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# Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation

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## Summary

**1.** Differential species responses to canopy gap formation may dominate organization of understorey plant community composition in many forests. Gap creation may enhance heterogeneity in understorey plant communities and could influence biodiversity patterns in young managed forests.

**2.** Our objective was to determine whether understorey plant communities exhibit patterns indicative of gap partitioning and to quantify environmental variables related to these patterns.

**3.** Patterns in understorey vegetation 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 understorey plant community composition was also assessed.

**4.** Understorey plant community composition differed significantly by location relative to gap in 0.4-ha gaps, but not 0.1-ha gaps, supporting the gap-size partitioning hypothesis.

**5.** The concurrent effects of ground-layer disturbance, gap size-related differences in resource gradient intensity, and pre-gap community composition and vegetation structure interact to influence the existence of gap partitioning in understorey plant communities.

**6.** Gap creation can influence small-scale heterogeneity in understorey plant communities and thus could be an important management tool in efforts to increase heterogeneity and biodiversity in stands and landscapes dominated by young, second growth forests.

*Key-words*: canopy gap, Douglas-fir, forest management, gap partitioning, herb layer, heterogeneity, Pacific Northwest, species composition, understorey vegetation

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## Introduction

Canopy gap formation is a common result of small-scale disturbance in forests, and can be an important factor regulating species distributions in forested landscapes (Watt 1947; Bormann & Likens 1979; Spies *et al.* 1990). In many forests, canopy gap formation is a major factor contributing to the maintenance of species diversity and vegetation structure in the overstorey canopy (Denslow 1980; Hibbs 1982; Brokaw 1985; Spies & Franklin 1989) and shrub and herb layers (Collins *et al.* 1985; Stewart 1988; Spies 1998; Roberts & Gilliam 2003). Knowledge of the effects of natural and anthropogenic disturbances on understorey plant communities is an essential element of sustainable management of forest landscapes (Halpern & Spies 1995; Roberts & Gilliam 1995; Battles *et al.* 2001).

The availability of many resources typically increases with gap formation, including light, soil moisture, nutrients, substrates (germination safe sites), and growing space (Canham & Marks 1985). The response of vegetation to variation in resource availability related to gap formation has been studied extensively in natural systems (Runkle 1981; Brokaw 1985; Moore & Vankat 1986; Stewart 1988; Bartemucci *et al.* 2006). The gap partitioning hypothesis is a theoretical framework

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that has been widely utilized to describe variation in tree species diversity in relation to forest canopy gaps and may also be useful in characterizing gap-scale patterns in understorey vegetation. Gap partitioning asserts that variation in tree species distributions can result from differential responses of species to environmental and resource gradients running from intact canopy into gaps (Ricklefs 1977; Denslow 1980). The gap-size partitioning hypothesis addresses the concept that resource gradients and associated partitioning are intensified as gap size increases (Denslow 1980; Whitmore 1989; Busing & White 1997).

Gap partitioning has received a great deal of attention in explaining diversity patterns in tropical forest ecosystems (Brokaw 1985, 1987; Denslow 1987; Schupp *et al.* 1989; Dalling *et al.* 1998; Kobe 1999). The concept has also been suggested in temperate forests as a tool to understand patterns in natural (Runkle 1982; Runkle & Yetter 1987; Lertzman 1992; Sipe & Bazzaz 1994, 1995; Busing & White 1997; Clinton 2003) and harvested gaps (Gray & Spies 1996, 1997; Coates 2000, 2002; Raymond *et al.* 2006). While the results of these investigations have been mixed, the majority of studies refute the existence of gap partitioning among canopy species in temperate forests. The failure of gap partitioning to explain patterns of temperate canopy species occurrence is likely to be related to the relatively low diversity and lack of adaptation to gap conditions in these canopy layers (Lertzman 1992; Coates 2002). The majority of these studies have likewise not supported gap-size partitioning among overstorey species in natural gaps of temperate forest systems (Lertzman 1992; Busing & White 1997). However, gap-size partitioning of overstorey species has been observed in gaps created by harvesting (Gray & Spies 1996; Coates 2002).

Although gap partitioning and gap-size partitioning hypotheses have not consistently explained distributions of overstorey species in temperate forests, they may be useful in describing patterns in understorey plant communities. The understorey in temperate coniferous forests of the Pacific Northwest USA generally exhibits higher diversity of species and functional groups than the overstorey (Halpern & Spies 1995; Bailey *et al.* 1998). Understorey species in these forests also generally exhibit greater niche specialization and therefore also a greater potential response in understorey community composition to resource gradients associated with gap formation (Roberts 2004). We therefore hypothesize that understorey plant communities in this region will be more likely than overstorey species to exhibit patterns related to resource gradients in gaps. Studies investigating understorey communities in gaps in temperate forests have, however, exhibited varied results. Responses of understorey plant growth, abundance and fecundity to gap formation have been illustrated in deciduous (Moore & Vankat 1986; Schumann *et al.* 2003) and coniferous forests (St Pierre 2000; Lindh *et al.* 2003). However, gap partitioning of understorey species composition has not been documented in either deciduous (Thompson 1980; Moore & Vankat 1986; Schumann *et al.* 2003) or coniferous forests (Anderson *et al.* 1969; London 1999).

The generally accepted model of vegetation composition in relation to the gap-phase disturbance regime combines the effects of niche partitioning along resource gradients and chance (Brokaw & Busing 2000). In understorey plant 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). We feel that this definition may need to be expanded to include specific disturbance effects. The response of potential gap species, especially those originating from the seed bank or dispersed seed, may be largely dependent on disturbance of the ground-layer, defined here as the ground surface and understorey vegetation layer (Collins & Pickett 1988a, 1988b; Roberts 2004). Filling of gaps entirely by pre-gap occupants has been associated with the absence of gap partitioning patterns (Hubbell *et al.* 1999; Brokaw & Busing 2000). Ground-layer disturbance provides gap-adapted species with more opportunities to colonize areas in which they can respond to gap formation. We hypothesize that harvest gaps may exhibit a greater propensity than natural gaps for gap partitioning in understorey plant communities due to greater disturbance of the ground-layer (Collins & Pickett 1988a, 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 understorey response to gap formation have generally concentrated on relatively small gap sizes (e.g. Moore & Vankat 1986), which may not have produced resource gradients capable of generating gap partitioning. We hypothesize that the understorey plant community in larger gap sizes may be more likely to exhibit gap partitioning than that in small gaps due to the existence of stronger resource gradients.

To test our hypotheses, we investigated variation in understorey plant communities in and around canopy gaps created in forest stands in western Oregon. We investigated patterns in two gap sizes, both of which were near the upper limit of common natural gap occurrences in the study area (Spies *et al.* 1990) and were expected to show strong gradients in resource availability (Canham *et al.* 1990). Our objectives included testing (i) whether gap partitioning exists in understorey plant communities, (ii) whether understorey vegetation patterns support gap-size partitioning, and (iii) whether disturbance of the understorey vegetation layer and ground surface is an important factor leading to the exhibition of gap partitioning in understorey plant communities. An understanding of the processes driving gap partitioning in understorey plant communities will facilitate the discussion of the role of gap creation in contributing to structural heterogeneity and species diversity in young, managed forests.

**Table 1.** Characteristics of DMS sites used in gap partitioning study. For more detail see (Cissel *et al.* 2006)

| | 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 (month/year) | 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) | *c.* 65 | *c.* 50 | > 50 | *c.* 45–50 |
| Mineral soil cover (%) | 1.1% | 0.9% | 3.0% | 4.9% |
| Site index (50 year) | 138 | 127 | 132 | 120 |

## Methods

### SITE DESCRIPTIONS

This study was part of the Density Management Study (DMS), an ongoing investigation of the effectiveness of thinning treatments in fostering development of late successional habitat features (Cissel *et al.* 2006). 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). All study stands were even-aged and dominated by 40–70-year-old Douglas-fir (*Psuedotsuga menziesii* (Mirb.) Franco) in a single canopy layer. One site (KM) had a small western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) component. Sites spanned a variety of elevations, aspects and stand histories. Site and treatment details are summarized in Table 1.

DMS 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 approximately 200 trees per hectare. Gap diameter to tree height ratios for the two gap sizes were approximately 1.0 and 2.0, respectively. Gap creation was implemented through operational harvesting and gap locations were determined by logging constraints not by condition of overstorey or understorey vegetation. Therefore, we believe that gap locations, while not randomly assigned within sites, reflect typical stand conditions in the region. Gaps that were used as landings for timber extraction were avoided in this study, but all gaps contained some ground-layer disturbance resulting from logging operations.

### STUDY DESIGN AND DATA COLLECTION

Gap transects used for sampling understorey vegetation, substrates and environmental variables were established between 1 July and 31 August 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 a fourth site (BL), resulting in a total of 15 gaps of each size. Transects originated at gap centre and extended 23 m beyond the gap edge, defined as the line extending between the boles of the nearest surrounding canopy trees, *sensu* Runkle (1982), into the surrounding forest understorey to the north/north-east (between 0 and 60°) and south/south-west (180° from N/NE bearing). Gaps were selected according to suitability for the transect layout, with the stipulation that transects avoid (at a distance greater than the total transect length) other gaps, leave islands (unthinned patches), or avoid the boundaries of the treatment or site. Understorey vascular plants (< 6 m in height) were sampled in plots (hereafter transect positions) made up of sets of five contiguous 4 m$^2$ square sampling quadrats (hereafter subplots) established parallel to transects (total transect position size was therefore 10 m by 2 m; see Fig. 1). Transect positions included: South Forest Matrix (SM; centred 54 m south of gap centre in 0.4-ha gaps and 36 m in 0.1-ha gaps, distances are approximate, actual distance depended on diameter of gap), South Edge (SE; *c.* 36 m, *c.* 18 m), South Gap Interior (SG; only in 0.4-ha gaps, *c.* 18 m), Gap Center (C), North Gap Interior (NG, only in 0.4-ha gaps), North Edge (NE), and North Forest Matrix (NM).

Ocular estimates of percentage cover were made for all vascular plant species in each subplot. Taxonomic nomenclature follows the USDA Plants Database (USDA-NRCS 2005). Percentage cover was also estimated for substrate types: litter, exposed mineral soil, coarse woody debris (> 2.5 cm diameter), stump/tree bole, and exposed rock. Data were averaged to the transect position level to account for lack of spatial independence of subplots.

Hemispherical canopy photographs were taken at subplot centres to characterize the understorey light environment. We used a Nikon Coolpix 4500 digital camera with FC-E8 Fisheye Converter Lens Attachment positioned at 1.5 m above the ground. Photographs were captured at dawn, dusk, or on days with uniform

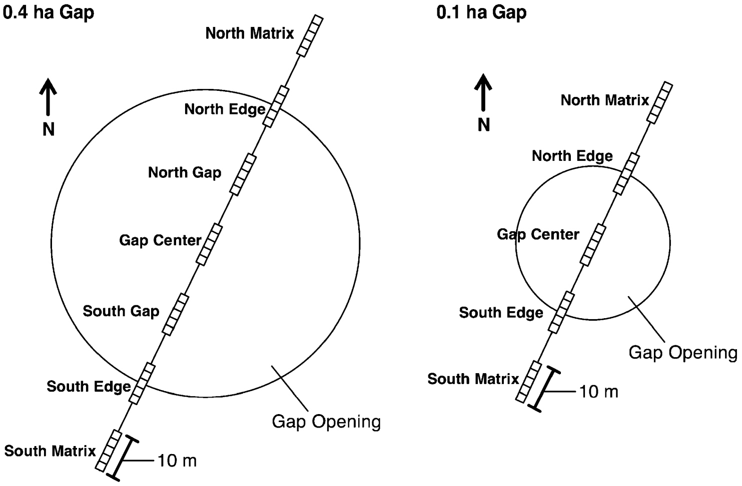

**Fig. 1.** Layout of gap-transects for both gap sizes; all elements are to scale. Figure illustrates an ideal case, in reality gaps were not perfectly round and actual distances along transects varied slightly. Orientation of gap transects is depicted as approximately NNE (22.5°), but varied between 0 and 60°.

cloud cover, 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). We used a projection function described by Frazer *et al.* (2001) to minimize lens projection distortion. Photos were analysed using Gap Light Analyser 2.0 (Frazer *et al.* 1999), and estimates of percentage canopy openness, leaf area index integrated over the zenith angles 0–60°, transmitted direct, diffuse, and total solar radiation (mol/m$^2$/d), and percentage transmitted direct, diffuse, and total solar radiation, were obtained.

## DATA ANALYSIS

### *Gap partitioning of community composition*

Tests of gap partitioning and gap-size partitioning in understorey plant species composition were made using multivariate techniques. To investigate species composition patterns, Non-metric Multi-dimensional Scaling ordination (NMS) was employed using the 'slow and thorough' autopilot setting in PC-ORD v 4.0 (McCune & Medford 1995). Species that occurred in less than 5% of plots were deleted from the analyses, species percentage cover was transformed using the arcsine square root transformation to improve data normality, and Sørensen distance was used in all multivariate analyses (McCune & Grace 2002). Correlation coefficients (Pearson's $r$) relating species abundances to ordination axes were calculated for each axis in the resulting solutions (McCune & Grace 2002). Plots were ordinated for the full data set (all sites) and subsequently for each site individually to allow us to examine the effect of transect position independent of the overwhelming differences in community composition among sites. We also investigated the relative contributions of species composition and cover to community patterns by converting the data sets from cover to presence/absence and re-running each NMS ordination to compare the effect of this change on results for each site.

To demonstrate the pattern and intensity of partitioning along the gap transects, we tested for differences in community composition among transect positions using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). This test allows for the use of non-euclidean distance measures (in this case Sørensen distance) as well as nested designs (McCune & Grace 2002). We accounted for nesting in the sampling design by considering each transect position to be nested within a transect and transects to be nested within sites. Transect distance was included as a covariate in PERMANOVA tests to account for spatial proximity of transect positions within a transect. However, 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). These three sites were also the sites that exhibited some evidence of partitioning in the NMS analysis. This method was applied using the PERMANOVA program (Anderson 2005).

### *Environmental variables and gap partitioning*

To investigate relationships between environmental variables and understorey vegetation patterns, canonical correspondence analysis (CCA) was performed on the two gap sizes separately. Environmental variables included in this analysis were selected to contrast the respective effects of gap (and gap size) related variation in resource availability and ground-layer disturbance on understorey vegetation patterns. Variables included in the analysis were: estimated percentage transmitted radiation, predicted soil moisture, percentage cover of slash (coarse woody debris), percentage cover of

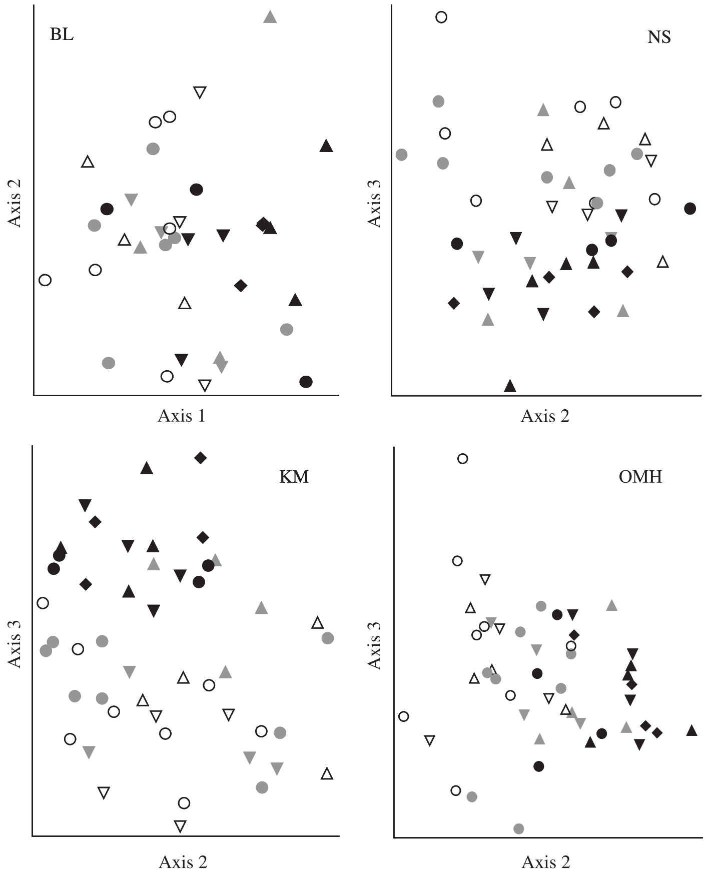

**Fig. 2.** NMS ordinations of transect plots on abundance of species for each site individually. Black symbols represent gap interior plots, grey symbols edge plots, and open symbols forest matrix plots. Triangles represent 0.4-ha gaps, circles 0.1-ha gaps.

exposed mineral soil, and distance to nearest road or skid trail. Soil moisture was predicted based on 6 years mean soil moisture response to gap creation on north–south transects across gaps (similar to those investigated in this study in size and diameter to tree height ratio) in western Oregon forests as described by Gray *et al.* (2002). All CCAs were run using default settings in PC-ORD (centred with unit variance), and Monte Carlo tests were performed to evaluate the significance of the species-environment relationships (H0: no linear relationship between matrices). Environmental variables were examined for collinearity using a correlation matrix and no instances of high correlation ($r > 0.5$) between variables were found.

## Results

### GAP PARTITIONING OF COMMUNITY COMPOSITION

### *NMS results*

The range of stand histories and ecoregions represented in this study were evident in NMS ordination of plots across the full data set as strong separation occurred among sites but not transect positions. After eliminating the influence of site differences on plant communities by ordinating each site individually, community composition separated among gap transect positions at three of the four sites. All individual site ordinations had three-dimensional solutions. The two axes from each solution that explained the greatest amount of variance from the original distance matrix are presented in Fig. 2.

At three of four sites (KM, NS, OMH) separation among transect positions was evident (Fig. 2). At each of these sites the axis along which partitioning was apparent explained much of the variation in community composition (Table 2). At the KM site the axis that illustrated gap partitioning (Axis 3) accounted for the majority of the variation in the community (Table 2) and was most strongly correlated with two species typical of open sites: *Digitalis purpurea* L. ($r = 0.629$, correlation with NMS axis) and *Rubus leucodermis* Dougl. ex Torr. & Gray ($r = 0.690$). At the OMH site, the gap partitioning axis (Axis 2) also explained the greater part of the total variation and was related to ruderal species such as *Hypochaeris radicata* L. ($r = 0.715$) and *Aira caryophylla* L. ($r = 0.486$). Axis 3 at OMH explained nearly as large a proportion of the variation as Axis 2 and was related to an elevation gradient at the site ($r = -0.515$) and to the native shrub

**Table 2.** Results of NMS ordinations, *P*-values were obtained from Monte Carlo tests of stress vs. 50 randomized runs of the data. 'Cover' is results with species represented by their percentage 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 $R^2$ | 13.5 | 19.1 | 19.3 | 33.2 | 21.8 | 24.9 | 14.3 | 38.2 |
| Axis 2 $R^2$ | 52.9 | 12.0 | 23.2 | 11.3 | 31.2 | 22.5 | 34.4 | 30.8 |
| Axis 3 $R^2$ | 15.4 | 38.8 | 37.8 | 27.6 | 28.7 | 29.0 | 33.9 | 11.9 |

*Gaultheria shallon* Pursh ($r = 0.658$). At NS, Axis 2 explained the greatest proportion of the variation (Table 2) and was correlated with the native fern *Polystichum munitum* (Kaulfuss) K. Presl ($r = 0.848$). Axis 3, the gap partitioning axis at NS, also explained a substantial amount of variation and was related to open site species such as *Rubus leucodermis* Dougl. ex Torr. & Gray ($r = 0.609$) and *Cirsium vulgare* (Savi) Ten. ($r = 0.608$).

In contrast, at BL no gap partitioning pattern was apparent (Fig. 2). The majority of variation at BL was explained by Axis 2, which suggests the influence of clonally spreading, rhizomatous species such as *Symphoricarpos* sp. Duham. ($r = -0.656$) and *Whipplea modesta* Torr. ($r = 0.615$). Species such as these dominated the understorey at the site and were likely to be present before gap creation.

Conversion of the data into presence/absence form had little effect on the conclusions of the ordination analyses at the three sites (KM, NS, OMH) that exhibited gap partitioning (Table 2). Therefore, abundance data were taken to be indicative of composition, and not merely differences in species cover between plots.

### *Comparison of transect positions*

Strong differences in community composition among transect positions were evident in large gaps but not small gaps, suggesting gap-size partitioning. Additionally, patterns and strengths of pairwise differences among positions varied between gap sizes and sites (Table 3). Community composition differed by transect position for the three sites included in the PERMANOVA analysis (which were also the sites that exhibited the strongest gap partitioning effect in the NMS analysis) in the large gaps ($F_{18,63} = 1.31$, $P = 0.005$). In contrast, community composition did not differ among transect positions in the small gaps ($F_{12,45} = 0.96$, $P = 0.629$). Pairwise comparisons of transect positions illustrated that differentiation in community composition occurred primarily between gap interior and forest matrix positions. However, gap edge positions and gap interior positions also differed from each other in a number of cases, typically exhibiting a north–south distinction in species composition (Table 3).

### ENVIRONMENTAL, RESOURCE AND DISTURBANCE VARIABLES IN RELATION TO GAP PARTITIONING

CCA analysis indicated that ground-layer disturbance and resource availability related to canopy removal interact to influence understorey community composition. In the large gaps, which exhibited gap partitioning, variables related to both ground-layer disturbance and resource availability were the strongest predictors of community composition (Table 4). Plots of the first two axes from CCA ordinations are presented in Figs 3 and 4. In the larger gaps, the sum of the canonical eigenvalues was 0.451 and the Monte Carlo test showed that all three axes were significant ($P = 0.01$). Two of the environmental variables, mineral soil cover and total transmitted radiation, were strongly related to understorey species composition (interset correlations > 0.5; Table 4). In the smaller gaps, the sum of the canonical eigenvalues was 0.343 and the Monte Carlo test showed that all three axes were significant ($P < 0.03$). Two of the environmental variables, transmitted radiation and predicted soil moisture, were strongly related to species composition (interset correlations > 0.5; Table 4). CCA ordinations explained relatively little of the overall community variation (Figs 3 and 4); this was probably related to large differences in community composition among sites. Although gap-related variables accounted for a relatively small portion of the total variation, the axes representing these variables were significant and the patterns exhibited are of interest.

## Discussion

### GAP PARTITIONING OF UNDERSTOREY COMMUNITY COMPOSITION

Within 5 to 7 years after gap creation, understorey plant communities showed differentiation in vegetation composition by gap position that was consistent with the predictions of the gap partitioning hypothesis. Previous studies of understorey plant responses to gap formation demonstrated little variation in community composition (Brewer 1980; Thompson 1980; Moore & Vankat 1986; Collins & Pickett 1988a; Schumann *et al.*

**Table 3.** Pairwise comparisons of transect positions from PERMANOVA tests. *Denotes *t*-values that were significant at the $P < 0.1$ level from Monte Carlo tests; no adjustments were made for multiple comparisons

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

**Table 4.** Inter-set correlations of environmental variables with CCA ordination axes for both gap sizes

| Variable | Axis 1 | Axis 2 |
|---|---|---|
| 0.4-ha gaps | | |
| Mineral soil cover | –0.551 | –0.173 |
| Coarse woody debris | 0.402 | 0.392 |
| Total transmitted radiation | –0.643 | 0.318 |
| Predicted soil moisture | –0.200 | 0.351 |
| Distance to road/skid trail | 0.371 | –0.110 |
| 0.1-ha gaps | | |
| Mineral soil cover | –0.126 | 0.126 |
| Coarse woody debris | 0.427 | –0.391 |
| Total transmitted radiation | –0.484 | –0.590 |
| Predicted soil moisture | 0.119 | –0.569 |
| Distance to road/skid trail | 0.286 | 0.138 |

2003). In these studies, just as at one of our sites, understorey responses to gap formation were generally characterized by increased cover of remnant species, rather than invasion by ruderal species. Therefore,

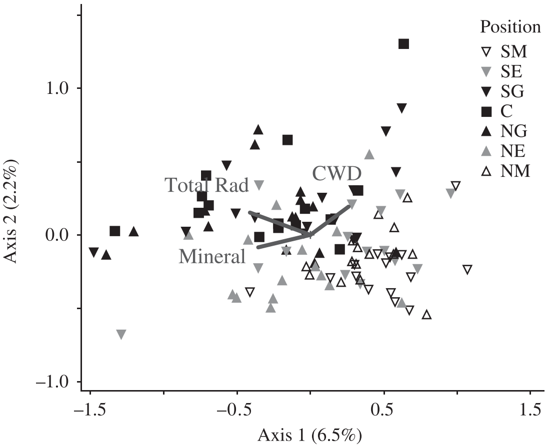

**Fig. 3.** CCA ordination diagram illustrating the distribution of transect position plots in ordination space for the 0.4-ha gaps. Correlated environmental variables are presented as vectors. Total Rad is total transmitted radiation, Mineral is cover of mineral soil, and CWD is cover of coarse woody debris.

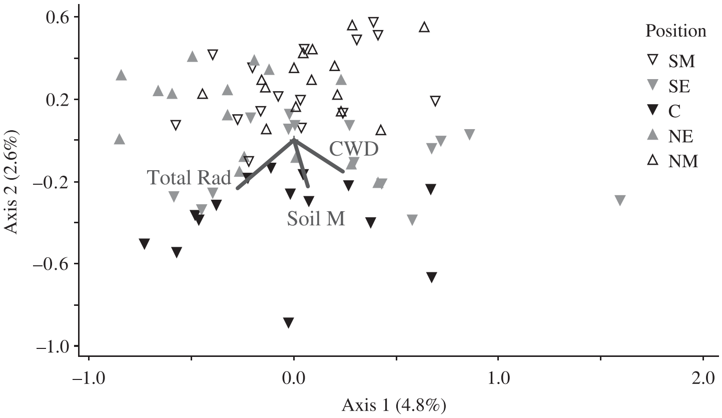

**Fig. 4.** CCA ordination diagram illustrating the distribution of transect position plots in ordination space for the 0.1-ha gaps. Correlated environmental variables are presented as vectors. Total Rad is total transmitted radiation, Soil M is predicted soil moisture, and CWD is cover of coarse woody debris.

vegetation community patterns in gaps may rely heavily on the condition of the understorey layer prior to gap formation.

Overstorey condition prior to gap creation can also affect the impact of gaps on understorey plant communities and this impact is likely to differ between forest types. In deciduous forests, light-demanding understorey species with a spring ephemeral growth form can persist under an undisturbed forest canopy (Collins *et al.* 1985; Moore & Vankat 1986). This pattern promotes pre-disturbance understorey 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). Species cover responses were minimal in deciduous forests of Ohio (Moore & Vankat 1986), Pennsylvania (Collins & Pickett 1988a, 1988b), Ontario (Reader & Bricker 1992), and New York (Goldblum 1997). In contrast to that of a deciduous forest, coniferous canopy cover, such as that in this study system, is persistent throughout the year, and ruderal and other light-demanding species are therefore more likely to be limited to gaps and edges (Nelson & Halpern 2005). Research in coniferous forests of the Pacific Northwest has typically illustrated strong responses in understorey vegetation cover, but not composition, related to gap creation (London 1999; St Pierre 2000; Lindh *et al.* 2003). In addition, the aforementioned studies generally investigated gaps that were both smaller and less disturbed than those in our study, which may help explain the absence of a gap partitioning response in understorey plant communities.

As expected, the greatest differentiation in community composition was between forest matrix and gap interior (C, SG, NG) positions. However, some differentiation between gap interior and gap edge positions was apparent and was frequently related to distinctions between north and south transect positions. This pattern is consistent with the pattern of variation in most environmental and resource gradients related to gap formation (Canham *et al.* 1990) and further demonstrates the influence of gap partitioning.

### GAP-SIZE PARTITIONING OF UNDERSTOREY COMMUNITY COMPOSITION

Gap-size partitioning was also exhibited in our study, as large gaps displayed greater partitioning of the understorey community than small gaps. Previous studies found little evidence of an influence of gap size on understorey community composition in deciduous forest gaps (Collins & Pickett 1988a, 1988b). However, an effect of gap size on growth and fecundity of understorey plants has been documented in Douglas-fir forests (St Pierre 2000). Gap-size partitioning of tree recruitment has also been demonstrated in experiments encompassing a wide range of gap sizes (Gray & Spies 1996, 1997; Coates 2000). Although our study included a limited range of gap sizes, we illustrated distinctly different patterns in compositional partitioning between gap sizes. Smaller gaps may not create strong enough gradients in resource differentiation to elicit a response in gap-associated species. Thus, we propose that gap partitioning of understorey plant communities is limited to certain gap sizes, which would vary among systems, but may be somewhat consistent in the relative strength of environmental and resource gradients they exhibit.

### DISTURBANCE, ENVIRONMENTAL AND RESOURCE VARIABLES IN RELATION TO GAP PARTITIONING

Our results support the hypothesis that vegetation responses to gap-phase disturbance are determined by a combination of the effects of niche partitioning and ‘chance’, which is represented in understorey plant communities by determination of species composition by gap capture of existing individuals and by stochastic seed dispersal (Brokaw & Busing 2000). Our results also suggest that disturbance of the ground surface and understorey vegetation layer is an integral component of vegetation response to gap formation (Beatty 2003). However, although the influence of ground-layer disturbance may facilitate differentiation in species composition, to be expressed these differences require strong resource partitioning, such as that found in larger gaps in our study. Ground-layer disturbance appears to foster expression of gap partitioning patterns in the understorey plant community by enabling germination and growth of gap adapted species in areas affected by gap formation.

### *Disturbance-related variables*

The influence of an interactive relationship between ground-layer disturbance and resource gradients on understorey plant community patterns was supported by analysis of the relationship between community composition and environmental variables. Patterns in understorey community composition were strongly related to disturbance-associated variables, especially exposed mineral soil (which resulted largely from harvesting-related ground surface disturbance and to a lesser extent from animal burrows; R. Fahey, personal observations). The relationship of understorey species distributions to ground disturbance in natural settings has been documented in other forest systems (Thompson 1980; Beatty 2003). 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 & Pickett 1988a). Another indicator of the importance of ground-layer disturbance would be an association between community composition and distance to roads or skid trails, which are extreme disturbances of all vertical stand layers (Roberts 2004). Roads and skid trails can be related to community composition because these features can act as an invasion pathway for early seral species (Parendes & Jones 2000; Berger *et al.* 2004). This relationship was not especially strong in our data, possibly in part because the overall abundance of invasive species was generally low (Fahey 2005). Cover of slash, another component of harvest disturbance, has been related to community composition in a study of responses of understorey species to green tree retention harvests in the Pacific Northwest (Nelson & Halpern 2005). Coarse woody debris cover, much of which was probably harvesting slash, was not strongly related to vegetation distributions in this study system, but may be more influential on sites without slash management.

The influence of gap formation on understorey plant communities may be strongly related to the vertical (or three-dimensional) distribution of disturbance intensity (Roberts 2004). In attempting to predict the effect of gap creation on understorey communities, it may be necessary to look beyond canopy removal as an indicator of gap influence. Disturbance of the ground-layer may be of primary importance to post-disturbance patterns of understorey vegetation (Beatty 2003). Quantification of the vertical distribution (including below-ground processes) of disturbance may make it possible to better predict the impact of gap creation on understorey communities.

### *Resource and environmental variables*

Ground-layer disturbance may be necessary for the initiation of gap partitioning patterns in understorey plant communities, but an interactive relationship with resource availability seems to best explain variation in community composition. The environmental and resource variables that were related to community composition patterns at each site (NMS axis correlations $> 0.5$) included both gap (transmitted radiation, leaf area index, soil moisture) and non-gap (slope, elevation) related variables. Leaf area index, which is negatively associated with the canopy opening, could be indicative of the influence of a number of resources, including nutrients, soil water and diffuse radiation, as well as some environmental variables such as soil and air temperature, and humidity. Separation of effects of this suite of gap-related variables may be quite difficult and further research may be warranted.

The Mediterranean climate of the Pacific Northwest USA is characterized by seasonal drought, and therefore availability of soil moisture may be especially influential on plant distributions in this region (St Pierre 2000; Lindh *et al.* 2003). Even in eastern deciduous forests, which have a less consistent pattern of seasonal drought, soil moisture can be a major factor affecting understorey cover in relation to gaps (Anderson *et al.* 1969; Moore & Vankat 1986). However, a study specifically investigating the influence of soil moisture on regeneration of canopy species in experimental gaps suggested that microsite variation superseded the larger scale effect of enhanced soil moisture availability (Gray & Spies 1997; Gray *et al.* 2002). Our results appear to support this finding as predicted soil moisture was not strongly related to community composition.

Although it was not possible to separate the range of within-gap variables that may be responsible for affecting species distributions, our results suggest that the influence of transmitted radiation was substantial. Total transmitted radiation was the variable most strongly related to community composition patterns in both gap sizes. Therefore, it appears that the potential for differentiation of community composition exists in areas influenced by ground-layer disturbance and that this differentiation is expressed only in the presence of high levels of available transmitted radiation.

## LIMITATIONS

Pre-disturbance species composition can have a profound influence on the make-up of the post-disturbance community (Connell & Slatyer 1977; Hughes & Fahey 1991; Nelson & Halpern 2005). We lack specific knowledge of the pre-treatment vegetation communities at these sites. This shortcoming makes it difficult to draw conclusions about the specific effects of gap creation, especially in relation to distributions of individual species, and we have therefore based our conclusions on the community as a whole (Nelson & Halpern 2005).

It is also important to note that we did not measure variation in nutrient dynamics, air and soil temperatures, or humidity, all of which may have influenced understorey plant communities (Canham & Marks 1985; Muller 2003). Time since gap formation may also affect the strength of gap influence on the understorey environment and plant community (Runkle 1982; Moore & Vankat 1986; Dirzo *et al*. 1992). Cover of understorey species may vary with gap age (Moore & Vankat 1986), and it is likely that species composition would also change over time in a gap environment (Brokaw 1985; Brokaw 1987; Schumann *et al*. 2003). As regeneration of canopy species fills gaps in the canopy and reduces resource availability to the understorey layer, the importance of certain species is likely to be reduced (Halpern 1989; Lindh & Muir 2004). Therefore, gap effects on understorey communities may be transient and the gap partitioning response observed here might be short-lived (Dyrness 1973; Halpern 1989). However, vestiges of partitioning patterns may persist for some time because not all understorey species will respond similarly to restoration of the overstorey canopy (Halpern 1989) and because the understorey layer may affect future tree regeneration (George & Bazzaz 2003; Royo & Carson 2006).

## Conclusions

Patterns consistent with gap-size partitioning in understorey plant communities were evident in harvest gaps created in young Douglas-fir forests of western Oregon. The expression of these patterns in understorey plant communities may be largely dependent on the concurrent influence of ground-layer disturbance, a strong resource gradient, and pre-disturbance vegetation composition and structure. Further investigation of the relationship between gap formation and understorey communities should account for these factors.

The existence of small-scale variation in understorey vegetation in gaps, as evidenced by gap partitioning, demonstrates that gap formation can create heterogeneity in understorey plant communities. This small-scale heterogeneity may indicate that gaps can influence stand and landscape heterogeneity, both in understorey plant communities and also in other taxa that rely on understorey vegetation for food or habitat (Levey 1988; Schowalter & Zhang 2005). Therefore, creation of gaps may have the potential for increasing overall stand heterogeneity and diversity. However, gap creation may also promote the establishment of exotic plant species in the presence of a seed source (Beggs *et al*. 2005; Fahey 2005). In designing management treatments, gap size and percentage of stand area allocated to gaps should be carefully considered and the correct prescription may depend greatly on management objectives and original stand condition. We believe that our general conclusions regarding the influence of ground-layer disturbance on understorey vegetation patterns may be applicable not only to created gaps but also to natural gaps in a variety of ecosystems. An understanding of understorey responses to gap formation will help further our overall knowledge of the effects of gaps on structural heterogeneity and biodiversity in forests.

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