect positions) made up of sets of five contiguous 4m^2 square sampling quadrates (subplots) established along the transect. This sampling design attempted to balance investigation of pattern at two scales, a small (10m) scale and a larger, transect level scale, this study investigated variation at both scales. Transect positions included: South Forest Matrix (SM; centered ~54m from gap center in 0.4ha gaps and ~36m in 0.1ha gaps), South Edge (SE; ~36m, ~18m), South Gap Interior (SG; only in 0.4 ha gaps, ~18m), Gap Center (C), North Gap Interior (NG, only in 0.4 ha gaps), North Edge (NE), and North Forest Matrix (NM) (Figure A2.1).

Ocular estimates of percent cover were made for all vascular plant species (with cover < 6m in height) in each subplot. Taxonomic nomenclature follows the USDA Plants Database (USDA-NRCS 2005). Maximum cover for each species was 100 percent, but cumulative cover of all plants could exceed 100 percent due to multiple vegetation layers. Percent cover was also estimated for substrate types: litter, exposed mineral soil, coarse woody debris, stump/tree bole, and exposed rock, and for growth form classes: ground-dwelling lichen, ground-dwelling bryophyte, fern, forb, grass, sedge/rush, low shrub, tall shrub, hardwood, and conifer. Data were averaged to the plot level for most analyses to account for lack of spatial independence of subplots. The exception to this was calculations of species turnover within positions.

Data analysis

To investigate the relationship between gaps and species diversity and turnover, we used an analysis of variance (ANOVA) with repeated measures in space to compare three measures of species diversity (α diversity), two measures of species turnover (β diversity), and abundance of exotic and late-successional species between transect position plots. The two gap sizes were analyzed separately. We employed an ANOVA model with repeated measures in space (along each transect), and blocked by site, using the MIXED procedure in SAS v 9.1 (SAS-Institute-Inc. 2005). The model used for this analysis was:

[6] $$Y_{ijk} = \mu + \beta_i + \lambda_{ijk} + P_l + \varepsilon_{ijkl}$$

where:

μ = the overall mean value of Y

β_i = the random effect of site that adds variability to the value of Y, i = 1,2,3,4.

λ_{ijk} = the random effect of transect k within site I, k = 1,2,3,4,5,6,7,8

P_l = the fixed effect of the lth level of position, l = 1,2,3,4,5,6,7 for large gaps and 1,2,3,4,5 for small gaps

ε_{ijkl} = the random effect among positions within transects,

and $\varepsilon_{ijkl} \sim MVN(0,\Sigma)$ and Σ =

$$\begin{array}{|c|c|c|c|c|}
\hline
\sigma^2_{11} & \sigma^2_{12} & \sigma^2_{13} & \sigma^2_{14} & \sigma^2_{15} \\
\hline
\sigma^2_{12} & \sigma^2_{22} & \sigma^2_{23} & \sigma^2_{24} & \sigma^2_{25} \\
\hline
\sigma^2_{13} & \sigma^2_{23} & \sigma^2_{33} & \sigma^2_{34} & \sigma^2_{35} \\
\hline
\sigma^2_{14} & \sigma^2_{24} & \sigma^2_{34} & \sigma^2_{44} & \sigma^2_{54} \\
\hline
\sigma^2_{15} & \sigma^2_{25} & \sigma^2_{35} & \sigma^2_{45} & \sigma^2_{55} \\
\hline
\end{array}$$

represents an unstructured covariance matrix among positions along a transect across the small gaps.

The Akaike Information Criteria (AIC;(Gotelli and Ellison 2004) statistic was used to select the most appropriate covariance structure for the models associated with each response variable. The covariance structures selected for each variable and used in the subsequent analyses are presented in Table 4.1. All comparisons of means were adjusted using the Tukey-Kramer procedure (Gotelli and Ellison 2004).

The three measures of α diversity were species richness (total number of species in each subplot averaged to the position level), Simpson's diversity index (Simpson 1949), and the Shannon-Wiener diversity index (MacArthur and MacArthur 1961). Simpson's diversity index was calculated as

$$[2]\quad D = 1 - \sum_{i=1}^{s} p_i^{\ 2}$$

where p_i is the proportion of total cover in species i and s is the total number of species in the subplot (Magurran 2004). This measure represents the likelihood that two randomly chosen units of cover will belong to different species, emphasizes common species, and is only minimally affected by presence of rare species (McCune and Grace 2002). The Shannon-Wiener diversity index was calculated as

$$[3]\quad H' = \sum_{i=1}^{s} p_i \ln p_i$$

where p_i is the proportion of total cover in species i (McCune and Grace 2002). This measure is based in information theory, and represents the amount of uncertainty involved in drawing from the species pool, where higher uncertainty equals greater diversity (McCune and Grace 2002). This measure is intermediate between species richness and Simpson's index in weighting of rare species (Magurran 2004).

The measures of β diversity were Whittaker's beta diversity index (Whittaker 1972), and total Sørensen's distance (McCune and Grace 2002) between subplots within each position group. Whittaker's beta diversity index was calculated as

$$[4]\quad \beta_w = S/\alpha$$

where S equals the total number of species recorded in a plot and α is the average number of species recorded in each subplot within that plot (McCune and Grace 2002). A value of Sørensen's distance for each position group was calculated between each subplot combination within the transect positions and summed and divided by the number of subplots. Sørensen's dissimilarity (distance) between subplots *i* and *h* was calculated as

[5]

$$D_{i,h} = \frac{\sum_{j=1}^{p} |a_{ij} - a_{hj}|}{\sum_{j=1}^{p} a_{ij} + \sum_{j=1}^{p} a_{hj}}$$

where a_{ij} is the abundance of species *j* in subplot *i,* a_{hj} is the abundance of species *j* in subplot *h,* and *p* is the total number of species in the two subplots (McCune and Grace 2002).

We also explored patterns of distribution and abundance of late successional and exotic species groups. For this purpose, we employed the same repeated measures ANOVA model in comparisons of total combined cover of species in these groups among transect positions.

We also related species diversity to species groupings (outlined below) to determine which components of the understory vegetation community were most strongly related to patterns in diversity and turnover. Spearman rank correlation coefficients between diversity and turnover measures and growth-form and life history strategy groups (Grime 1977) were calculated using PROC CORR in SAS v9.1 (SAS-Institute-Inc. 2005). Growth form groups were: ferns, grasses, sedges/rushes, herbs, low shrubs, tall shrubs, and trees. Life history strategy groups followed Grime (1977) and were classified as: ruderals, competitors, and stress tolerators. Species were assigned to groups based on life-history and growth form attributes based on Hitchcock and Cronquist (1973). Classifications for all species can be found in Table A4.1.

Results

Understory plant species diversity was highest in gap interiors, and differences between transect positions seemed to due to the differential presence of rare species, which in this analysis were species with low total cover rather than low frequency. Species richness, which is highly influenced by rare species was consistently greater in gap interior positions than in forest matrix positions, but not edge positions (Table 4.1, Figures 4.1 and 4.2). The Shannon index weights rare species more strongly and exhibited stronger differences among positions than the Simpson index (Table 4.1). The Simpson and Shannon diversity indices differed by position only in the larger gaps and in general the south gap interior and gap center positions had higher diversity than the forest matrix positions with both measures (Figures 4.1 and 4.2).

All three diversity measures were most strongly correlated (positively) with the ruderal species group in the large gap size (Table 4.2). Species richness and the Shannon index followed this pattern in the small gaps, but the Simpson diversity index was most strongly related to the competitor species group in the small gaps (Table 4.3). Apparently the rare species that were driving species diversity patterns were primarily ruderal species. In addition, the grass and herb growth forms were most strongly correlated with species richness, which weights rare species most highly, in both gap sizes (Tables 4.2 and 4.3). Ruderal species as defined for this study most commonly exhibit one of these two growth forms, and therefore would be expected make up a significant portion of the cover in both groups.

Table 4.1. Repeated measures ANOVA results for all sites and all variables. Covariance types are: AR = autoregressive with all positions correlated, UN(x) = unstructured with x positions correlated, TOEP(x) = banded toeplitz with x positions correlated. * denotes p < 0.05 for Type 3 test of fixed effects.

Gap Size	*Variable*	*Covariance Type*	*df*	*F*	*p*
0.4 ha					
	Richness	AR	6,84	4.29	0.001*
	Simpson	UN(2)	6,84	4.89	<0.001*
	Shannon	TOEP(4)	6,84	3.49	0.004*
	Whittaker	TOEP(1)	6,84	2.86	0.014*
	Sorensen	TOEP(3)	6,84	6.54	<0.001*
	Exotic	UN(1)	6,84	6.20	<0.001*
	Late-successional	UN(1)	6,84	3.64	0.003*
	Native early seral	UN(3)	6,84	20.88	<0.001*
0.1 ha					
	Richness	TOEP(1)	4,56	4.65	0.003*
	Simpson	TOEP(1)	4,56	0.34	0.849
	Shannon	TOEP(1)	4,56	0.72	0.583
	Whittaker	TOEP(1)	4,56	1.70	0.164
	Sorensen	AR	4,56	5.98	<0.001*
	Exotic	UN(5)	4,56	5.88	0.001*
	Late-successional	TOEP(2)	4,56	0.88	0.482
	Native early seral	TOEP(3)	4,56	3.01	0.025

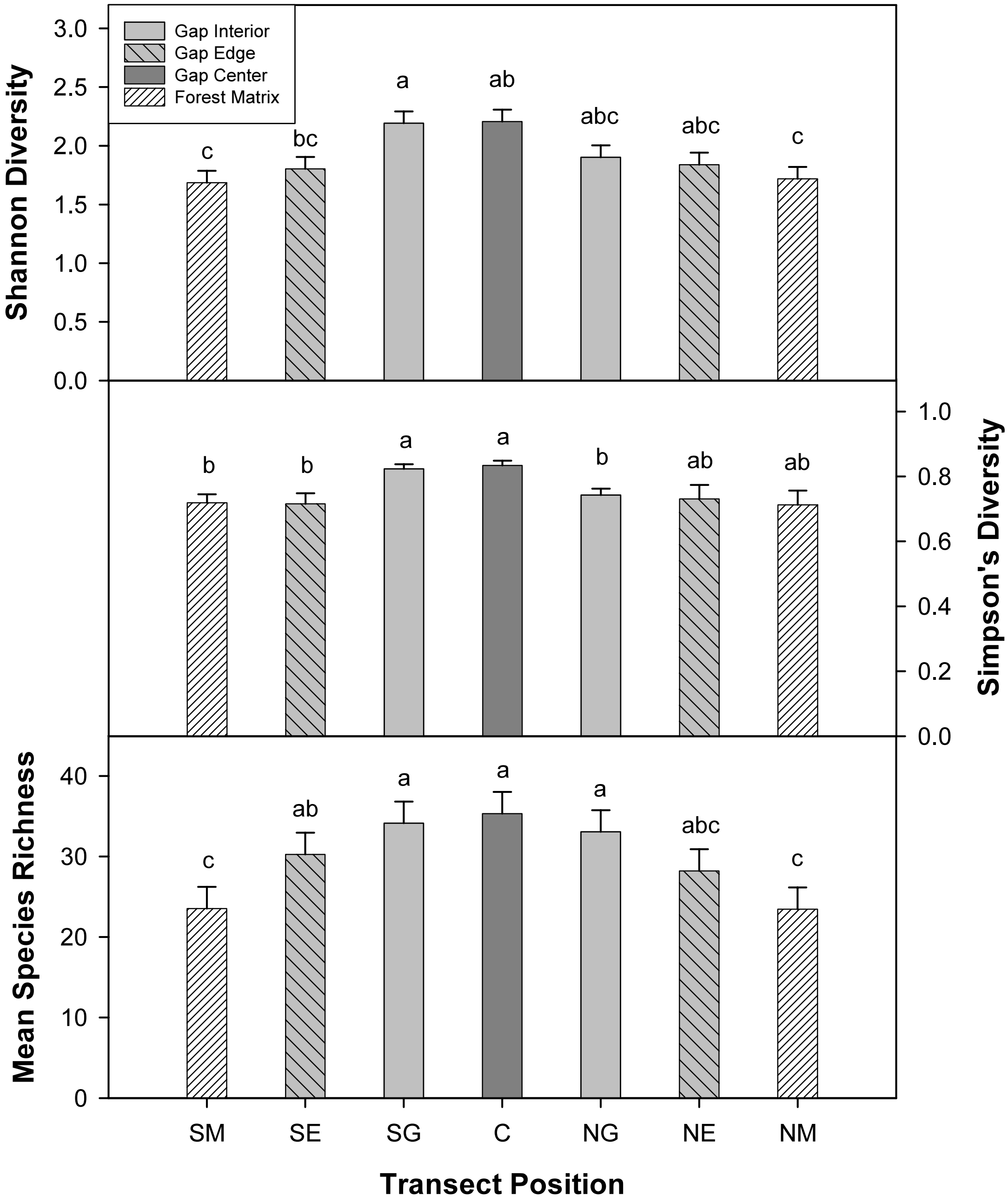

Figure 4.1a. Least squares mean values of species richness, Simpson's diversity, and the Shannon-Wiener diversity index for each transect position in the 0.4ha gaps. Results of position comparisons are indicated by letters above bars, positions sharing letters are not significantly different from each other at the $p < 0.05$ level. Error bars represent standard errors for each position.

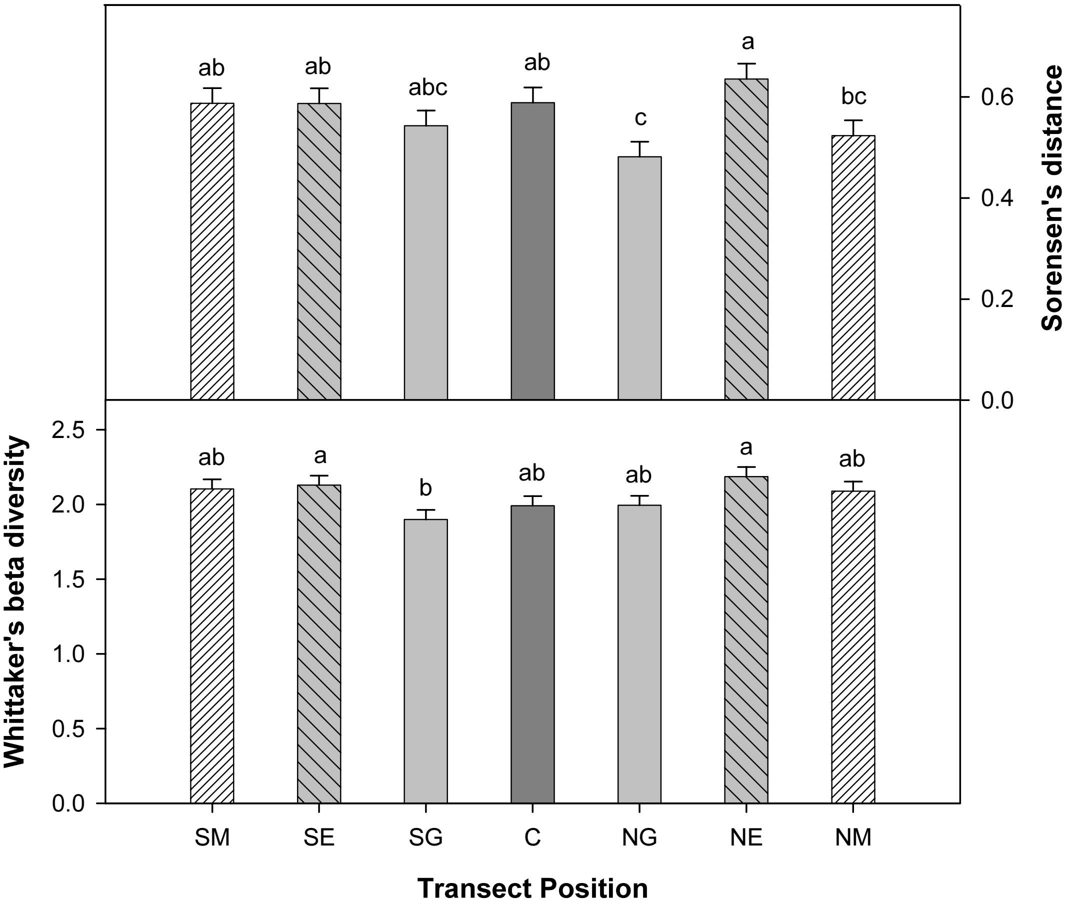

Figure 4.1b. Least squares mean values of Whittaker's beta diversity and Sorensen's distance for each transect position in the 0.4ha gaps. Results of position comparisons are indicated by letters above bars, positions sharing letters are not significantly different from each other at the $p < 0.05$ level. Error bars represent standard errors for each position.

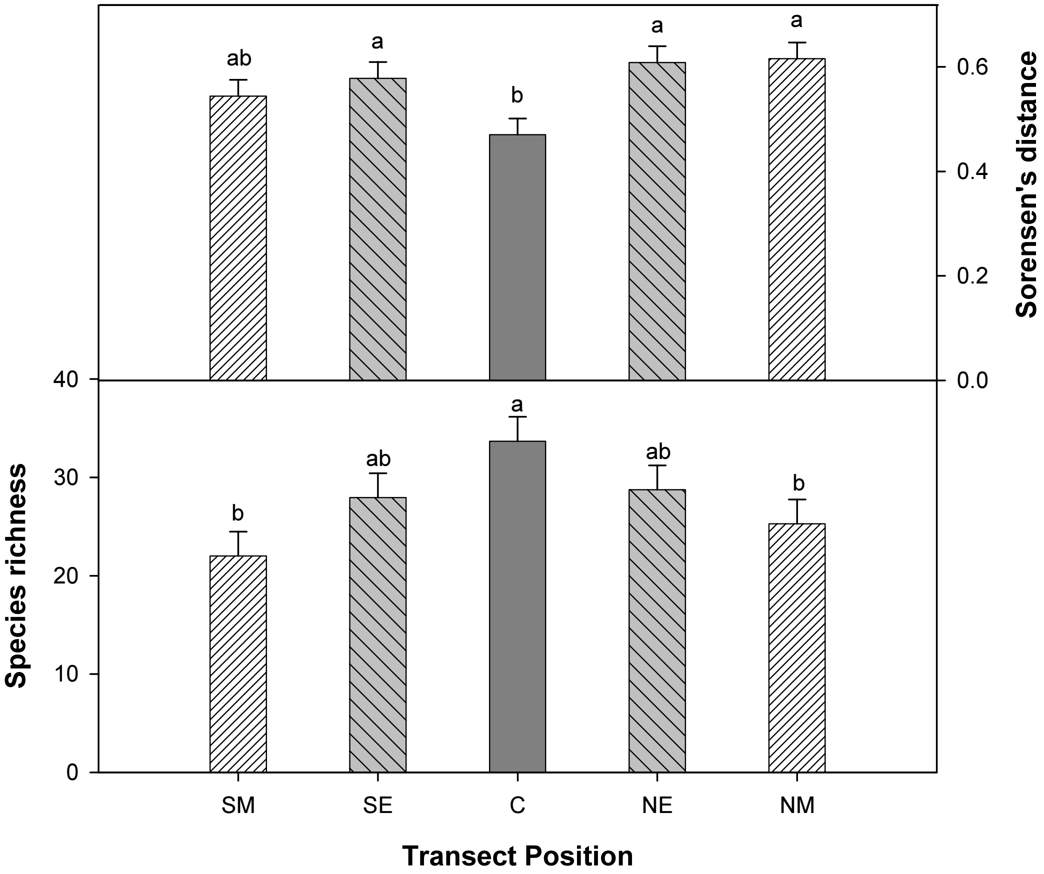

Figure 4.2. Least squares mean values of species richness and Sorensen's distance, for each transect position in the 0.1ha gaps. Results of position comparisons are indicated by letters above bars, positions sharing letters are not significantly different from each other at the $p < 0.05$ level. Error bars represent standard errors for each position.

Table 4.2. Spearman rank correlations of species diversity and turnover measures with species growth form and life history strategy groups in 0.4ha gaps. * denotes $p < 0.05$.

	Richness	*Simpson*	*Shannon*	*Whittaker*	*Sorensen*
Ruderal	0.5114*	0.5578*	0.6387*	-0.2962*	-0.0409
Competitor	0.3520*	0.3932*	0.3514*	-0.3632*	-0.3773*
Stress-tolerator	0.1162	-0.0778	-0.1031	0.0774	-0.1685
Fern	-0.3997*	-0.5044*	-0.4719*	0.2615*	0.1963*
Grass	0.6897*	0.6447*	0.4928*	-0.1970*	-0.0727
Herb	0.4252*	0.5463*	0.5199*	-0.2856*	-0.0959
Low Shrub	0.1858	0.2314*	0.3095*	-0.2942*	-0.3774*
Sedge/Rush	0.3798*	0.3882*	0.2548*	-0.0781	0.0904
Tree	-0.0208	0.0763	0.1420	-0.1366	0.1816
Tall Shrub	-0.1103	-0.1317	-0.1043	0.2026*	0.0017

Table 4.3. Spearman rank correlations of species diversity and turnover measures with species growth form and life history strategy groups in 0.1ha gaps. * denotes $p < 0.05$.

	Richness	*Simpson*	*Shannon*	*Whittaker*	*Sorensen*
Ruderal	0.7358*	0.3552*	0.4743*	0.2591*	-0.0137
Competitor	0.4914*	0.4389*	0.4708*	-0.1466	-0.2347*
Stress-tolerator	-0.0683	0.0214	-0.0516	-0.2370*	0.0271
Fern	-0.0451	-0.0977	-0.0406	-0.1398	-0.0495
Grass	0.5243*	0.5462*	0.4585*	0.2489*	-0.0400
Herb	0.4973*	0.4547*	0.4189*	-0.0088	0.0401
Low Shrub	0.3912*	0.4454*	0.4430*	-0.2684*	-0.2518*
Sedge/Rush	0.3010*	0.0027	-0.1165	0.4646*	0.1963*
Tree	0.0207	0.0441	0.0456	-0.1007	-0.0138
Tall Shrub	-0.1124	0.0030	0.0667	-0.1061	0.0900

Small scale variability, as described by species turnover across the 10m long transect position plots, was lowest in gap interiors in both gap sizes. Whittaker's β diversity index was lower in the south gap position than the gap edges in the large gaps (Figure 4.1b), but did not differ among positions in small gaps (Table 4.1). In large gaps, Sorensen distance was higher in the north edge position than in the north matrix or north gap positions (Figure 4.1). In small gaps, the highest values for this measure were found in the north matrix, north edge, and south edge positions, all of which were significantly greater than the gap center position (Figure 4.2). Species turnover was negatively correlated with cover of competitor species and low shrubs in both gap sizes (Tables 4.2 and 4.3), suggesting that these measures were strongly affected by the presence of dominant shrub layers, especially in the large gaps. Overall though, edge locations did not exhibit consistently higher species turnover than matrix positions in either gap size.

Exotic species cover was higher in gap interior positions than forest matrix positions in both gap sizes (Tables A5.1 and A5.2), but was generally relatively low across all locations (Figures 4.3 and 4.4). Cover of native early seral species was also highest in gap interior positions, and was always much greater than that of exotic species (Figures 4.3 and 4.4). This relationship held at all sites except OMH, where exotic species made up a larger component of cover in gap interiors than did native early seral species (Figures A6.1 and A6.2).

Abundance of late successional species varied among transect positions only in the large gaps (Table 4.1), where gap interior positions had lower cover than forest matrix positions (Table A5.1). Late-successional species cover was low in all positions in both gap sizes, but especially in gap interior positions (Figures 4.3 and 4.4).

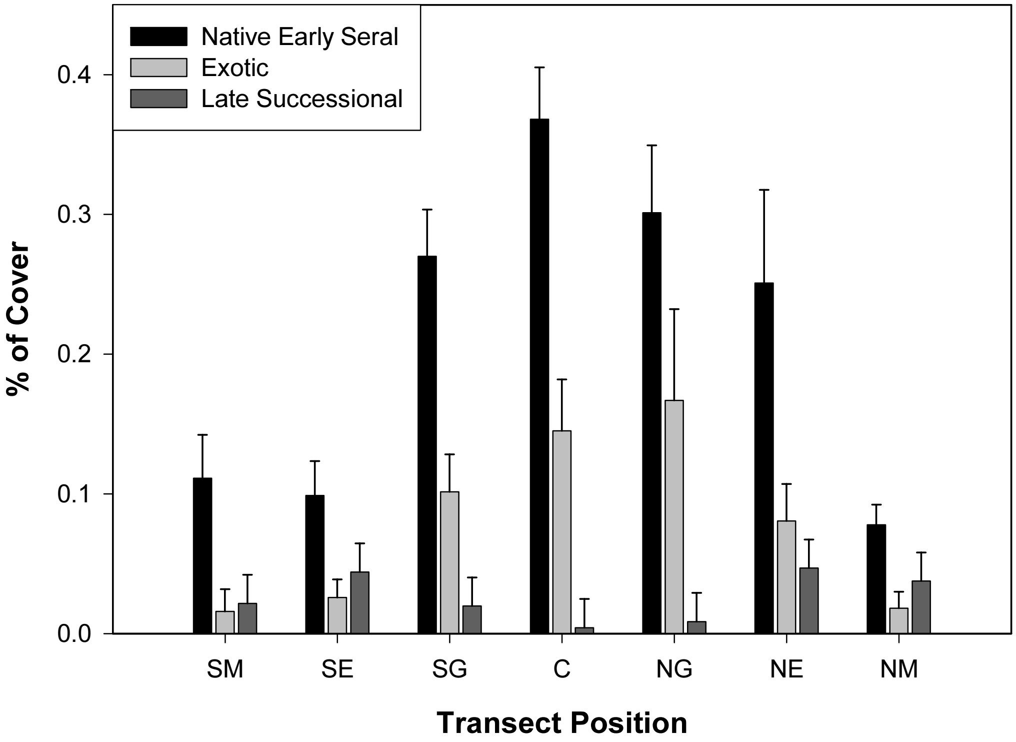

Figure 4.3. Mean proportion of total cover in species groups by transect position in the 0.4ha gaps. Error bars represent standard errors.

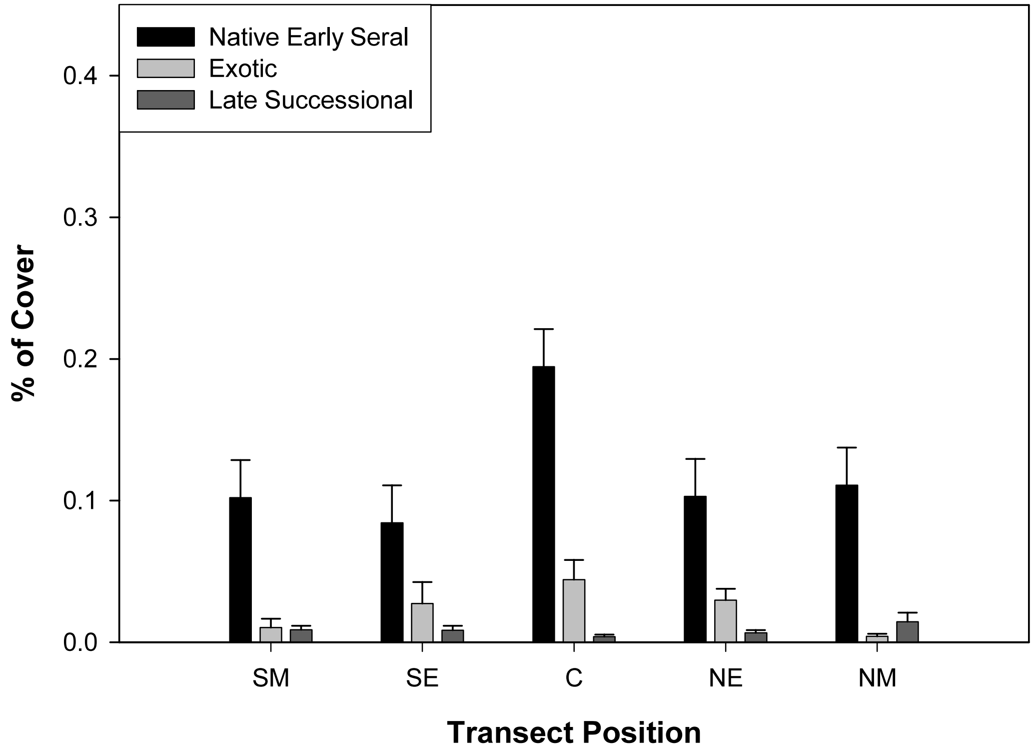

Figure 4.4. Mean proportion of total cover in species groups by transect position in the 0.1ha gaps. Error bars represent standard errors.

In summary, all species diversity measures were greater in gap interior positions than forest matrix positions in the large gaps. In the small gaps, only species richness differed between the gap interior and forest matrix. In both gap sizes, measures that weighted rare species more strongly exhibited greater differences among positions. Gap edges did not exhibit higher small scale species turnover than the surrounding forest matrix. Species diversity patterns were dominated by differential abundances of ruderal species, while species turnover was highest in the absence of high cover of competitor species. Abundance of exotic species was greatest in gap interiors in both gap sizes. Late-successional species were negatively related to large gaps, but did not vary with respect to small gaps.

Discussion

Gap creation may result in diversification of the understory vegetation community at a small scale. The presence of gap openings appears to have influenced species diversity, but this influence is likely transient and may not affect large scale diversity patterns. Small scale heterogeneity in understory vegetation communities may be negatively affected by gap creation. The presence of gaps may be an important factor regulating the abundance of exotic species. Gaps also appear to have an influence on abundance of late successional species, but only in larger gaps.

Disturbance type and intensity resulting in gap formation may affect the subsequent response in understory vegetation communities. Gap formation did not increase small scale understory species diversity in other studies which focused on natural gaps (Moore and Vankat 1986, Dirzo et al. 1992) but did increase understory diversity in one study that focused on harvest gaps (Schumann et al. 2003). Our results support the notion that harvest gaps may increase understory diversity in the short term, and suggest that this effect may be related to disturbance of the ground and understory layer (Chapter 2). The diversity pattern in our study was strongly related, especially in the larger gap size, to cover of ruderal species. Ruderals were also shown to drive species compositional patterns in these large, highly disturbed gap openings (Chapter 2). Other studies have shown short term increases in understory plant species diversity in relation to forest harvesting and related these changes to the influence of ruderal and early seral species (Thomas 1999, Battles et al. 2001, Schumann et al. 2003). Influence of gaps on diversity patterns may also be greater in larger gaps (Brokaw and Scheiner 1989, Schumann et al. 2003), an effect that is also probably largely related to the influence of ruderal species.

Although at the small scale there was higher diversity inside gaps related to gap creation, Berryman et al. (2005) found that this effect was not exhibited in stand scale (between treatment) analyses in the same DMS stands included in our study. One reason for this disparity may be the association of higher diversity levels with rare species in our gaps. Rare species are less likely to be encountered in a stand level survey and would therefore be less likely to influence diversity patterns at that scale. The lack of a large scale effect of gap creation could also be related to the relatively minor proportion of the treatment area taken up by gaps or the lack of a large gap influence on the surrounding forest (see Chapter 3). In general, our findings supported the hypothesis that gaps would positively influence small scale understory plant species diversity.

Edge locations may not function as transition zones in the understory vegetation community. Our results only lend moderate support to the notion of gap edges as small scale ecotones within a forest (Eysenrode et al. 2002), as these areas did not have higher species turnover than the surrounding forest understory. On a very small scale (~10m) heterogeneity in the vegetation community is lower inside gaps than in the forest matrix surrounding the gaps. Berryman et al. (2005) found no evidence for lower species turnover in treatments containing gaps when data were analyzed at the treatment level. The reasons for lack of an effect of low turnover in the gap interior on stand level analyses are probably much the same as those outlined above in regards to species diversity.

Gap formation may have a positive influence on the abundance of exotic plant species, but will not necessarily result in exotic dominated communities. Exotic species were generally relatively low in abundance across all sites and gaps compared to native early seral species. High abundance of exotics, such as that exhibited at the OMH site, may be related to the presence of a local seed source or to a higher degree of soil disturbance (Chapter 2), both of which are often viewed as important variables in determining susceptibility to exotic species invasion (Mack et al. 2000, Thysell and Carey 2001, Beggs and Puettmann in review). The presence of relatively large amounts of exotic cover at the OMH site supports the idea that gaps can act as centers of establishment for exotic plant species (Goldblum and Beatty 1999). In a similar study in western Oregon greater cover of exotic species was not apparent in gaps (Beggs and Puettmann in review). Our results support the hypothesis that exotic species cover can be positively related to gap interiors, especially in larger gap sizes, and in the presence of ground-layer disturbance and seed sources. However, at all sites other than OMH, the abundance of native early seral species far outweighed that of exotic species, suggesting that relative importance of exotics in these gaps may be low.

Large, highly disturbed gaps may have a negative influence on the abundance of late successional species. The overall low levels of late successional associated species across our entire study precluded strong conclusions related to the hypothesis of a negative relationship between these species and gaps. However, a trend of lower abundance was evident, especially in the large gap size. A negative relationship between gap interiors and growth and fecundity of the late-successional associate *Trillium ovatum* in western Oregon has been established (St. Pierre 2000). Beggs and Puettmann (in review) also found that a number of late successional species were less frequent in gap interiors. The same study, in contrast to our findings, demonstrated that some late successional species showed an affinity for gap edge habitats.

Gap age also affects the strength of influence on the understory community (Runkle 1982, Moore and Vankat 1986, Dirzo et al. 1992). Cover of understory species can differ with gap age (Moore and Vankat 1986), and it is likely that species diversity and the importance of exotic and late-successional species would change over time in gaps as resource availability changes (Runkle 1982, Brokaw 1985, Brokaw 1987). Under open, clearcut conditions, the importance of ruderal and early seral species, which affected species diversity patterns in our study system, has been shown to peak around year seven post-disturbance (Halpern 1989). Gaps in our study (6-7 years post-harvest) may therefore be near peak abundances of ruderal species. As regeneration of canopy species fills gaps and reduces light availability to the understory layer, importance of light demanding species is likely to be reduced (Halpern 1989, Lindh and Muir 2004). Gap effects on understory species diversity may, therefore, also be transient and the importance of both early seral and exotic species may decline over time (Halpern 1989).

Limitations

Although the data we present suggest that gap creation has influenced understory communities, pre-disturbance species composition can have a profound influence on the makeup of the post-disturbance community (Hughes and Fahey 1991, Nelson and Halpern 2005). We lack specific knowledge of the pre-treatment vegetation communities at these sites. This shortcoming makes it difficult to draw definitive conclusions about the direct effects of gap creation on species diversity and community composition (Nelson and Halpern 2005). We also did not determine the number of stems of each species on each plot, which precludes us from making inferences about the relationship between diversity and density in gap locations. Density has been shown to be the driving factor in higher diversity patterns found among tree species in gap locations in tropical forests (Denslow 1995).

Conclusions

Gap formation in young managed forests appears to be highly influential on patterns of understory plant species diversity. Small-scale understory plant species diversity may be heightened by gap formation, especially in the short term. Enhanced species diversity appears to be driven by establishment of ruderal, native, early seral species, and to a lesser extent, by exotic species. Patterns in understory vegetation communities may be transient, as many species are likely to drop out as tree regeneration develops and the overstory canopy is renewed. In general though, forest management treatments including gaps appears, in the short term, to result in enhanced small-scale understory vegetation community species diversity and increased abundance of native dominated early successional habitat.

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CHAPTER 5: CONCLUSIONS

Conclusions

This study investigated patterns in understory vegetation communities related to harvest gaps created as part of a thinning regime in western Oregon. The goal of this research was to investigate the role of gaps in influencing small scale heterogeneity and diversity in understory communities in thinned forest stands. A relationship between harvest gaps and variation in understory communities has been established by Beggs and Puettmann (in review). The more detailed and spatially explicit findings of this study support their conclusion that gaps influence small scale heterogeneity in thinned forest stands.

Creation of canopy gaps in young managed forests appears to have significant influences on understory vegetation community dynamics. Gap partitioning of understory vegetation community composition may result when canopy gaps are formed in young forests. Partitioning seems to be related to an interactive relationship between ground-layer disturbance and resource partitioning. Partitioning in understory community composition in harvest gaps may depend on initiation by disturbance, and may not be as likely to occur in less disturbed systems, such as naturally formed gaps (Moore and Vankat 1986, Collins and Pickett 1988a, Collins and Pickett 1988b).

Gap influence on understory vegetation resulting from the creation of canopy gaps in young forests appears to be limited almost entirely to within gap areas. Large gaps may have some influence beyond the physical gap area, but small gaps may have no influence beyond their physical extent. Thinning in the forest matrix surrounding gap openings may result in low levels of gap influence and patch contrast at gap edges. Understory vegetation distributions may be a useful measure of gap extent influence and gap partitioning in managed systems, although the high degree of variability in understory responses may be detrimental to their widespread applicability in this role.

Harvest gaps in young stands generally support a native dominated or mixed native and exotic early seral community where differentiation in the understory community is not precluded by expansion of a dominant clonal shrub layer. Understory plant species diversity appears to be greater in gaps than in thinned forest. Diversity patterns seem to be related to establishment of native early seral species, and to a lesser extent, exotic species. Heterogeneity in understory communities may be diminished at a very small scale in gap areas. However, neither the enhancement of diversity nor decrease in species turnover observed at small scales are evident in stand level treatment comparisons (Berryman et al. 2005). In addition, any and all gap effects on understory vegetation communities may be transient, as many species are likely to drop out as advance regeneration fills gaps (Halpern 1989).

All partitioning effects were much more strongly expressed in large gaps. Smaller gaps appear to be more easily dominated by expansion of competitor species and seem to lack the substantial ruderal component seen in large gaps (Bazzaz and Pickett 1980). Small gaps for the most part may also be less influenced by the exotic species component that was prevalent in large gaps. Extent of gap influence appears to be greater in large gaps than in small gaps and may not scale linearly with gap size. Strong differences in response to gap creation may also exist between stands and differences in pre-harvest community composition and harvesting methods seem to play a large role in post-harvest community makeup (Berger 2004).

In general, gap creation appears to enhance understory vegetation community heterogeneity, species diversity, and abundance of native dominated early successional habitat in young stands. Inclusion of gaps in silvicultural treatments in young Douglas-fir forests in western Oregon may result in increased small scale structural diversity and heterogeneity in the understory layer. However, creation of large gaps may increase the propensity for exotic species establishment in young managed stands and could have deleterious effects on the abundance of late-successional associated plant species in the short term. The use of smaller gap sizes in silvicultural treatments may still result in diversification of the understory vegetation layer, but may be less likely to promote the establishment of early seral and exotic understory plant species.

Future research

Research into the relationship between harvest gap creation and understory vegetation communities should focus on spatial coherence between ground-layer disturbance following harvest, resource gradients, and development of understory communities. A detailed spatial approach may more definitively illustrate the relative contributions of gap partitioning and ground-layer disturbance in patterning gap understory communities. In addition, it would be advantageous to have pre-treatment vegetation, substrate, and environmental data to form a baseline from which to evaluate changes in species composition and the variables related those changes (Nelson and Halpern 2005). It would also be informative to follow changes in community pattern over time while simultaneously monitoring environmental variation related to gap closure, and root regrowth. Better measures of belowground resource availability would likely shed some light on the processes driving community composition in gaps (Muller 2003). In addition, detailed study of seed banks and life-history traits would help illustrate the relative importance of different components of the communities in structuring post-disturbance composition (Halpern 1989, Halpern et al. 1999). Studies incorporating a broader array of gap sizes would further understanding of the differences seen between gap sizes here, and may assist managers in decisions regarding optimal gap sizes for various management objectives.

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APPENDICES

Appendix 1

Table A1.1. Characteristics of DMS sites used in gap partitioning study. For more detail see (Cissel et. al 2006). Site index at 50 years from (King 1966).

	Bottomline	*Keel Mountain*	*North Soup*	*OM Hubbard*
Latitude (N)	43°46’20”	44°31’41”	43°33’57”	43°17’30”
Longitude (W)	123°14’11”	122°37’55”	123°46’38”	123°35’00”
Elevation (m)	236-369	659-768	159-411	394-783
Aspect	NW-NE	SW-NW	NW-N	NE-N
Slope	0-30%	0-30%	0-60%	30-60%
Annual precipitation (cm)	127	165	216	178
Logging Method	Cable yard	Cable/Ground	Cable yard	Tractor/Cable
Treatment Date (mo/yr)	7-11/1997	7/1997-9/1998	8/1998-9/1999	7-11/1997
Soil texture	Clay loam	Loam	Clay loam	Loam/Clay
Stand Age (years)	~65	~50	>50	~45-50
Mineral soil cover (%)	1.1%	0.9%	3.0%	4.9%
Site Index	138	127	132	120

Appendix 2

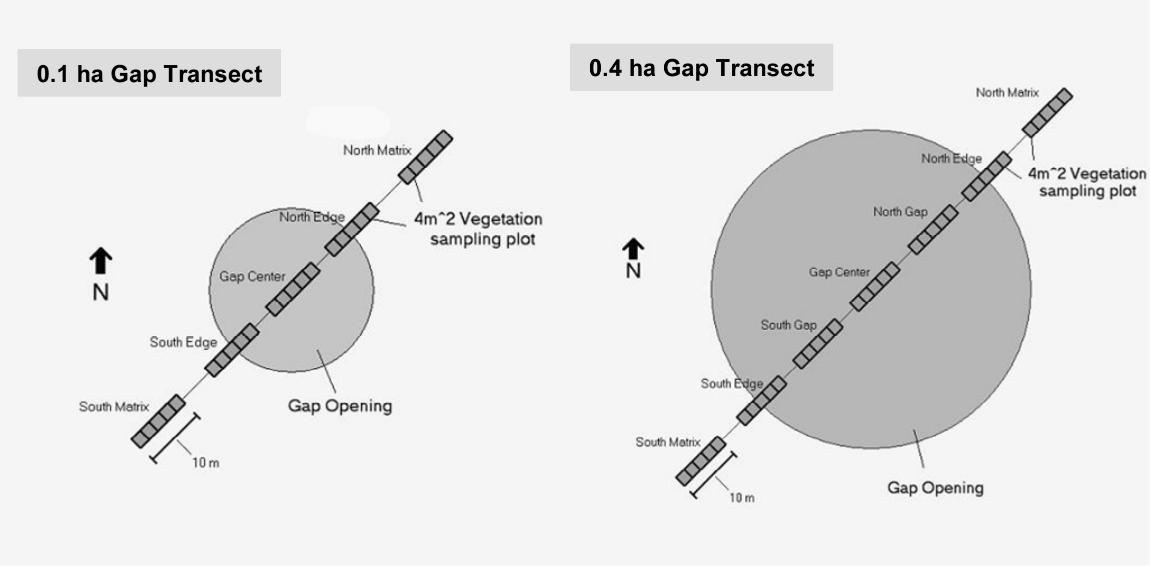

Figure A2.1. Gap transect set up for both gap sizes, all elements are to scale. Transect direction as depicted is 45°, actual transect directions varied between 0 and 45°. Distance between position groups varied slightly because gaps were not perfectly round.

Appendix 3

Table A3.1. Pairwise comparisons of transect positions from PERMANOVA tests, bolded values are significant at the $p < 0.1$ level from Monte Carlo tests.

		Keel Mountain		*North Soup*		*OM Hubbard*	
Position 1	Position 2	t	p	t	p	t	p
0.4 ha Gap							
SM	SE	0.7723	0.860	0.6326	0.807	0.8321	0.741
SM	SG	1.5788	0.027	0.8231	0.883	1.3521	0.053
SM	C	1.7938	0.029	0.9524	0.573	1.5072	0.057
SM	NG	1.7181	0.029	1.0889	0.229	1.4504	0.056
SM	NE	1.3347	0.083	0.9950	0.570	1.3356	0.116
SM	NM	0.8777	0.632	0.7942	0.970	1.0956	0.262
SE	SG	1.4746	0.060	0.7801	1.000	1.3804	0.114
SE	C	1.7882	0.027	0.9080	0.761	1.5028	0.090
SE	NG	1.6128	0.027	1.2015	0.059	1.4584	0.061
SE	NE	1.1799	0.174	1.0270	0.403	1.1549	0.198
SE	NM	0.7759	0.837	1.2392	0.085	1.0106	0.486
SG	C	0.8514	0.678	0.5043	1.000	0.6068	0.944
SG	NG	0.8326	0.749	0.7616	1.000	0.8254	0.793
SG	NE	0.8695	0.831	1.0642	0.405	1.2597	0.091
SG	NM	1.3919	0.027	1.3453	0.060	1.6318	0.056
C	NG	0.8341	0.744	0.6657	0.971	0.8751	0.772
C	NE	1.0763	0.376	1.0116	0.513	1.3667	0.028
C	NM	1.6460	0.026	1.2864	0.085	1.8044	0.054
NG	NE	0.7859	0.745	1.0738	0.402	1.0595	0.287
NG	NM	1.4111	0.031	1.4260	0.061	1.7362	0.032
NE	NM	0.8684	0.831	1.1156	0.258	1.3558	0.090
0.1 ha Gap							
SM	SE	0.7977	0.750	0.9543	0.462	0.9106	0.629
SM	C	1.6349	0.059	1.2531	0.116	1.4344	0.031
SM	NE	1.1609	0.195	0.9848	0.574	1.0946	0.285
SM	NM	0.9496	0.568	1.0748	0.307	0.8711	0.735
SE	C	1.1905	0.169	1.0802	0.396	1.1413	0.178
SE	NE	1.1087	0.203	1.2024	0.148	0.6093	1.000
SE	NM	0.9525	0.482	1.0627	0.285	0.6949	1.000
C	NE	1.3038	0.146	1.4005	0.056	0.9818	0.463
C	NM	1.1626	0.255	1.2441	0.142	1.2434	0.092
NE	NM	0.7318	0.721	0.7322	0.746	0.7939	0.859

Appendix 4

Table A4.1. Habitat preference, origin, growth-form, duration, life history strategy group (Grime 1977) classification of 176 species encountered in transect study plots. Habitat preference: F = forest understory; O = open site; I = intermediate. Origin: N = native; E = exotic. Growth form: F = fern; H = herb; G = grass; LS = low shrub; SR = sedge/rush; T = tree; TS = tall shrub. Duration: A = annual; B = biennial; P = perennial. Life history strategy: COM = competitor; RUD = ruderal; ST = stress-tolerator; N = not-classified.

Species	*Habitat preference*	*Origin*	*Growth form*	*Duration*	*Grime*
Abies grandis	F	N	T	P	N
Acer circinatum	F	N	TS	P	ST
Acer macrophyllum	F	N	T	P	N
Achlys triphylla	F	N	H	P	ST
Adiantum aleuticum	F	N	F	P	ST
Adenocaulon bicolor	F	N	H	P	ST
Agrostis capillaris	O	E	G	P	RUD
Agrostis exarata	O	N	G	P	RUD
Agoseris grandiflora	O	N	H	P	RUD
Agoseris sp.	--	--	H	P	--
Aira caryophyllea	O	E	G	A	RUD
Alnus rubra	I	N	T	P	RUD
Anemone deltoidea	F	N	H	P	ST
Anaphalis margaritacea	O	N	H	P	RUD
Arctostaphylos columbiana	I	N	LS	P	N
Arbutus menziesii	I	N	T	P	N
Asarum caudatum	F	N	H	P	ST
Asyneuma prenanthoides	I	N	H	P	N
Aster sp.	--	--	H	--	--
Athyrium filix-femina	F	N	F	P	ST
Blechnum spicant	F	N	F	P	ST
Boykinia occidentalis	F	N	H	P	ST
Bromus carinatus	O	N	G	A/B/P	COM
Bromus sp.	--	--	G	A/B/P	--
Bromus vulgaris	F	N	G	P	ST
Carex deweyana	I	N	SR	P	N
Carex hendersonii	I	N	SR	P	N
Cardamine oligosperma var. oligosperma	O	N	H	A/B	RUD
Carex sp.	--	--	SR	--	--
Campanula scouleri	F	N	H	P	COM
Cerastium arvense	I	N	H	P	RUD
Centaurium muehlenbergii	O	N	H	A/B	RUD
Ceanothus velutinus var. hookeri	I	N	TS	P	COM
Chamerion angustifolium	O	N	H	P	RUD
Chrysolepis chrysophylla var. chrysophylla	O	N	T	P	--
Chimaphila menziesii	F	N	LS	P	ST

Table A4.1 (continued)

Species	*Habitat preference*	*Origin*	*Growth form*	*Duration*	*Grime*
Cirsium arvense	O	E	H	P	RUD
Cirsium sp.	--	--	H	--	--
Cirsium vulgare	O	E	H	P	RUD
Clinopodium douglasii	F	N	H	P	ST
Claytonia sibirica	I	N	H	A/P	RUD
Cornus canadensis	I	N	LS	P	ST
Corylus cornuta var. californica	F	N	TS	P	COM
Collomia heterophylla	O	N	H	A	RUD
Cornus nuttallii	F	N	T	P	ST
Crepis capillaris	O	E	H	A/B	RUD
Cynosurus cristatus	O	E	G	P	N
Cynosurus echinatus	O	E	G	A	RUD
Dactylis glomerata	O	E	G	P	COM
Deschampsia elongata	O	N	G	P	N
Dicentra formosa	F	N	H	P	ST
Digitalis purpurea	O	E	H	B	RUD
Disporum hookeri / D. smithii	F	N	H	P	ST
Dryopteris arguta	I	N	F	P	ST
Elymus glaucus ssp. jepsonii	O	N	G	P	RUD
Epilobium ciliatum	O	N	H	P	RUD
Epilobium minutum	O	N	H	A	RUD
Equisetum arvense	O	N	H	P	N
Erigeron sp.	--	--	H	--	--
Erechtites minima	O	E	H	A/P	RUD
Festuca occidentalis	F	N	G	P	ST
Festuca sp.	--	--	G	--	--
Festuca subulata	I	N	G	P	N
Fragaria sp.	O	N	H	P	--
Frangula purshiana	F	N	T/TS	P	--
Fragaria vesca ssp. bracteata	O	N	H	P	COM
Galium aparine	O	N	H	A	RUD
Gaultheria shallon	F	N	LS	P	COM
Galium trifidum	F	N	H	P	ST
Galium triflorum	F	N	H	P	ST
Geranium carolinianum	I	N	H	A/B	RUD
Geranium sp.	--	--	H	--	--
Goodyera oblongifolia	F	N	H	P	ST
Hieracium albiflorum	F	N	H	P	N
Hieracium sp.	--	--	H	--	--
Hierochloe occidentalis	O	N	G	P	N
Holodiscus discolor	I	N	TS	P	COM
Holcus lanatus	O	E	G	P	N
Hypericum perforatum	O	E	H	P	RUD

Table A4.1 (continued)

Species	*Habitat preference*	*Origin*	*Growth form*	*Duration*	*Grime*
Hypochaeris radicata	O	E	H	P	RUD
Hydrophyllum tenuipes	F	N	H	P	N
Iris tenax	O	N	H	P	N
Juncus effusus	O	N	SR	P	N
Juncus sp.	--	--	SR	--	--
Linnaea borealis	F	N	LS	P	COM
Listera caurina	F	N	H	P	ST
Lilium columbianum	I	N	H	P	N
Lonicera ciliosa	F	N	LS	P	N
Lotus crassifolius	F	N	H	P	COM
Lonicera hispidula	I	N	LS	P	COM
Lotus micranthus	O	N	H	A	RUD
Lolium perenne ssp. multiflorum	O	E	G	A/B/P	RUD
Luzula comosa	O	N	SR	P	N
Luzula parviflora	I	N	SR	P	N
Lupinus sp.	--	--	H	--	--
Luzula sp.	--	--	SR	--	--
Madia sp.	--	--	H	--	--
Madia exigua	O	N	H	A	RUD
Madia gracilis	O	N	H	A	RUD
Mahonia nervosa	F	N	LS	P	COM
Madia sativa	O	N	H	A	RUD
Maianthemum stellatum	F	N	H	P	ST
Mentha arvensis	I	N	H	P	N
Medicago lupulina	O	E	H	A/P	RUD
Microseris sp.	--	--	H	--	--
Mitella sp.	--	--	H	--	--
Moehringia macrophylla	I	N	H	P	N
Myosotis laxa	I	N	H	A/B/P	RUD
Mycelis muralis	O	E	H	A	RUD
Nemophila parviflora	I	N	H	A	RUD
Osmorhiza berteroi	F	N	H	P	N
Oxalis oregana	F	N	H	P	ST
Oxalis suksdorfii	I	N	H	P	N
Petasites frigidus var. palmatus	I	N	H	P	N
Pedicularis racemosa	F	N	H/LS	P	N
Phleum pratense	O	E	G	P	COM
Piperia elegans ssp. elegans	F	N	H	P	N
Plantago lanceolata	O	E	H	A/B/P	RUD
Polystichum munitum	F	N	F	P	N
Prunus emarginata	I	N	T/TS	P	N
Prunella vulgaris	O	E	H	P	N
Pseudognaphalium canescens ssp. microcephalum	O	N	H	B/P	RUD
Pseudotsuga menziesii	I	N	T	P	N

Table A4.1 (continued)

Species	*Habitat preference*	*Origin*	*Growth form*	*Duration*	*Grime*
Pteridium aquilinum	O	N	F	P	COM
Ranunculus sp.	--	--	H	--	--
Ranunculus uncinatus var. parviflorus	O	N	H	A/P	ST
Rhododendron macrophyllum	F	N	LS/TS	P	N
Ribes lacustre	F	N	LS	P	COM
Ribes sanguineum	I	N	LS	P	COM
Rosa gymnocarpa	I	N	LS	P	COM
Rumex acetosella	O	E	H	P	RUD
Rubus discolor	O	E	LS	P	COM
Rubus laciniatus	O	E	LS	P	COM
Rubus lasiococcus	F	N	LS	P	ST
Rubus leucodermis	O	N	LS	P	COM
Rubus parviflorus	O	N	LS	P	COM
Rubus spectabilis	O	N	LS	P	COM
Rubus ursinus	I	N	LS	P	COM
Salix sp.	--	--	T/TS	P	--
Sambucus racemosa	F	N	TS	P	COM
Senecio jacobaea	O	E	H	P	RUD
Senecio sylvaticus	O	E	H	A	RUD
Senecio vulgaris	O	E	H	A/B	RUD
Sonchus asper	O	E	H	A	RUD
Stellaria calycantha	I	N	H	A/P	N
Stellaria crispa	I	N	H	P	N
Stachys mexicana	I	N	H	P	N
Symphoricarpos sp.	--	--	LS	P	COM
Synthyris reniformis	F	N	H	P	ST
Taxus brevifolia	F	N	T	P	ST
Taraxacum officinale	O	E	H	P	RUD
Tellima grandiflora	F	N	H	P	ST
Thermopsis montana	O	N	H	P	N
Thalictrum occidentale	F	N	H	P	ST
Thuja plicata	F	N	T	P	N
Tiarella trifoliata var. trifoliata	F	N	H	P	ST
Tiarella trifoliata var. unifoliata	F	N	H	P	ST
Toxicodendron diversilobum	O	N	LS	P	COM
Tolmiea menziesii	F	N	H	P	ST
Trientalis borealis	F	N	H	P	ST
Trisetum canescens	F	N	G	P	COM
Trillium ovatum	F	N	H	P	ST
Trifolium repens	O	E	H	P	RUD
Tsuga heterophylla	F	N	T	P	N
Umbellularia californica	O	N	T/TS	P	COM

Table A4.1 (continued)

Species	*Habitat preference*	*Origin*	*Growth form*	*Duration*	*Grime*
Vancouveria hexandra	F	N	H	P	ST
Vaccinium membranaceum	I	N	TS	P	COM
Vaccinium ovatum	O	N	TS	P	COM
Vaccinium parvifolium	F	N	TS	P	ST
Veratrum californicum var. caudatum	I	N	H	P	N
Veronica officinalis	O	N	H	P	N
Vicia americana ssp. americana	I	N	H	P	N
Viola glabella	F	N	H	P	ST
Viola sempervirens	F	N	H	P	N
Whipplea modesta	F	N	LS	P	COM
Xerophyllum tenax	F	N	H	P	ST

Appendix 5

Table A5.1. Pairwise comparisons for species group ANOVAs for the 0.1ha gaps. Bolded numbers represent significant comparisons at $p < 0.05$.

Variable	*Position 1*	*Position 2*	*t Value*	*p*
Native early seral	SM	SE	0.46	0.991
Native early seral	SM	C	-2.79	0.054
Native early seral	SM	NE	-0.02	1.000
Native early seral	SM	NM	-0.23	0.999
Native early seral	SE	C	-2.81	0.051
Native early seral	SE	NE	-0.56	0.980
Native early seral	SE	NM	-0.71	0.954
Native early seral	C	NE	2.34	0.148
Native early seral	C	NM	2.52	0.100
Native early seral	NE	NM	-0.20	1.000
Exotic	SM	SE	-1.03	0.838
Exotic	SM	C	-2.25	0.176
Exotic	SM	NE	-2.22	0.189
Exotic	SM	NM	1.23	0.735
Exotic	SE	C	-1.08	0.816
Exotic	SE	NE	-0.14	1.000
Exotic	SE	NM	1.51	0.561
Exotic	C	NE	0.89	0.900
Exotic	C	NM	2.86	0.045
Exotic	NE	NM	3.47	0.009
Late successional	SM	SE	0.08	1.000
Late successional	SM	C	1.04	0.837
Late successional	SM	NE	0.47	0.989
Late successional	SM	NM	-1.18	0.762
Late successional	SE	C	1.01	0.851
Late successional	SE	NE	0.40	0.995
Late successional	SE	NM	-1.26	0.717
Late successional	C	NE	-0.59	0.976
Late successional	C	NM	-2.22	0.188
Late successional	NE	NM	-1.74	0.419

Table A5.2. Pairwise comparisons for species group ANOVAs for the 0.4ha gaps. Bolded numbers represent significant comparisons at $p < 0.05$.

Variable	*Position 1*	*Position 2*	*t Value*	*p*
Native early seral	SM	SE	0.33	1.000
Native early seral	SM	SG	-3.12	0.038
Native early seral	SM	C	-5.29	< 0.001
Native early seral	SM	NG	-3.35	0.020
Native early seral	SM	NE	-2.10	0.363
Native early seral	SM	NM	0.93	0.966
Native early seral	SE	SG	-3.46	0.014
Native early seral	SE	C	-6.19	< 0.001
Native early seral	SE	NG	-3.60	0.009
Native early seral	SE	NE	-2.42	0.204
Native early seral	SE	NM	0.66	0.994
Native early seral	SG	C	-2.05	0.392
Native early seral	SG	NG	-0.56	0.998
Native early seral	SG	NE	0.29	1.000
Native early seral	SG	NM	5.56	< 0.001
Native early seral	C	NG	1.14	0.914
Native early seral	C	NE	2.53	0.163
Native early seral	C	NM	6.39	< 0.001
Native early seral	NG	NE	0.77	0.987
Native early seral	NG	NM	5.48	< 0.001
Native early seral	NE	NM	2.61	0.137
Exotic	SM	SE	-0.78	0.987
Exotic	SM	SG	-3.22	0.029
Exotic	SM	C	-3.52	0.012
Exotic	SM	NG	-2.32	0.249
Exotic	SM	NE	-2.45	0.190
Exotic	SM	NM	-0.20	1.000
Exotic	SE	SG	-3.04	0.048
Exotic	SE	C	-3.36	0.019
Exotic	SE	NG	-2.19	0.314
Exotic	SE	NE	-2.22	0.296
Exotic	SE	NM	1.15	0.910
Exotic	SG	C	-1.03	0.947
Exotic	SG	NG	-0.95	0.962
Exotic	SG	NE	0.62	0.996
Exotic	SG	NM	3.44	0.015
Exotic	C	NG	-0.30	1.000
Exotic	C	NE	1.52	0.730
Exotic	C	NM	3.62	0.009
Exotic	NG	NE	1.26	0.868
Exotic	NG	NM	2.31	0.250
Exotic	NE	NM	2.60	0.139

Table A5.2 (continued).

Variable	*Position 1*	*Position 2*	*t Value*	*p*
Late successional	SM	SE	-0.78	0.987
Late successional	SM	SG	-3.22	0.029
Late successional	SM	C	-3.52	0.012
Late successional	SM	NG	-2.32	0.249
Late successional	SM	NE	-2.45	0.190
Late successional	SM	NM	-0.20	1.000
Late successional	SE	SG	-3.04	0.048
Late successional	SE	C	-3.36	0.019
Late successional	SE	NG	-2.19	0.314
Late successional	SE	NE	-2.22	0.296
Late successional	SE	NM	1.15	0.910
Late successional	SG	C	-1.03	0.947
Late successional	SG	NG	-0.95	0.962
Late successional	SG	NE	0.62	0.996
Late successional	SG	NM	3.44	0.015
Late successional	C	NG	-0.30	1.000
Late successional	C	NE	1.52	0.730
Late successional	C	NM	3.62	0.009
Late successional	NG	NE	1.26	0.868
Late successional	NG	NM	2.31	0.250
Late successional	NE	NM	2.60	0.139

Appendix 6

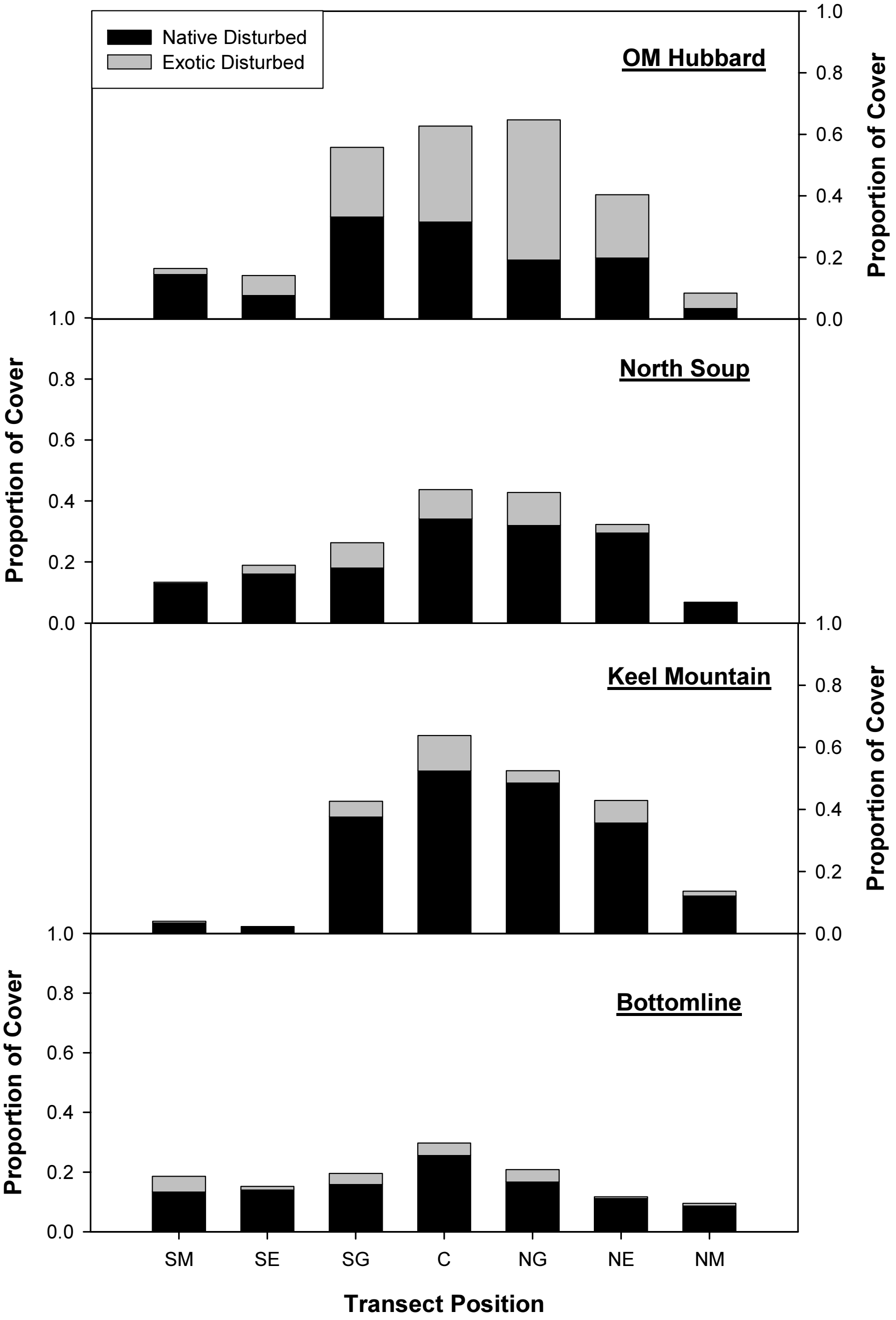

Figure A6.1. Cover of exotic and native early seral species by transect position in the 0.4ha gaps for each site.

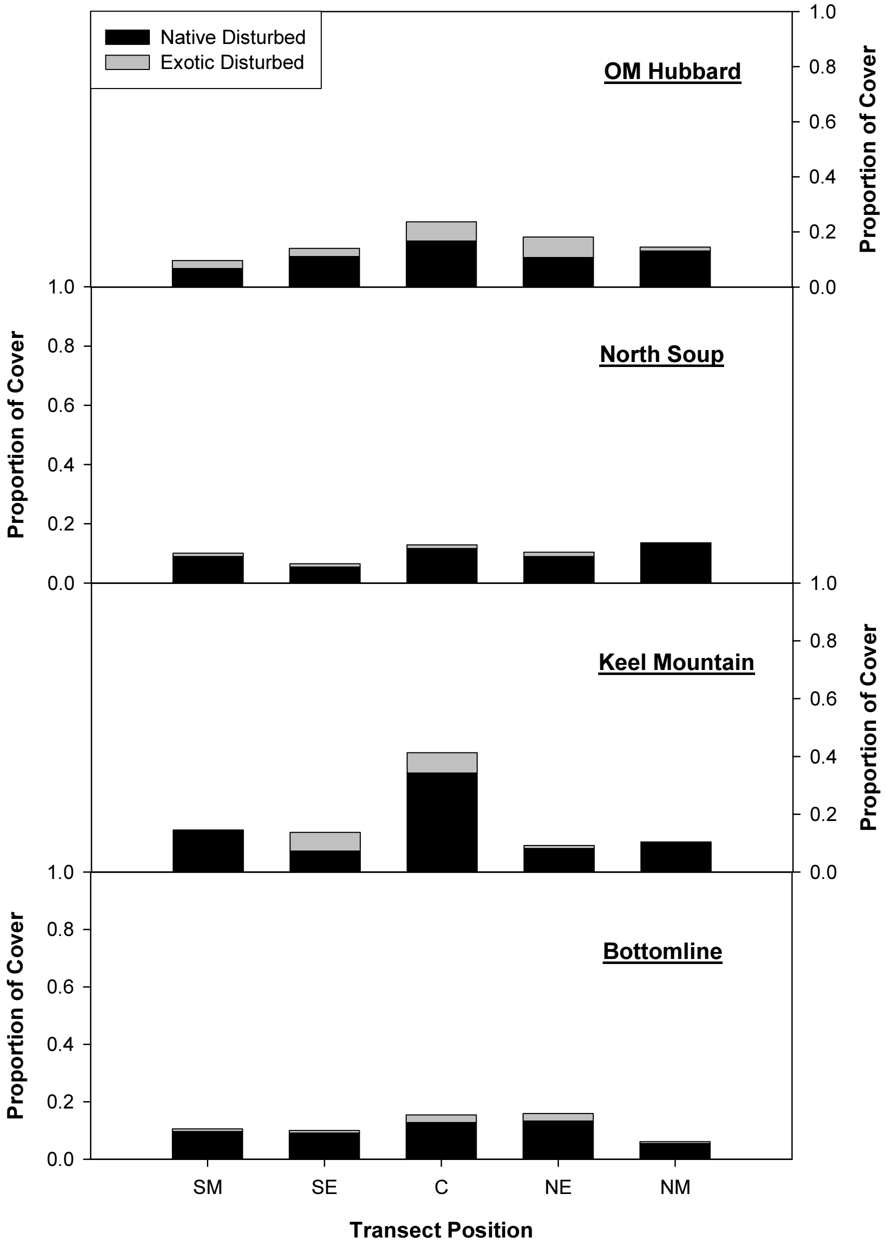

Figure A6.2. Cover of exotic and native early seral species by transect position in the 0.1ha gaps for each site.