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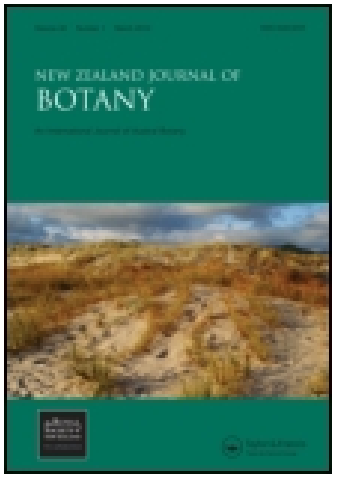

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Variable retention management influences biomass of Misodendrum and Usnea in Nothofagus pumilio southern Patagonian forests

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RESEARCH ARTICLE

Variable retention management influences biomass of *Misodendrum* and *Usnea* in *Nothofagus pumilio* southern Patagonian forests

Rosina Soler[a]*, Guillermo Martínez Pastur[a], María Vanessa Lencinas[a] and Mauricio Rosenfeld[b]†

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Variable retention systems (retention of some existing trees in different densities along with significant elements of the original forest after logging) aim to mitigate the impact of harvesting in native temperate forests, improving biodiversity conservation in managed stands. This study evaluates the effect of variable retention harvesting on epiphytic lichens (*Usnea barbata*) and mistletoes (*Misodendrum punctulatum*) in *Nothofagus pumilio* forests. The abundance of these canopy-dwelling species can be estimated by measuring their litter fall. We quantified mistletoe, lichen and tree litter fall monthly for 3 years. Tree and lichen biomasses were influenced by canopy cover, being higher in primary forests than in harvested stands. However, aggregated retention showed the highest mistletoe biomass production. Furthermore, mistletoe biomass increased while lichen biomass decreased over the years after harvesting. Variable retention was useful in maintaining both lichen and mistletoe biomass after harvest, but aggregates were not enough to maintain the original level of lichen populations. Forest harvesting with variable retention generates positive (litter input) and negative (decline of host growth) effects of mistletoes and epiphytic lichens at community level, which should be evaluated during conservation and management planning.

Keywords: aggregated retention; canopy communities; epiphytic lichen; hemiparasitic plants; litter fall; mistletoe

Introduction

Harvesting influences the entire forest system under management, modifying biodiversity levels in the understorey, soil and canopy communities (Franklin et al. 1997; Lindenmayer & Franklin 2002). Silviculture focused on sustainable forest management seeks to conserve biodiversity at different levels. However, most worldwide monitoring programmes mainly assess the species changes and impacts at the understorey level (Halpern & Spies 1995; Luque et al. 2010; Gustafsson et al. 2012). Among the poorly studied groups, epiphytic lichens and vascular plants growing in tree crowns are sensitive to changes in tree density and canopy disturbances (Storaunet et al. 2008; Humphrey et al. 2009; Zotz & Bader 2009).

Harvesting that opens the canopy modifies the microclimate (Promis et al. 2010) and processes such as litter contribution and decomposition (Caldentey et al. 2001), while facilitating tree seedling recruitment and growth (Martínez Pastur et al. 2011a). During the last 20 years, new alternatives have been proposed to better integrate wood production and biodiversity conservation. The variable retention system, a stand-level conservation approach, is extensively used in Europe, North America, Latin America and Australia. Current applications use the terms aggregated (or group) retention and

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dispersed retention to indicate different spatial distributions of retained pre-harvest structures (e.g. living trees or coarse woody debris) (Gustafsson et al. 2012). Approaches and levels of retention, which take into account natural disturbance dynamics (Franklin et al. 1997), differ depending on local context. In southern Patagonia, variable retention proposes to retain 30% of the original forest as aggregated retention (in one circular patch per hectare) and 15% as dispersed retention (evenly distributed individual trees); and dispersed and aggregated retention are applied together across the harvest unit (Martínez Pastur et al. 2009). Most of the natural structures and their associated organisms are maintained through retention, but little is known about how harvesting affects the continuity and complexity of the tree layer, nor the abundance and distribution of species that grow on canopy trees, such as parasites and epiphytes.

Misodendrum (mistletoe) and *Usnea* (old man's beard lichen) are two common elements in the canopy of *Nothofagus* forests in southern Patagonia. The genus *Misodendrum*, endemic to the sub-Antarctic forests (Rossow 1982), comprises eight species of hemiparasitic plants. Four species are present in the forests of Tierra del Fuego (Orfila 1978; Moore 1983; Tercero Bucardo & Rovere 2010), where *Misodendrum punctulatum* is the most abundant parasite of *Nothofagus pumilio* and *Nothofagus antarctica*, colonizing small branches and tree stems (Tercero Bucardo & Rovere 2010). The genus *Usnea* is a fruticose epiphytic lichen that generally grows hanging from tree branches, resembling grey or greenish hair (Clerc 1998). *Usnea* occurs in upland areas throughout the world, including Tierra del Fuego. This lichen grows on *Nothofagus* trees, where *Usnea barbata* is the most abundant and widespread species (Hawksworth & Moore 1969). In addition to being endemic components in native temperate forests, both lichens and mistletoes are ecologically important as food, shelter and nesting material for wildlife (Calvelo et al. 2006; Díaz & Kitzberger 2006; Soler Esteban et al. 2011). Parasitic plants and lichens may also provide a benefit to other plant species by enhancing soil fertility and nutrient cycling through tree litter fall (Essen et al. 1996, March & Watson 2007, 2010; Fischer et al. 2013). Consequently, changes in the biomass of canopy communities can have various effects on many ecosystem processes.

In southern Patagonia, studies have shown that variable retention is useful in improving the conservation of biodiversity and ecological processes in managed forests (Lencinas et al. 2009, 2011, 2012; Simanonok et al. 2011). However, these studies do not examine canopy communities such as hemiparasitic plants (aerial stem) and lichens. The objective of this study was to define the impact of forest harvesting on mistletoes (*M. punctulatum*) and epiphytic lichens (*U. barbata*) in *N. pumilio* forests managed with variable retention (aggregated and dispersed retention) and compare it with primary unmanaged forests. We expect to detect changes in the litter fall biomass of these organisms along the canopy cover gradient produced by variable retention (aggregated and dispersed) harvesting compared with natural canopies in unmanaged stands. Tested hypotheses were: (i) lower levels of canopy retention (dispersed retention) reduces *M. punctulatum* and *U. barbata* litter fall, whereas higher levels of canopy retention (aggregated) maintain similar values to unmanaged forests; and (ii) litter fall production increases with years after harvesting as a result of the occurrence of new colonization in the harvested forests.

Materials and methods

Southern Patagonian Nothofagus pumilio *forests*

At the austral extreme of South America, Tierra del Fuego Island, shared between Chile and Argentina, hosts the world's southernmost forested ecosystems. *Nothofagus pumilio* is the main tree component of these forests in the central portion of the island. This species has a wide natural distribution from 36°50′ to 55°02′S. Among the three types of *Nothofagus* found in southern Patagonia, *N. pumilio* forests are mainly used for timber harvesting activities because of their good yield characteristics (Martínez Pastur et al. 2007). In these forests, wind-throw is the primary natural disturbance, creating canopy gaps throughout the forest (Rebertus & Veblen 1993).

The climate of the central zone of Tierra del Fuego is cold because of oceanic influences and is

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characterized by short summers and long, snowy and frozen winters. Mean monthly air temperatures range from −3 to 9 °C (minimum and maximum temperatures in July and February, respectively) with only 3 months per year free of mean daily temperatures below 0 °C. The growing season of these forests is approximately 5 months while soil and minimum mean air temperature are both above 0 °C (Barrera et al. 2000). Precipitation can reach up to 600 mm yr^{-1} and the annual average wind speed outside forests is 8 km h^{-1}, reaching up to 100 km h^{-1} during storms (Martínez Pastur et al. 2009). The areas occupied by forests are mostly of glacial origin, consisting of loess and alluvial materials in the foothills, which form acid brown soils (Frederiksen 1988).

Studied sites and forest structure characterization

The study was conducted in a permanent plot established at Los Cerros Ranch (54°18′S, 67°49′ W), within a large area of pure (monospecific) *N. pumilio* forests (115 ha) harvested during 2005. Seventy years ago this area was subject to low-intensity selective cutting. Following the harvest period, the plot was undisturbed until 2004 when a variable retention system was implemented, which continues today with an average harvest of 100 ha $year^{-1}$. The variable retention method applied in Tierra del Fuego generates areas of different canopy openness and micro-environmental conditions (Martínez Pastur et al. 2009). This system retains one circular aggregate of 30-m radius per hectare (30 m^2 ha^{-1} basal area), and evenly dispersed dominant trees are retained (10–15 m^2 ha^{-1} basal area) between the aggregates. For this study, nine sampling sites were selected: (i) three sectors at the interior of retained aggregates (AR) in three different stands, (ii) three sectors of dispersed retention (on the harvested forest 20 m away from the aggregates' influence) (DR), and (iii) three unmanaged stands of primary forests (5–10 ha each) (PF). Study sites of AR and DR were established in stands harvested 2 years before the onset of this study.

Forest structure of each sampling site was characterized through six forest plots using the point sampling method (BAF 6) (Bitterlich 1984). We measured the diameter at breast height (DBH) (trees > 5 cm) for all trees within the plot, to estimate the basal area (BA) (m^2 ha^{-1}), quadratic mean diameter (QMD) (cm), tree density (TD) (n ha^{-1}), and total over-bark volume (TOBV) (m^3 ha^{-1}) of each stand. The dominant height (DH) was measured in three dominant trees per plot by using a TruPulse 200 laser rangefinder (Laser Technology, Centennial, CO, USA). Furthermore, canopy cover (CC) (%) was estimated through hemispherical photographs of the forest overstorey (for equations and methodologies see Martínez Pastur et al. 2011a,b).

Biomass quantification

We sampled litter fall production for three consecutive years starting two years after harvesting (2007–2009). The use of this litter fall sampling method permits an accurate assessment of epiphytic macrolichen diversity and biomass production at the stand level (McCune 1994; March & Watson 2007), as it provides a ground-based technique to carry out hypothesis testing with reasonable statistical power. This method is also useful because it provides a good idea of canopy communities often overlooked because of inaccessibility (Essen & Renhron 1998). Ten circular traps were placed along a 50-m transect in each stand at 1.8 m above the ground. Transects within variable retention areas were placed at the centre of the aggregates, to represent the innermost situation of AR, and to avoid the AR–DR edge influence. The traps used were plastic buckets, 27.5 cm in diameter and 30.0 cm in depth. Litter fall biomass was collected monthly (except during winter, when pooled samples included June to September) and manually classified as: (i) *N. pumilio* litter (leaves, fine branches and reproductive structures), (ii) mistletoe (leaves, fine branches and seeds), and (iii) epiphytic lichen (alive and dead thallus). All this material was dried in an oven at 70 °C until constant weight, and weighed with a precision of ± 0.0001 g. The litter fall biomasses of *N. pumilio*, mistletoe and epiphytic lichen were expressed as kg ha^{-1}.

Table 1 Analyses of variance for basal area (BA) (m^2 ha^{-1}), canopy cover (CC) (%), dominant height (DH) (m), quadratic mean diameter (QMD) (cm), tree density (TD) (n ha^{-1}), and total over-bark volume (TOBV) (m^3 ha^{-1}) for primary and retention treatments in *Nothofagus pumilio* forests.

Treatments	BA	CC	DH	QMD	TD	TOBV
PF	71.5 b	88.2 b	21.4 a	53.5 a	510.5 b	788.8 b
AR	78.5 b	82.2 b	23.8 b	56.1 a	505.2 b	953.8 b
DR	13.0 a	45.7 a	23.4 b	74.2 b	42.4 a	157.9 a
F(*P*)	91.51 (<0.001)	29.43 (<0.001)	7.18 (0.002)	11.30 (0.001)	42.71 (<0.001)	98.45 (<0.001)

PF, primary forest; AR, aggregated retention; DR, dispersed retention; *F*, Fisher's test; *P*, probability. Letters in each column indicate differences by Tukey's test ($P < 0.05$).

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Data analysis

One-way analyses of variance (ANOVAs) were carried out to analyse forest structure variables, with forest treatment as the factor. Repeated measures ANOVAs were carried out to test differences between forest treatments (AR, DR and PF) and years after harvesting (2007 = 2, 2008 = 3 and 2009 = 4). The response variables were: (i) *N. pumilio* (NP), *M. punctulatum* (MI) and *U. barbata* (US) (kg ha^{-1} $year^{-1}$) litter fall biomass; (ii) ratios of MI/NP and US/NP; (iii) ratios of MI/BA and US/BA (kg m^{-2} BA^{-1}). When the sphericity test was significant, the Greenhouse & Geisser (1959) univariate adjustment was applied to evaluate within-subjects effects. After performing the ANOVAs, a post hoc Tukey's test was used for each mean comparison ($P < 0.05$).

Results

Forest structure was significantly different in harvested stands compared with unmanaged primary forests (Table 1). PF presented lower DH than the managed areas (21.4 vs. 23.8 m). The other variables did not present significant differences between PF and AR, but were significantly different from DR. This treatment reduced their BA to 16%–18%, CC to 52%–55%, TD to 8% and TOBV to 16%–20% of the non-harvest areas (PF and AR) for DR, while QMD increased by 1.3.

The monthly sequence of litter fall biomass varied among forest treatments and between the mistletoe and epiphytic lichen (Fig. 1). Mistletoe litter fall biomass in PF and DR showed a peak during December (3.24 and 4.37 kg ha^{-1}, respectively) whereas in AR the high litter fall biomass

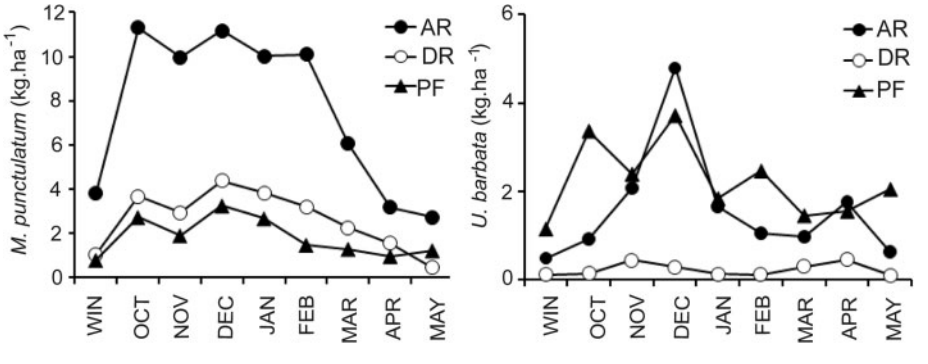

Figure 1 Mean values of monthly litter fall biomass of **A**, *Misodendrum punctulatum* and **B**, *Usnea barbata* in primary forests (PF) and variable retention (AR: aggregated, and DR: dispersed) in *Nothofagus pumilio* forests. WIN, winter period between June and September.

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was observed from October to February (9.97–11.3 kg ha^{-1}) compared with other months (2.72–6.06 kg ha^{-1}). Stands with large canopy cover (PF and AR) showed a peak of lichen litter fall during December (3.71 and 4.79 kg ha^{-1}, respectively) compared with other months (0.92–2.72 kg ha^{-1}), whereas in DR this litter fall biomass was lower and more homogeneous through the year (0.10–0.46 kg ha^{-1}).

Nothofagus pumilio litter fall biomass was related to the canopy cover gradient (Table 2, Fig. 2A). The highest value was found in PF with 4084 ± 350 kg ha^{-1} year^{-1} (average ± standard error), followed by AR with 3301 ± 588 kg ha^{-1} year^{-1} and DR with 1063 ± 270 kg ha^{-1} year^{-1}. Interannual variations ranged from 2.5 to 3.0 ton ha^{-1} year^{-1}, but no significant differences were detected (Table 2).

Mistletoe litter fall biomass significantly differed among the studied treatments (Table 2, Fig. 2B). Lower values were observed in PF and DR, while the higher amount was recorded at AR. However, MI/NP ratio was significantly higher in managed stands (AR and DR) compared with PF, which indicates a greater mistletoe litter fall biomass per tree litter fall biomass unit. The MI/BA ratio presented marginal significant differences (F = 4.50; P = 0.064) following the same trend between control and harvested areas (Table 2). Annual variation was also observed, with the mistletoe litter fall being significantly greater 4 years after harvesting. A significant interaction between treatment and year on MI/BA was found only in DR and this ratio showed high variation over time (Fig. 3).

Lichen litter fall biomass followed the same trend as tree litter (Table 3, Fig. 2C). The highest value was recorded in PF, followed by AR and DR, with significant differences between the three treatments (Table 3). The US/NP and US/BA ratios did not present significant differences, but showed the same trend described before. Lichen litter significantly decreased with years after harvesting, being similar between the 3rd and 4th years. However, there were significant interactions between treatment and year for *U. barbata* biomass and related ratios (US/NP and US/BA). These interactions occurred because there was no response of *U. barbata* litter fall to harvesting (both AR and DR), whereas the only significant increase of *U. barbata* litter fall occurred in unmanaged forests (Fig. 3).

Discussion

Although there have been few studies on the impacts of forest harvesting focused on canopy communities of temperate forests (Essen et al. 1996;

Table 2 Repeated measures analysis of variance for litter fall biomass of *Nothofagus pumilio* (NP) (kg ha^{-1} year^{-1}) and *Misodendrum punctulatum* (MI) (kg ha^{-1} year^{-1}) at stand level, and the ratios MI/NP and MI/BA (kg m^{-2} BA), where BA is the basal area (m^2 ha^{-1}) of control (PF), aggregated retention (AR) and dispersed retention (DR).

Effect *(df)*	NP F (*P*)	MI F (*P*)	MI/NP F (*P*)	MI/BA F (*P*)
Between-subject effectsTreatments *(2)*	11.07 (0.009)	6.35 (0.032)	13.32 (0.006)	4.49 (0.064)
Within-subject effects Years *(2)*	2.76 (0.139)	9.97 (0.003)	6.81 (0.010)	17.63 (<0.001)
Interaction Treatments × Years *(4)*	1.84 (0.230)	2.07 (0.147)	2.55 (0.094)	4.53 (0.018)
Mean values of litter fall and ratios				
PF	4084.63 c	18.57 a	0.48 a	0.21
AR	3301.45 b	79.77 b	2.52 b	1.12
DR	1063.66 a	26.43 ab	2.62 b	0.82
2	2935.02	34.45 a	1.41 a	0.56 a
3	2595.32	35.29 a	1.86 ab	0.60 a
4	2919.40	55.03 b	2.34 b	0.98 b

Years after harvesting: 2 (2007), 3 (2008) and 3 (2009). F(*P*) = *F* test with significance level between parentheses. Different letters within columns represent significant differences by Tukey's test (P < 0.05).

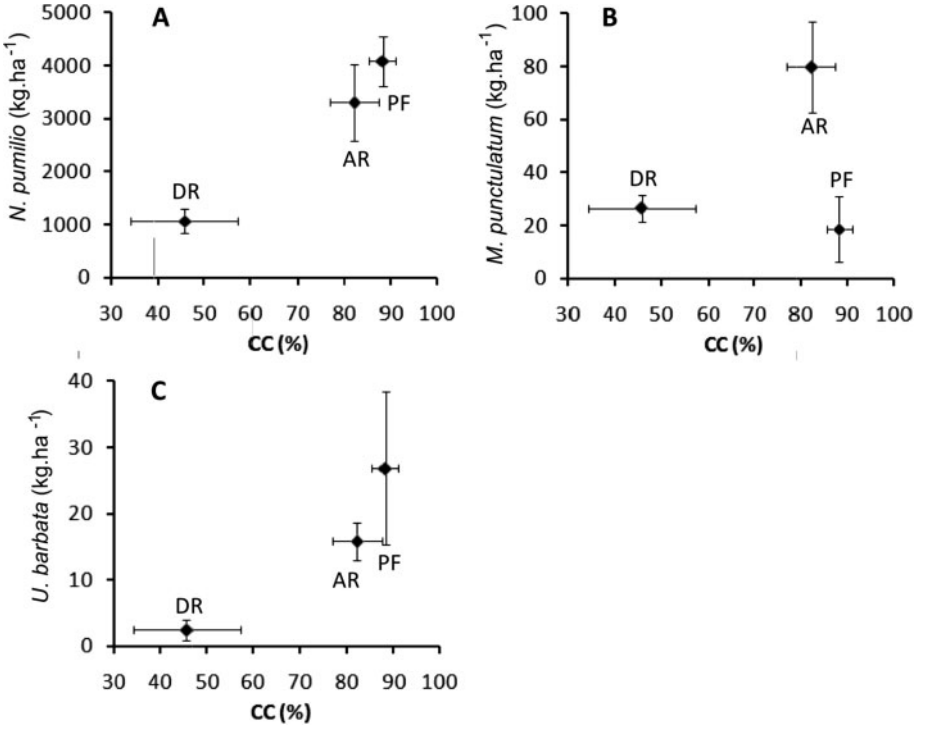

Figure 2 Mean values of annual litter fall biomass of **A**, *Nothofagus pumilio*; **B**, *Misodendrum punctulatum*; and **C**, *Usnea barbata* related to canopy cover (CC) in primary forests (PF) and variable retention (AR: aggregated, and DR: dispersed). Bars indicate the standard deviation of means.

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Table 3 Repeated measures analysis of variance for litter fall biomass of *Usnea barbata* (US) (kg ha^{-1} $year^{-1}$) at stand level, and the ratios US/NP and US/BA (kg m^{-2} BA), where BA is the basal area (m^2 ha^{-1}) of control (PF), aggregated retention (AR), and dispersed retention (DR).

Effect *(df)*	US F (*P*)	US/NP F (*P*)	US/BA F (*P*)
Between-subject effects Treatments *(2)*	17.90 (<0.001)	2.55 (0.157)	2.10 (0.202)
Within-subject effects Years *(2)*	8.55 (0.005)	2.82 (0.099)	4.95 (0.027)
Interaction Treatments × Years *(4)*	7.63 (0.002)	5.30 (0.010)	5.98 (0.007)
Mean values of litter fall and ratios			
PF	26.79 c	0.66	0.30
AR	15.80 b	0.42	0.22
DR	2.42 a	0.25	0.07
2	18.85 b	0.52	0.24 b
3	12.12 a	0.42	0.17 a
4	14.05 a	0.40	0.19 ab

Years after harvesting: 2 (2007), 3 (2008) and 3 (2009). F(*P*) = F test with significance level between parentheses. Different letters within columns represent significant differences by Tukey's test ($P < 0.05$).

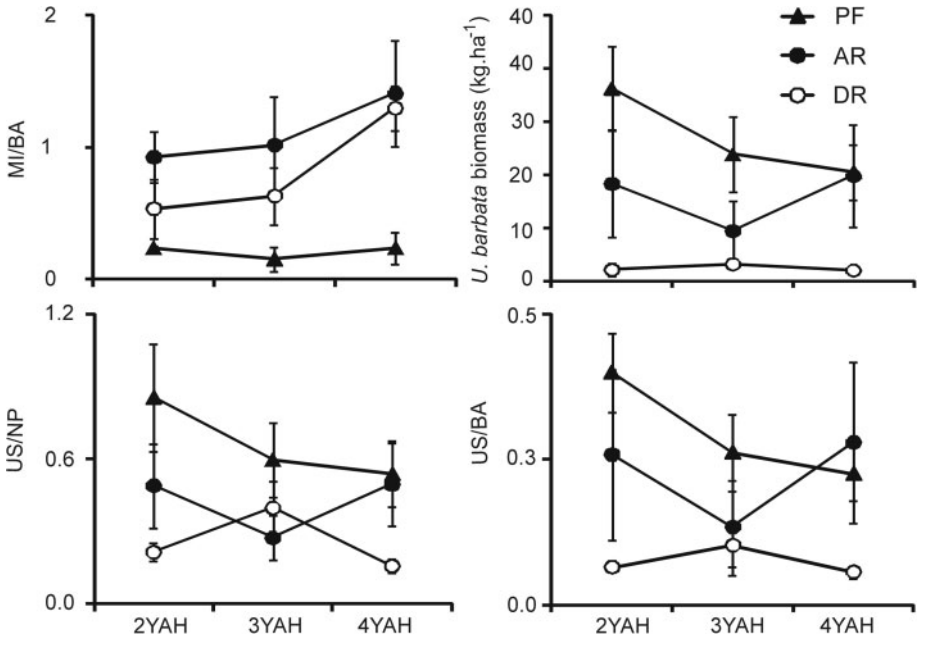

Figure 3 Treatment × years interaction plot detected with repeated measures analyses of variance described in Tables 2, 3, for MI/BA, *Usnea barbata* biomass, US/NP and US/BA ratios. Bars indicate the interactions standard error.

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Essen & Renhron 1998; Rheault et al. 2003; Storaunet et al. 2008; Humphrey et al. 2009; Zotz & Bader 2009), they affirm the potential of these groups as relevant indicators of forest habitat disruption. Our results suggest that variable retention harvesting modifies the biomass production of mistletoes and epiphytic lichens in temperate *Nothofagus* forests. The alteration of forest structure recorded in this work, the structural diversity (dispersed and aggregated retention) created by the forestry retention described by Martínez Pastur et al. (2009), and the resulting modifications to microclimate conditions (Baker & Read 2011; Martínez Pastur et al. 2011a) create new habitat conditions for the organisms living at the treetop in managed environments. However, we detected different responses of *U. barbata* and *M. punctulatum* to aggregated and dispersed retention. Here, high litter production was understood as an increase of mistletoe and lichen biomass in the canopy (c.f. March & Watson 2007), while a decline of litter reflected the opposite.

Increase of mistletoe biomass production after harvesting

Whereas we had hypothesized that harvesting would decrease *M. punctulatum* biomass production proportionally to the canopy cover gradient, which results from variable retention compared with natural canopies in unmanaged stands, we instead observed a four-fold increase of mistletoe production under similar canopy cover (80%) after harvesting. Our results showed that mistletoe biomass greatly increases in AR within the harvested area, being totally different to the values recorded in unmanaged forests. Moreover, the lower level of canopy retention at DR did not reduce the litter production compared with unmanaged forests. This result could be a result of mistletoe biomass falling because of the damage induced by high-intensity winds in *N. pumilio* stands after harvesting (Cellini 2010; Promis et al. 2010) coupled with higher tree density in AR (hence greater chance of infection) than in DR. Wind intensity could also be responsible for

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the monthly pattern observed for biomass fall. For this study area, Cellini (2010) reported higher wind speed during October and summer months, which is also the maximum *Misodendrum* sp. seed dispersal period (Tercero Bucardo & Kitzberger 2004).

As we expected, mistletoe litter fall biomass increased with years after harvesting, probably due to growth of those individuals established before harvesting rather than new infections. Considering that *M. punctulatum* have a multi-year incubation period (4–6 years) before aerial structures appear (Tercero Bucardo & Kitzberger 2004), it is probable that this study only registered the growth response of individuals already established in the original forests. The new climatic conditions (e.g. increased light availability) generated by forest management would probably benefit mistletoe aerial shoot production. Similarly, Noetzli et al. (2003) state that increasing light levels in thinned silver fir (*Abies alba*) forests in Switzerland may improve the growth of white mistletoe (*Viscum album*).

Traditionally, mistletoe infestation has been recognized as having a direct negative impact on host performance by reducing the growth rate of commercially valuable timber species or causing host-death. In Patagonian forests, high mistletoe loads have direct effects on both radial growth and architecture in *N. pumilio* individuals (Henríquez-Velásquez et al. 2012). Moreover, in young infected trees the stem quality could also be reduced by the dieback of weakened host branches, which is more likely than snapping caused by wind or snow and increasing insect and fungus attacks (Henríquez-Velásquez et al. 2012). From the perspective of negative cost for the host, the excessive *M. punctulatum* production in *N. pumilio* aggregates (assuming litter production correlated with mistletoe biomass in the canopy, March & Watson 2007) can lead to undesirable consequences for the future timber quality of retained trees. However, recent research findings highlight the key role of mistletoe species in many forest ecosystems through direct and indirect effects at the community-level (Mathiasen et al. 2008; Watson 2009). For example, the hemiparasitic *Amyema miquelii* contributed to the litter fall input, ground nutrient dynamic, and increased plant biomass in the understorey of *Eucalyptus* forests in Australia (March & Watson 2007). In Patagonian forests, austral parakeets (*Enicognathus ferrugineus*) fed heavily on buds, flowers and foliage of *Misondendrum* sp. during the winter (Díaz & Kitzberger 2006), while a high proportion of the guanaco (*Lama guanicoe*) winter diet comprises this hemiparasitic plant in Tierra del Fuego (Soler Esteban et al. 2011). This, along with other evidence from around the world led to the proposal that mistletoes as ecological keystones (Mathiasen et al. 2008). Because of this, it is important to consider the divergent roles of these plants because any gains in timber production coming from the removal of infested trees should be weighed against the likely losses in ecosystem function.

Lower levels of canopy retention reduces epiphytic lichen biomass

As we expected, lower levels of canopy retention (dispersed retention) reduce the *U. barbata* biomass production while a higher level of canopy retention (aggregates and unmanaged stands) produces higher lichen litter. Hence, litter production of *U. barbata* in this study was closely related to tree canopy cover and consequently, to *N. pumilio* litter production. However, we did not detect differences among treatments when *U. barbata* biomass was analysed considering the basal area of *N. pumilio* stands. This finding indicates that biomass production was subject to tree density and tree canopy cover. Both of these variables can be assumed to be good predictors of the amount of substrate available to this lichen in *Nothofagus* forests, which is one of the most important factors (substrate quality and its availability) in determining the epiphytic lichen abundance in the forest canopy (Essen et al. 1996). Furthermore, timber practices have strong impacts on substrate quality (e.g. bark depth, branch diameter) by reducing those structural features of old-growth forest that favour growth of fruticose pendulous species such as *Usnea* sp. (Essen et al. 1996). However, the retention forestry approach is intimately linked to the concept of biological legacies (Franklin et al. 1997), which refers to the maintenance of pre-harvest structures,

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such as old trees. The variable retention systems studied here modified the spatial heterogeneity (e.g. canopy stratification, patches of original forest) and compositional diversity (e.g. understorey plant diversity, coarse woody debris) of managed sectors, which promotes biocomplexity throughout the system (Carey 2003). While dispersed retention represents the most significant modification to the forest structure, the aggregated retention could maintain similar conditions to unmanaged forests (Martínez Pastur et al. 2009). However, more studies about the influence of substrate availability (branch characteristics, distance between remnant trees, spatial configuration of aggregates) linked to tree retention design (dispersed, aggregated or both combined) are needed.

Lichen abundance in forests is also controlled by environmental conditions (Essen & Renhron 1998; Rheault et al. 2003). Epiphytic lichens are very sensitive to changes in solar radiation and water availability because they are poikilohydric organisms, meaning that they are inefficient at controlling their water content and light capture (Belinchón et al. 2007). For *Usnea* sp., excessive sun and dry conditions limit its growth both in coniferous forests of North America (Rheault et al. 2003) and in deciduous (*Quercus pyrenaica*) forests of Europe (Belinchón et al. 2007). In this study we did not include climatic variables and their modifications after harvest, but there is considerable evidence that the canopy opening of *N. pumilio* forests in southern Patagonia increases solar radiation levels (Promis et al. 2010; Martínez Pastur et al. 2011a,b) and decreases air humidity levels (Cellini 2010). As expected, the changes in the micro-climate produced by forest harvest seem to have negative effects on epiphytic lichen communities. These negative effects also increase over the years after harvesting in our study. The decreases in the litter production through time could be an effect of wind break-off and mortality due to light-damage, which has also been observed in other temperate forests (Storaunet et al. 2008). Variable retention produces a gradient from humid-shadow sectors inside the aggregates to dry-sunny conditions in the dispersed retention (Cellini 2010; Martínez Pastur et al. 2011a,b). These micro-climate conditions offer the epiphytic lichens different sites to develop, but on average the litter fall biomass levels of harvested areas, both in aggregated and dispersed retention, are lower than in primary forests.

Forest management implications

Biodiversity conservation in managed forests aims to maintain the richness and abundance of the species at the same level of primary forests through the maintenance of structural heterogeneity (Martínez Pastur et al. 2009, 2011b) at spatial and temporal scales (Halpern & Spies 1995; Gustafsson et al. 2012). In this study, variable retention influences mistletoe and epiphytic lichen communities in different ways, increasing or decreasing their litter fall biomass production.

Litter is a key component in nutrient cycling, determining the availability of essential nutrients which, in turn, affect tree productivity and understorey plant diversity, along with dynamics and interactions among animal populations (Essen et al. 1996; Caldentey et al. 2001; March & Watson 2010; Fischer et al. 2013). Consequently, changes in litter fall can have critical effects on many ecosystem processes. In temperate forests of North America, Europe and Australia the litter contribution by mistletoes and lichens seems to be very important (Essen et al. 1996; March & Watson 2007). However, in our study the input of *M. punctulatum* and *U. barbata* only represented 2% of all litter production (45, 95 and 29 kg in PF, AR and DR, respectively). Although the two species represent a small component of the biomass, they made an important contribution to the spatial and temporal patterns of litter fall. While *N. pumilio* had a massive leaf fall during autumn (March, April and May) typical of broadleaved temperate *Nothofagus* forests (Moore 1983; Barrera et al. 2000), mistletoe and lichen contribute most to the litter in late spring and summer, thus displaying complementarity with host litter fall. This highlights how mistletoe and lichens can be important seasonal sources of nutrients to a deciduous forest ecosystem. This pattern has also been observed in *Eucalyptus* sp. forests (Australia), where the litter contribution from

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Amyema miquelii extended the period of high litter fall by several months (March & Watson 2007).

The variable retention harvest system was designed to include mitigation areas (aggregated retention) with similar characteristics to those of primary forests (e.g. basal area, canopy cover and *N. pumilio* litter fall biomass). These aggregates have been useful in maintaining much of the original diversity in the managed areas (Carey 2003; Lencinas et al. 2011, 2012), but not at the same level as primary forests. For these reasons, new alternatives must be considered to guarantee the maintenance of the original levels of biodiversity. The epiphytic lichen *U. barbata* can survive in the harvested forests, mainly inside the aggregates, but their size (60 m diameter) is not enough to maintain the population levels found in the primary forest. As a potential solution, the aggregate size could be larger than the actual sizes.

Misodendrum punctulatum was preserved after harvesting, both in aggregates and dispersed retention. As mentioned before, mistletoe might provide important ecological benefits and be desirable to some managers; however the excess of mistletoe in managed forests increasing year to year is undesirable for many foresters and timber companies. To avoid economic losses, the extraction of remnant individuals with high-infection levels in post-harvest stand management has been proposed. However, previous work in Europe has dismissed the removal of infected trees as a regulation strategy of mistletoe dynamics, because enhanced light conditions after tree extractions may improve the growth of mistletoe on neighbour individuals (Noetzli et al. 2003). Hence, it is important to further analyse the causes of mistletoe biomass increase in order to determine the ecological roles of hemiparasitic plants in productive forested areas. Also, more studies about the design of post-harvest variable retention practices are necessary to improve its implementation in the southern Patagonian forests to achieve conservation objectives, and increase forest health at the stand and landscape level.

References

Baker SC, Read SM 2011. Variable retention silviculture in Tasmania's wet forests: ecological rationale, adaptive management and synthesis of biodiversity benefits. Australian Forestry 74: 218–232.

Barrera MD, Frangi JL, Lichter LL, Perdomo MH, Pinedo LB 2000. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. Journal of Vegetation Science 11: 179–188.

Belinchón R, Martínez I, Escudero A, Aragón M, Valladares F 2007. Edge effects on epiphytic communities in a Mediterranean *Quercus pyrenaica* forest. Journal of Vegetation Science 18: 81–90.

Bitterlich W 1984. The relascope idea. Relative measurements in forestry. London, Commonwealth Agricultural Bureaux. 242 p.

Caldentey J, Ibarra M, Hernández J 2001. Litter fluxes and decomposition in *Nothofagus pumilio* stands in the region of Magallanes, Chile. Forest Ecology and Management 148: 145–157.

Calvelo S, Trejo A, Ojeda V 2006. Botanical composition and structure of hummingbird nests in different habitats from northwestern Patagonia (Argentina). Journal of Natural History 40: 589–603.

Carey AB 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. Forestry 76: 127–136.

Cellini JM 2010. Estructura y regeneración bajo distintas propuestas de manejo de bosques de *Nothofagus pumilio* (Poepp. et Endl.) Krasser en Tierra del Fuego, Argentina [Relationship between forest structure remaining after the harvesting of *Nothofagus pumilio* (Poepp. et Endl.) Krasser, and its natural regeneration dynamic in Tierra del Fuego, Argentina]. PhD thesis. La Plata University, Buenos Aires. 157 p.

Clerc P 1998. Species concepts in the genus *Usnea* (lichenized Ascomycetes). Lichenologist 30: 321–340.

Díaz S, Kitzberger T 2006. High *Nothofagus* flower consumption and pollen emptying in the southern South American austral parakeet (*Enicognathus ferrugineus*). Austral Ecology 31: 759–766.

Essen PA, Renhorn KE, Pettersson RB 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications 6: 228–238.

Essen PA, Renhron KE 1998. Edge effects on an epiphytic lichen in fragmented forests. Conservation Biology 12: 1307–1317.

Fischer JP, Phoenix GK, Childs DZ, Press MC, Smith SW, Pilkington MG, et al. 2013. Parasitic plant litter input: a novel indirect mechanism influencing plant community structure. New Phytologist 198: 222–231.

Franklin JF, Berg DR, Thornburgh DA, Tappeiner JC 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm KA, Franklin JF eds. Creating a forestry

for the 21st century. Washington, Island Press. Pp. 111–139.
Frederiksen P 1988. Soils of Tierra del Fuego. A satellite-based land survey approach. Folia Geographica Danica 18: 1–159.
Greenhouse S, Geisser S 1959. On methods in the analysis of profile data. Psychometrika 32: 95–112.
Gustafsson L, Baker SC, Bauhus J, Beese WJ, Brodie A, Kouki J, et al. 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62: 633–645.
Halpern CB, Spies TA 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5: 913–934.
Hawksworth DL, Moore DM 1969. Some lichens from Tierra del Fuego and their chemical constituents. Bryologist 72: 247–251.
Henríquez-Velásquez C, Henríquez JM, Aravena JC 2012. Damage caused by mistletoe *Misodendrum punctulatum* Banks Ex Dc. on architecture and radial growth of *Nothofagus pumilio* (Poepp. et Endl.) Krasser forests of southern Chile. Austral Ecology 37: 816–824.
Humphrey J, Ray D, Brown T, Stone D, Watts K, Anderson R 2009. Using focal species modelling to evaluate the impact of land use change on forest and other habitat networks in western oceanic landscapes. Forestry 82: 119–134.
Lencinas MV, Martínez Pastur G, Cellini JM, Busso C 2012. Improvement in conservation value of insect communities in South Patagonian forests managed with variable retention. In: Thangadurai D, Busso C, Abarca Arenas L, Jayabalan S eds. Frontiers in biodiversity studies. New Delhi, IK International Publishing House. Pp. 118–130.
Lencinas MV, Martínez Pastur G, Gallo E, Cellini JM 2009. Alternative silvicultural practices with variable retention improve bird conservation in managed South Patagonian forests. Forest Ecology and Management 258: 472–480.
Lencinas MV, Martínez Pastur G, Gallo E, Cellini JM 2011. Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests. Forest Ecology and Management 262: 1236–1250.
Lindenmayer DB, Franklin JF 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Washington, Island Press. 351 p.
Luque S, Martínez Pastur G, Echeverría C, Pacha MJ 2010. Overview of biodiversity loss in South America: a landscape perspective for sustainable forest management and conservation in temperate forests. In: Li C, Lafortezza R, Chen J eds. Landscape ecology and forest management: challenges and solutions in a changing globe. Beijing, HEP-Springer. Pp. 352–379.
March WA, Watson DM 2007. Parasites boost productivity: effects of mistletoe on litter dynamics in a temperate Australian forest. Oecologia 154: 339–347.
March WA, Watson DM 2010. The contribution of mistletoes to nutrient returns: evidence for a critical role in nutrient cycling. Austral Ecology 35: 713–721.
Martínez Pastur G, Cellini JM, Lencinas MV, Barrera M, Peri PL 2011b. Environmental variables influencing regeneration of *Nothofagus pumilio* in a system with combined aggregated and dispersed retention. Forest Ecology and Management 261: 178–186.
Martínez Pastur G, Lencinas MV, Cellini JC, Peri PL, Soler R 2009. Timber management with variable retention in *Nothofagus pumilio* forests of Southern Patagonia. Forest Ecology and Management 258: 436–443.
Martínez Pastur G, Lencinas MV, Peri PL, Moretto A, Cellini JM, Mormeneo I, et al. 2007. Harvesting adaptation to biodiversity conservation in sawmill industry: technology innovation and monitoring program. Journal of Technology Management & Innovation 2: 58–70.
Martínez Pastur G, Peri PL, Cellini JM, Lencinas MV, Barrera M, Ivancich H 2011a. Canopy structure analysis for estimating forest regeneration dynamics and growth in *Nothofagus pumilio* forests. Annals of Forest Science 68: 587–594.
Mathiasen RL, Nickrent DL, Shaw DC, Watson DM 2008. Mistletoes: pathology, systematics, ecology, and management. Plant Disease 92: 988–1006.
McCune B 1994. Using epiphyte litter to estimate epiphyte biomass. The Bryologist 97: 396–401.
Moore D 1983. Flora of Tierra del Fuego. London, Anthony Nelson. 338 p.
Noetzli KP, Müller B, Sieber TN 2003. Impact of population dynamics of white mistletoe (*Viscum album* spp. *abietis*) on European silver fir (*Abies alba*). Annals of Forest Science 60: 773–779.
Orfila EN 1978. Misodendraceae de la Argentina y Chile. Buenos Aires, Fundación Elías y Ethel Malamud. 73 p.
Promis A, Caldentey J, Ibarra M 2010. Microclima en el interior de un bosque de *Nothofagus pumilio* y el efecto de una corta de regeneración [Microclimate within a *Nothofagus pumilio* forest and the effects of a regeneration felling.]. Bosque 31: 129–139.
Rebertus A, Veblen T 1993. Structure and tree-fall gap dynamics of old-growth Nothofagus forests in Tierra del Fuego, Argentina. Journal of Vegetation Science 4: 641–654.
Rheault H, Drapeau P, Bergeron Y, Esseen PA 2003. Edge effects on epiphytic lichen in managed black spruce forests of eastern North America. Canadian Journal of Forest Research 33: 23–32.

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Rossow RA 1982. Sinopsis de las Misodendraceae [Overview of Misodendraceae]. Parodiana. 1: 245–270.

Simanonok MP, Anderson CB, Martínez Pastur G, Lencinas MV, Kennedy JH 2011. A comparison of impacts from silviculture practices and North American beaver invasion on stream benthic macroinvertebrate community structure and function in *Nothofagus* forests of Tierra del Fuego. Forest Ecology and Management 262: 263–269.

Soler Esteban R, Martínez Pastur G, Lencinas MV, Borrelli L 2011. Differential forage use between large native and domestic herbivores in Southern Patagonian *Nothofagus* forests. Agroforestry Systems 85: 587–594.

Storaunet KO, Rolstad J, Toeneiet M, Rolstad E 2008. Effect of logging on the threatened epiphytic lichen *Usnea longissima*: a comparative and retrospective approach. Silva Fennica 42: 685–703.

Tercero Bucardo N, Kitzberger T 2004. Establishment and life history characteristics of the southern South American mistletoe *Misodendrum punctulatum* (Misodendraceae). Revista Chilena de Historia Natural 77: 509–521.

Tercero Bucardo N, Rovere AE 2010. Patrones de dispersión de semillas y colonización de *Misodendrum punctulatum* (Misodendraceae) en un matorral postfuego de *Nothofagus antarctica* (Nothofagaceae) del noroeste de la Patagonia [*Misodendrum punctulatum* (Misodendraceae) seed dispersal and colonization patterns on a *Nothofagus antarctica* (Nothofagaceae) post-fire shrubland from Northwestern Patagonia]. Revista Chilena de Historia Natural 83: 375–386.

Watson DM 2009. Parasitic plants as facilitators: more Dryad than Dracula? Journal of Ecology 97: 1151–1159.

Zotz G, Bader MY 2009. Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Progress in Botany 70: 147–170.

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