



Effects of canopy gaps on forest floor vascular and non-vascular plant species composition and diversity in an uneven-aged *Nothofagus betuloides* forest in Tierra del Fuego, Chile

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Abstract: Canopy gaps modify the environmental conditions available for plant growth in forests. Small canopy gaps are frequent in *Nothofagus betuloides* forests of Tierra del Fuego. Our objective was to study whether the forest floor vascular and non-vascular plant species composition and diversity are influenced by the occurrence of small-scale disturbances due to changes in the below-canopy solar radiation transmittances and forest floor heterogeneity (cover of litter, bare soil and fallen woody debris classed in three decay stages) in a *N. betuloides* forest located in south western Tierra del Fuego (53°59'S, 69°58'W). The vegetation was sampled in and around 13 canopy gaps (47 m² on average). Following a light gradient, 65 plots (2 × 2 m) were established. The cover of all plant species was recorded using Londo's scale. Species richness and total cover were calculated for each of the following taxonomical groups: spermatophyta (monocotyledons, dicotyledons), pteridophyta, bryophyta, marchantiophyta, anthocerotophyta and lichens. There were 63 species found on the forest floor. Marchantiophyta was the most diverse group with the highest species richness (6.6 species per plot). The vegetation on the forest floor was very homogeneous in species composition, richness and species diversity. The ordination analysis (NMS) showed that the community composition was weakly influenced by the patterns of below-canopy solar radiation transmittances and substrate heterogeneity. MRPP analysis of the community composition did not reveal differences in plant species assemblages between positions along transects running from areas beneath closed canopy to the open centres of canopy gaps. The marchantiophyte *Chiloscyphus magellanicus* was the only species which can be considered to be an indicator species; it was more likely to occur in gap centres (more open conditions). We conclude that these small canopy gaps do not very much modify the forest floor communities and the communities can be considered relatively stable.

Abbreviations: IDWD–Intermediate Decayed Fallen Woody Debris, LDWD–Least Decayed Fallen Woody Debris, MDWD–Most Decayed Fallen Woody Debris, MRPP–Multi-response Permutation Procedure Analyses, NMS–Non-metric Multidimensional Scaling, PAI–Plant Area Index.

Nomenclature: Zuloaga et al. (2008) for vascular plants; Müller (2009) for bryophytes; Hässel de Menéndez and Rubies (2009) for marchantiophytes and anthocerotophytes; and Galloway and Quilhot (1998) for lichens.

Introduction

Many forests experience frequent, small-scale canopy disturbances caused by single or multiple tree-falls creating gaps that over time affect large areas (Spies et al. 1990). The gaps modify existing microsites on the forest floor and create new ones accompanied by an increase in light, water and soil nutrients (Canham and Marks 1985) thereby creating different microsites (Collins et al. 1985).

Much attention has been focused on the changes to vascular plant species composition and diversity due to small-scale canopy disturbances (Collins et al. 1985, Busing and White 1997, De Grandpré et al. 2011). However, less clear are the effects of natural small-scale canopy gaps on bryophyte species composition and diversity (Jonsson and Esseen 1990, Kimmerer and Young 1996, Kimmerer 2005). None-

theless, it has been suggested that the bryophyte species composition is affected by the abundance and properties of substrates available for colonization on the forest floor (McAlister 1995, Crites and Dale 1998, Mills and Macdonald 2004). Because we only have limited knowledge of the processes that influence the spatial structure and dynamics of bryophyte communities (Kimmerer and Young 1996, Kimmerer 2005), this paper contributes to the understanding of the effects of natural, small-scale canopy gaps on the forest floor vascular and non-vascular species composition and diversity due to changes in solar radiation transmittances and substrate conditions (microsites).

Most of the studies related to natural canopy disturbances have focused on the dynamics of woody species regeneration in South American *Nothofagus* dominated forests (e.g., Veblen 1989, Rebertus and Veblen 1993, Fajardo and de Graaf

2004). In these studies of natural canopy gaps, other forest floor plant species (i.e., herbs, ferns, and bryophytes) have been largely ignored.

Nothofagus betuloides dominated forests are the world's southernmost evergreen forest type (Promis et al. 2008). These forests are very dense, and general descriptions of the forest floor have shown that only a few vascular plant species and a thick cover of lower plants (up to 100% of coverage) dominate here. The many fallen decaying tree trunks occur as massive mounds covered by extensive, deep, spongy carpets of liverworts, mosses, filmy ferns, and lichens. Epiphytes grow on the stems and branches of the trees (Pisano 1977, Roig et al. 1985, Promis et al. 2008).

Small-scale canopy gaps are the most frequent fine-scale disturbances in these forests of Tierra del Fuego (Rebertus and Veblen 1993, Rebertus et al. 1993, Veblen et al. 1996, Promis 2009). *N. betuloides* has been found to be capable of establishing in small canopy gaps (Rebertus and Veblen 1993, Gutiérrez 1994, Arroyo et al. 1996, Promis 2009). At the same time, Pisano (1971) showed that a shrub layer dominated by *Gaultheria mucronata* and *Empetrum rubrum* variable in abundance and height can be found in *N. betuloides* forest canopy gaps. However, the effects of small-scale canopy gaps on forest floor non-vascular plant species richness for these forests, has not yet been studied.

Along with the knowledge gap concerning ground vegetation in natural *N. betuloides* forests of Tierra del Fuego, there is also an intensifying demand for both the utilisation and the preservation of these forests (Cruz and Caldenteu 2007). One reason for the creation of the Cape Horn Biosphere Reserve was due to the uniqueness of the non-vascular flora occurring in the sub-Antarctic Magellanic ecosystems (Rozzi et al. 2008). Therefore, it is of great value: (1) to benchmark the natural biodiversity of these forest types and (2) to understand the role of one of the most frequent natural disturbances for this forest type - small-scale canopy gaps that maintain or change the forest floor plant species diversity.



Figure 1. Map of southern Patagonia showing Tierra del Fuego and the forest studied on the Río Cónдор (modified from Promis et al. 2008).

We expected that the forest floor vegetation would be influenced by the occurrence of small-scale disturbances due to changes in solar radiation transmittances and substrate conditions. Related to this assumption, the following questions were addressed: (1) how do natural small-scale disturbances affect the forest floor plant species richness, diversity and abundance, (2) how do changes in the solar radiation transmittances and substrate conditions produced by the small-scale disturbances modify the forest floor plant species composition, and (3) are there forest floor plant species that indicate environmental differences between disturbed and undisturbed areas under the canopy layer?

Methods

Study area

The study was conducted in an uneven-aged, evergreen, pure *N. betuloides* forest (20 ha, 1,362 trees ha⁻¹, 105 m² ha⁻¹ basal area). The forest had neither a history of human activities nor were there any signs of such. The evergreen *N. betuloides* forest type, here grows on shallow soils characterized by a surface layer, up to 20 cm thick, of partially decomposed organic matter covering a podzolic soil. The shrub layer is species poor but there is a very dense layer of epiphytic ferns, mosses and liverworts, especially on the slowly decaying fallen tree trunks (Promis et al. 2008). The forest is located at the 'Estancia Olguita' on the southeastern bank of the Río Cónдор (53°59' S, 69°58' W), between 180 and 212 m. a.s.l. and on the southwestern Chilean side of Tierra del Fuego (Fig. 1).

The area is part of the Northern Antitropical sub-zone with a mean air temperature of 9.0-9.5 °C in the warmest month of the year remaining above zero in the coldest month. The mean annual rainfall lies between 500-600 mm but can reach up to 900 mm. The wind direction is commonly west to southwest with speeds averaging between 14-22 km h⁻¹ and with a maximum wind speed in summer of more than 100 km h⁻¹ (Tuhkanen 1992).

The study area is part of the subalpine zone where the relief is characterised by valleys, deepened and U shaped by glaciers, running parallel to the Andes (Frederiksen 1988).

Selection of canopy gaps

In the forest dominated by *N. betuloides*, the forest floor vegetation under thirteen canopy gaps (used previously for a canopy gap and disturbance dynamics research project, Promis 2009) was studied. The gap soil conditions represent the typical upland podzolic soils of this forest type being well-drained, and shallow (<50 cm). A 'gap' was defined as the horizontal projection of a canopy opening to the ground surface (Runkle 1982) larger than 20 m² in area. It was considered a closed gap if the vegetation growing below the opening was more than 2 m tall (Brokaw 1982). In a previous study canopy gap sizes between 21 and 98 m² and a mean area of 51 m² were measured in this pure *N. betuloides* forest

(Promis 2009). The thirteen gaps selected for this study correspond with this size range (in average 47 m^2 with a range between 21 and 92 m^2). Their mean expanded gap area (definition according to Runkle 1982) was 167 m^2 with a range between 110 and 278 m^2 . An analysis of the canopy gap ages revealed that they were created at different times. Eight were classified as old (gaps created > 15 years ago), two as middle-aged (created between 6 and 15 yrs. ago) and three as young (created less than 6 yrs. ago). The gap age was estimated by using sapling release dates based on bud scale scar counts and by assessing the decay stage of the gap-maker trees (trees that caused canopy opening, Runkle 1982).

Forest floor vegetation sampling

The forest floor vegetation was sampled in a total of 65 plots placed inside and around the edge of the 13 canopy gaps during the summer of 2006. Following a gradient of light conditions, five plots per gap (Fig. 2) were established. One plot was located in the centre of the gap, one on the southeast gap edge, one on the northwest gap edge, one below the undisturbed canopy to the southeast and another one to the northwest of the GAP. The plots in undisturbed canopy positions (southeast and northwest) were located at a distance of half the height of the highest tree in the vicinity of the gap ($26 \text{ m} \pm 0.9$; average \pm SE). This distance was measured from the base of the trees at the edges of the canopy gap. Because all canopy gaps had different shapes and sizes, the distance between the positions of gap centre, southeast gap edge and northwest gap edge in the different gaps was not constant for all gaps.

Within each plot, the cover of each forest floor vegetation taxonomical group (monocotyledons, dicotyledons, pteridophyta, bryophyta, marchantiophyta, anthocerotophyta and lichens) and the combined cover by plant species was visually estimated using the Londo scale (Londo 1984).

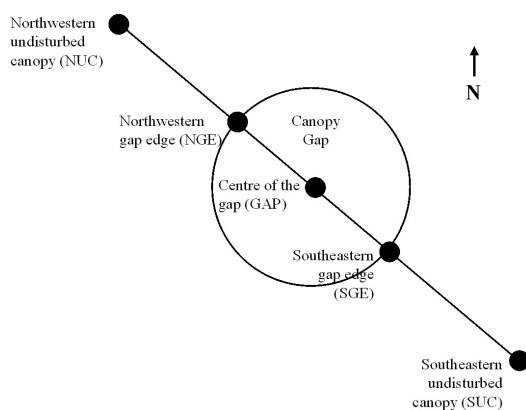


Figure 2. Transect layout and plot locations within the canopy gaps. The circular shape of the canopy gap does not reflect reality as all gaps analysed had different shapes and therefore the distances between the plot locations on the transect were not constant.

The bryophyta, marchantiophyta, anthocerotophyta and lichen species were collected and later identified in the laboratory under a microscope.

Environmental variables

The direct and diffuse below-canopy solar radiation transmittances and the plant area index (PAI) were estimated indirectly using hemispherical photographs. One hemispherical photograph was taken at each plot centre. A Nikon Coolpix 990[®] digital camera (Nikon Corporation, Tokyo, Japan) fitted with a Nikon FC-E8[®] fisheye converter (Nikon Corporation, Tokyo, Japan) was used to take photos from approximately 1.3 m above the ground. The images were analysed using HemiView version 2.1 (Delta-T Devices, Cambridge, UK) (Rich et al. 1999). The digital images were processed and analysed following a standard protocol for the evaluation of hemispherical photographs described by Promis et al. (2011). As hemispherical photographs do not distinguish between opaque objects (e.g., branches) and photosynthetic tissue (leaves), PAI was considered to be the sum of all canopy elements blocking out light (Holst et al. 2004).

The substrate heterogeneity, within all plots, was assessed by estimating the cover of litter, exposed mineral soil and fallen woody debris. Based on the structural characteristics of the wood, a three-class system for describing the degree of decay of fallen woody debris ($> 10 \text{ cm}$ diameter) was applied: a) least decayed fallen woody debris (LDWD), having hard wood into which a knife can only penetrate a few millimetres; b) intermediate decayed fallen woody debris (IDWD), the wood structure ranges from fairly hard to fairly soft, a knife can penetrate less than 2 cm ; c) most decayed fallen woody debris (MDWD), with wood structure from soft to very soft where a knife penetrates more than 2 cm .

Data analysis

In order to contrast the variation in PAI and the substrate heterogeneity, the cover estimated for each of them in the centre of the canopy gaps, the two gap edges and beneath the closed canopy were compared using the non-parametric Friedman test and the Wilcoxon test as a post-hoc test (Sokal and Rohlf 2000), because the data did not meet the requirements of normality and homogeneity of variances.

Species richness was calculated as the number of all species in each plot, and the Simpson's diversity index was used to calculate the species diversity (McCune and Grace 2002). To test for statistical differences in the overall species richness, diversity and abundance (estimated as the mean coverage) by taxonomical groups between areas in canopy gaps and beneath undisturbed canopies, the non-parametric Friedman test and the Wilcoxon test as a post-hoc test (Sokal and Rohlf 2000) were used. This statistical analysis was performed using SPSS 15.0 for Windows (SPSS Inc.).

A non-parametric multi-response permutation procedure (MRPP; Zimmerman et al. 1985) based on Sørensen distance (McCune and Grace 2002) was used to test for compositional

differences between canopy gap centres, canopy gap edges, and under undisturbed canopies. A descriptor of within-group homogeneity, compared to the random expectation is given by the statistic A . When $A=1$ all items are identical within groups; if $A=0$, the heterogeneity within groups equals expectation by chance. However, if there is less agreement within groups than expected by chance, then $A < 0$.

Indicator species analysis (Dufrêne and Legendre 1997) including a Monte Carlo randomization test (based on 1000 permutations) (McCune and Mefford 1999) was performed to identify forest floor plant species that might be associated with disturbed or non-disturbed locations. The method combines the forest floor plant species relative frequency and the abundance within the studied groups in and around canopy gaps reflecting the faithfulness of a species to a group (Berryman and McCune 2006). Indicator species for a location were considered at the $p < 0.05$ level and with an observed indicator value greater than 25 (Dufrêne and Legendre 1997).

To visualize the vegetation pattern, non-metric multidimensional scaling (NMS; Kruskal 1964) was used. We chose NMS because it is known to be a robust ordination method (McCune and Grace 2002). To be consistent with the other analysis we used Sørensen distance. The NMS was performed with 250 random starting configurations and the same number of runs with the original data set and six axes. The final solution was selected based on the most stable solution with the lowest dimensionality and 500 iterations and with the lowest final stress compared with the randomization test. A preliminary Detrended Correspondence Analysis revealed a gradient length of 2.97. For the ordination analysis, species that occurred in less than 5% of the plots were removed. Because of their rare occurrence in the dataset they do not provide any insight into the pattern of the vegetation (McCune and Grace 2002), therefore, 27 rare species (out of a total of 63 species) were removed for this analysis. An outlier analysis (with a cut-off of 2.5 standard deviations) of the vegetation and environmental matrixes was performed using Sørensen distance confirmed the consistency of the data set.

The MRPP, the indicator species analysis and the NMS analysis were performed using PC ORD version 5.0 (McCune and Mefford 1999).

Results

Environmental variables

PAI ranged between 2.3 and 6.1. The higher values came from the canopy gaps and from the gap edges (4.2 – 4.5 on average) (Table 1). The values did not differ significantly between locations within the gaps, but there was a difference in PAI values between positions in the gaps and those under the closed canopy. Here the values were significantly lower (3.0 – 3.1 on average).

Only minor spatial differences in the substrate heterogeneity were found within the canopy gaps and the surrounding

undisturbed canopy in the *N. betuloides* forest (Table 1). In general, the most frequent substrate was litter with a median cover between 50 and 75%. However, neither litter, exposed mineral soil, IDWD nor MDWD differed significantly between any of the gaps and undisturbed canopy situations. But the LDWD showed some differences. The highest, but not significantly different amounts were found in the gap centres and at gap edges (median between 5.0 and 15%). Lower coverage of LDWD was estimated beneath the undisturbed canopies (median between 0.0 and 5.0%), which also were not statistically different (Table 1).

Species richness and abundance

Sixty three species were found growing on the forest floor in this pure and uneven-aged *N. betuloides* forest. When arranged by taxonomical groups in decreasing order, there were 17 bryophytes, 17 marchantiophytes, 12 lichens, 8 dycotyledons, 5 pteridophytes, 3 monocotyledons and 1 anthocerotophyte (Table 2). Seedlings of *N. betuloides*, the marchantiophyte *Gakstroemia magellanica*, *Chiloscyphus magellanicus* and *Plagiochila obovata*, and the bryophyte *Dicranoloma robustum* were the five most abundant species (Appendix).

The average number of forest floor species per plot (species richness) was highest for the marchantiophytes (6.6 species), followed by dycotyledons (2.5 species), and lowest for the anthocerotophytes (0.2 species) (Table 2). On the other hand, the highest coverage was for the marchantiophytes (44.0% of the forest surface) followed by the dycotyledons (27.7%) and bryophytes (15.3%) (Table 2).

A large number of rare species (occurring between one and three times in the sample) were recorded (43% of the total number of species). Bryophytes and lichens were the taxonomical groups that showed the highest percentage of rare species with 53 and 58% of the total species recorded (Appendix).

Effects of gap partitioning on species composition

Out of the entire forest floor flora (63 species), 4 species were recorded only in canopy centres, 8 only in the gap edges, and 7 were only found below undisturbed canopies. However, all of these plant species were rare, and only showed up between one and three times in the sample (Fig. 3).

Generally, no significant differences were found in the species richness (median between 14 and 15 species per plot) and species diversity (median between 0.82 and 0.84) when the different locations in and around the canopy gaps were compared (Table 3). The forest floor species abundance was highest in the canopy gaps (median 100%), gap edges (median between 97 and 100%) and beneath the undisturbed canopy to the northwest (median 80%); however, there were no significant differences. The species abundance recorded beneath the undisturbed canopy to the southeast, by contrast, was significantly lower (median of 77%) (Table 3).

Table 1. Descriptive statistics for plant area index (PAI) and the coverage (%) of the substrate heterogeneity by plot estimated in the forest – in gaps, at gap edges (SEG is southeast and NGE northwest from the gap centre) and beneath undisturbed canopies (SUC and NUC). Q1 and Q3 are the lower and upper quartiles. Identical letters indicate no significant difference between the different locations in the forest (Friedman test and Wilcoxon test as a post-hoc test, $p < 0.05$, $n = 13$).

Variable		GAP		Gap Edge		Undisturbed canopy		Friedman's test
				SGE	NGE	SUC	NUC	
Plant area index (PAI)	Q1	3.6	3.2	3.2	2.8	2.8	$Fr = 13.85$, $df = 4$, $p = 0.01$	
	Median	4.7a	4.2a	4.5a	3.1b	3.1b		
	Q3	5.4	5.1	5.2	3.2	3.3		
Exposed bar mineral soil (BS)	Q1	0.0	0.0	0.0	0.0	0.0	$Fr = 3.50$, $df = 4$, $p = 0.48$	
	Median	0.0a	0.0a	0.0a	0.0a	0.0a		
	Q3	0.0	0.0	0.0	0.0	0.0		
Litter (L)	Q1	40.0	40.0	22.5	50.0	50.0	$Fr = 3.61$, $df = 4$, $p = 0.46$	
	Median	60.0a	55.0a	50.0a	65.0a	75.0a		
	Q3	75.0	80.0	75.0	85.0	87.5		
Least decay fallen woody debris (LDWD)	Q1	5.0	2.5	0.0	0.0	0.0	$Fr = 15.75$, $df = 4$, $p = 0.00$	
	Median	10.0a	15.0a	5.0a	5.0b	0.0b		
	Q3	42.5	35.0	42.5	10.0	0.0		
Intermediate decay fallen woody debris (IDWD)	Q1	2.5	5.0	2.5	5.0	0.0	$Fr = 6.66$, $df = 4$, $p = 0.16$	
	Median	5.0a	10.0a	5.0a	10.0a	5.0a		
	Q3	15.0	10.0	20.0	20.0	5.0		
Most decay fallen woody debris (MDWD)	Q1	0.0	2.5	5.0	0.0	5.0	$Fr = 2.39$, $df = 4$, $p = 0.67$	
	Median	5.0a	5.0a	10.0a	20.0a	10.0a		
	Q3	12.5	20.0	15.0	32.5	35.0		

Table 2. Species richness (average species per plot) and abundance (average species cover in% per plot). The standard error is in brackets.

Taxonomical Groups [Total number of species]		Species richness	Abundance
Spermatophytes – Dicotyledons [8]	Mean	2.5 (0.1)	27.7 (0.3)
	Range	1-6	2.0-100
Spermatophytes – Monocotyledons [3]	Mean	0.4 (0.1)	0.6 (0.0)
	Range	0-2	0.0-4.0
Pteridophytes [5]	Mean	1.1 (0.1)	7.3 (0.2)
	Range	0-3	0.0-70.0
Bryophytes [17]	Mean	2.4 (0.2)	15.3 (0.1)
	Range	0-5	0.0-34.0
Marchantiophytes [17]	Mean	6.6 (0.2)	44.0 (0.2)
	Range	1-9	10.0-72.0
Anthocerotophytes [1]	Mean	0.2 (0.1)	0.2 (0.0)
	Range	0-1	0.0-4.0
Lichens [12]	Mean	0.8 (0.1)	0.9 (0.0)
	Range	0-3	0.0-3.0
All species [63]	Mean	14.1 (0.4)	84.2 (0.2)
	Range	3-23	34.0-100

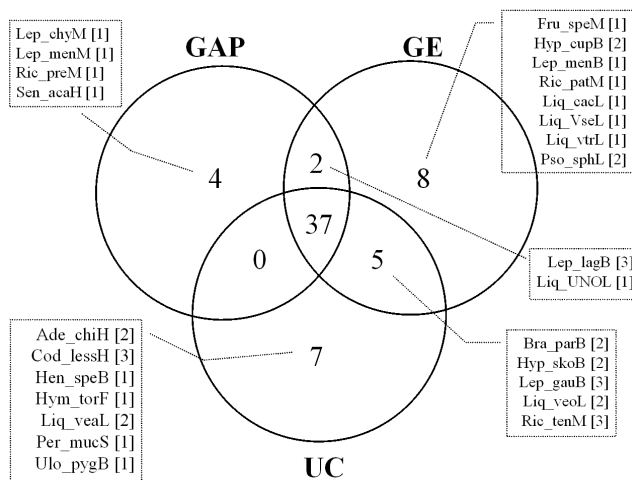


Figure 3. Venn diagram showing species occurrence in gap centres (GAP), gap edges (GE) and undisturbed canopies (UC). In text boxes the species acronym (Appendix). In brackets are the number of plots in which the species occurred.

Table 3. Species richness, species diversity and species abundance in canopy gaps, gap edges (SEG is southeast and NGE northwest from the gap centre) and beneath undisturbed canopies (SUC and NUC). Q1 and Q3 are the lower and upper quartiles. Identical letters indicate no significant difference between the different locations (Friedman test and Wilcoxon test as a post-hoc test, $p < 0.05$, $n = 13$).

		GAP		Gap Edge		Undisturbed canopy		Friedman's test
				SGE	NGE	SUC	NUC	
<i>Species richness</i>								
Total number of species		42	45	43	40	41		$Fr = 3.13$, df = 4, $p = 0.54$
	Q1	13.0	11.0	12.5	11.0	11.0		
Average species per plot	Median	14.0a	15.0a	14.0a	15.0a	15.0a		
	Q3	17.5	17.5	16.0	17.0	15.0		
<i>Species diversity</i>								
Average Simpson's diversity index	Q1	0.80	0.80	0.81	0.81	0.79		$Fr = 1.91$, df = 4, $p = 0.75$
	Median	0.83a	0.84a	0.83a	0.84a	0.82a		
	Q3	0.84	0.87	0.86	0.88	0.84		
<i>Species abundance</i>								
Average species cover per plot (%)	Q1	73	84	79	64	61		$Fr = 10.64$, df = 4, $p = 0.03$
	Median	100ab	100a	97ab	77b	80ab		
	Q3	100	100	100	99	100		

Table 4. Non-metric multidimensional scaling (NMS) correlations for the 8 environmental variables with the first 3 ordination axes. r is the Pearson's correlation with ordination axes. This optimal three-dimensional solution had a stress value of 16.22 ($p = 0.004$).

Environmental variables	Axis 1	Axis 2	Axis 3
	r	r	r
Direct below-canopy solar radiation transmittance	-0.073	0.129	0.192
Diffuse below-canopy solar radiation transmittance	0.213	0.077	-0.107
PAI	0.124	-0.088	-0.057
Litter	-0.149	-0.063	0.280
BS	0.071	-0.013	-0.041
LDWD	0.288	-0.137	-0.080
IDWD	-0.167	0.027	-0.030
MDWD	0.025	0.212	-0.214
Coefficients of determination	0.35	0.28	0.16
Cumulative % variance explained	35	63	79

The MRPP analysis of the community composition did not reveal differences in plant species assemblages between the positions along transects running from areas beneath undisturbed canopy to the centre of canopy gaps ($A = -0.001$, $p = 0.478$); this was additionally confirmed by the pairwise post-hoc comparisons.

Results for the indicator species analysis showed that only the marchantiophyte *C. magellanicus* was more likely to occur in the gap centres (observed indicator value = 28.8, $p = 0.034$) (Appendix). The abundance (added cover classes) of *C. magellanicus* was higher in the gap centres reflecting a strong gap influence. There were no species associated with other positions along the transects, namely gap edges or undisturbed canopies (Appendix).

The NMDS confirmed the results of the MRPP. There were no clear patterns in the vegetation composition related to the different gap positions nor was there a clear gradient related to the slightly changing environmental conditions. A three-dimensional solution described 79% of the variance in the species composition (Table 4 and Fig. 4). The proportion of variance explained for each ordination axis was 35% for Axis 1, 28% for Axis 2, and 16% for Axis 3. Furthermore,

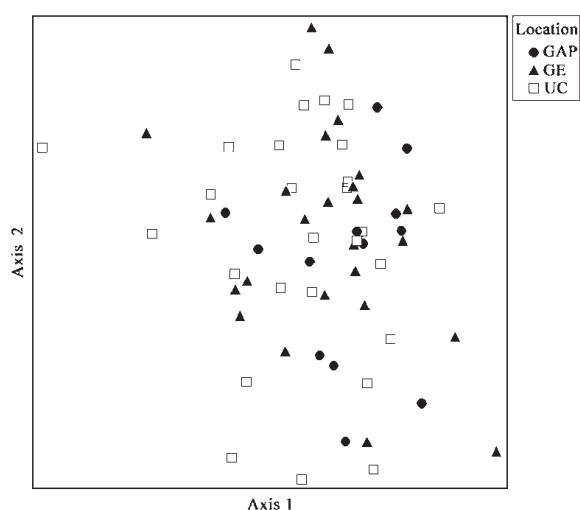


Figure 4. NMS ordination diagram of the vegetation composition. The symbols are the plots. GAP = gap centre; GE = gap edge (southern and north-western together); UC = undisturbed canopy (south-eastern and north-western together).

the community composition was only weakly related to the environmental variables measured. The axes were weakly correlated to the environmental variables (litter, exposed mineral soil, IDWD, LDWD, MDWD, PAI and below-canopy direct and diffuse solar radiation transmittances) ($r < 0.288$) (Table 4).

Discussion

Relationships between environmental factors and species richness, diversity and composition

The decrease in vascular plant species diversity with an increase in latitude observed in the northern hemisphere's boreal forest (Hart and Chen 2006), was also observed in our study with a relatively low vascular species diversity. The central-south zone of Chile (31–42°S) has the highest vascular plant species richness while the lowest is farther south (43–56°S) (Bannister et al. 2011). However, Rozzi et al. (2008) reported the highest bryophyte richness at the southernmost tip of the continent and this same richness of non-vascular plant species was found in our study where the highest species diversity belonged to the marchantiophytes and bryophytes.

Previous studies in temperate and boreal forests found that differences in vascular and non-vascular plant species diversity in natural forests is influenced by the formation or presence of gaps in the canopy layer (Jonsson and Esseen 1990, Busing and White 1997). However, we found only a few differences in the forest floor plant species richness, diversity and abundance, and no changes in the forest floor plant species composition in small canopy gaps located in our *N. betuloides* forest study area. Similar findings have been also documented by Kimmerer and Young (1996) and Kimmerer (2005).

In general, the vegetation studies in the Patagonian *Nothofagus* forests have been purely descriptive (Pisano 1977, Moore 1983, Roig et al. 1985). From these works we know that the vascular and non-vascular plant species found in canopy gaps and beneath the undisturbed canopy are typical forest species of wet areas and shaded forests. Furthermore, the majority of the non-vascular species can be found growing on decaying woody debris (Greene et al. 1985, Hässel de Menéndez and Solari 1985, Matteri 1985). As Kent (2012) pointed-out, in many parts of the world the vegetation description is extremely generalised, which is the case here.

A similar study conducted in a South American *Nothofagus* forest found that gap size and location did not have an effect on herb and shrub species richness (Damascos and Rapoport 2002). Similarly, in the boreal forest small canopy gaps have resulted in little changes in the vascular plant species composition (Hart and Chen 2006). This might be explained by the small environmental differences (i.e., solar radiation transmittances, nutrient availability) between the canopy gaps and under the undisturbed forest canopy (Anderson and Leopold 2002, Damascos and Rapoport 2002, Fahy and Puettmann 2007). In this study, the transmission of

direct solar radiation into the *N. betuloides* forest was measured as being between 3.2% and 19.4% of the above canopy solar radiation, and between 3.2% and 16.7% for the diffuse solar radiation showing a solar radiation gradient as well as a difference in PAI between canopy gaps and the surrounding undisturbed canopy in the *N. betuloides* forest (Promis et al. 2010). Their effects on the forest floor vegetation did not include a shift in species composition. Furthermore, increases in the below-canopy solar radiation in canopy gaps must not cause increases in soil resource (water, nutrient) availability (Bauhus 2009).

However, the presence of a gap in the canopy does not only increase the solar radiation on the forest floor, wind also has greater access and creates microsites by disturbing the forest floor and by causing additional woody debris to be knocked to the ground (Ulanova 2000). It has been argued before that the abundance and properties of substrates available for colonization on the forest floor are strong predictors of bryophyte species composition (McAlister 1995, Crites and Dale 1998, Mills and Macdonald 2004). In the *N. betuloides* forest, no big changes were found in the substrate heterogeneity in canopy gaps. Only the amount of the least decayed fallen woody debris in canopy gaps was statistically significant higher than under the undisturbed canopy. This is likely the consequence (broken branches etc.) of the falling gap-makers or the presence of whole or parts of trees that have fallen down after the creation of the gap. However, this change in substrate availability was not found to influence the plant community composition in this study.

Hart and Chen (2006) stated that small canopy gaps could influence important shifts in the non-vascular species composition by favouring species which have propagules present in the disturbed area. In this study an increase in the marchantiophyte *C. magellanicus* was related to canopy gaps (Appendix). *C. magellanicus* has a temperate South American pattern of distribution, associated with the Andinopatagonian – subantarctic island areas (Hässel de Menéndez and Rubies 2009). It is only known that *C. magellanicus* occurs as a thick bryophyte carpet that covers the forest floor in *N. betuloides* forests including rocks, stream banks and sometimes it is even found submerged in bog pools (Hässel de Menéndez and Solari 1985, Hässel de Menéndez 1999), but we do not have any information about the species dispersal, and the effects of micro-environmental changes on its distribution.

Nevertheless, the attempts to understand shifts in the forest floor vegetation diversity, dynamics and composition, should take into account factors such as the time since the last disturbance and the disturbance history (Messier et al. 2009), although this is difficult to assess when pristine and native forests are studied. The gaps studied covered the whole age range from 6 to >15 years, but the majority were classed as old (8 gaps out of 13), 3 as recent and 2 as middle aged. Therefore, our results suggest that the species composition is relatively resilient to these small scale disturbances. Furthermore, the uneven-aged canopy structure suggests many dec-

ades of stability with only the occasional creation of small canopy gaps (Promis 2009).

Conclusions

The composition of the forest floor vegetation, its species richness and diversity shows a high resistance to gap creation and seems to be very well adapted to these small changes. Neither vascular plant species nor non-vascular plant species showed a shift in species composition due to the small environmental changes produced by the canopy gaps. It might just as well be that climatic conditions are the dominating influence that describe vegetation patterns and composition and in this case that the high precipitation and the high humidity do not change the microclimate enough in the small gaps. As in many other studies examining the effects of canopy gaps in pristine forests, this one has shown itself to be difficult due to the ascertaining of the differences in the times when the gaps were created. Therefore, further studies are required to try to understand the temporal patterns involved in the creation of canopy gaps on the forest floor species composition.

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Appendix

List of species by taxonomical group, abundance (average of the cover class) and frequency. The file may be downloaded from the web site of the publisher at www.akademai.com.