



Original article

Mistletoes and epiphytic lichens contribute to litter input in *Nothofagus antarctica* forests



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ABSTRACT

Litter input is one of the key components that define nutrient cycling in forests and the majority of studies only consider the tree components of litterfall. However, epiphytic species can play a crucial role in litter input throughout the growing season. This work evaluates changes in litter production by mistletoe (*Misodendrum* sp.) and epiphytic lichen (*Usnea* sp.), related to crown cover in mature unmanaged, second-growth and managed (thinned for silvopastoral use) forests in Tierra del Fuego (Argentina). We used plastic traps to collect litterfall biomass from trees, lichens and mistletoes on a monthly basis over three consecutive years. Tree litter was considerable during autumn (March to May), which is typical of *Nothofagus* deciduous species in the Southern hemisphere. In contrast, peak litterfall from mistletoes and lichens occurred during spring and summer seasons. Tree litter (1954–3398 kg dry matter ha⁻¹ year⁻¹) was correlated with crown cover gradient being highest in second-growth forests and lowest in thinned sites. While litter input from mistletoes did not vary among forest types (307–333 kg dry matter ha⁻¹ year⁻¹), lichen litter (11–40 kg dry matter ha⁻¹ year⁻¹) was higher in unmanaged and thinned mature forests despite differences in tree crown cover. Contrary to what we expected, the management practices investigated here did not affect the biomass of canopy communities compared to unmanaged mature forests. Mistletoes and lichens significantly increased the spatial (forest type) and temporal complexity (extended period of falling) of litterfall in *Nothofagus antarctica* forests. This study provides a starting point to understand the ecological relevance of canopy communities in the Patagonian forests of southern Argentina.

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1. Introduction

The key role of litter as one of the most important resources influencing ecological processes in forest ecosystems (e.g., carbon and nutrient cycling, regulation of soil microclimate, vegetation composition) has been widely recognized (Frangi et al., 2005; Sayer, 2006). Great effort has been made to quantify the contribution of litter from trees (leaves, branches, reproductive structures), while input from epiphytes, lianas and parasites have received less attention. Because non-terrestrial organisms in the canopy also provide organic material to the forest soil via abscised structures, it should be considered an important source of nutrient-rich litter

input in some ecosystems (Fisher et al., 2013).

Forest canopies are complex and host a large diversity of organisms (Nadkarni et al., 2004). Among these, epiphytic lichens and mistletoes are two characteristic features of forest canopies in many temperate and boreal areas (Esseen et al., 1996; Watson, 2001; Mathiasen et al., 2008). Distribution and abundance of these organisms can be influenced by canopy structure, tree age (Esseen et al., 1996; Storaunet et al., 2008) or stand density (Tercero-Bucardo and Kitzberger, 2004; Mathiasen et al., 2008; Noetzli et al., 2003). Thus, spatial configuration at the local level determines not only the occurrence of canopy organisms, but also their abundance, and therefore their litter input.

Though they often appear constant and immutable over time, forest canopies are dynamic and change in structure and function, mainly due to developmental age and disturbance (Barrera et al., 2000; Nadkarni et al., 2004). Under natural conditions, overstorey tree structure varies widely at tree (e.g., tree architecture) and stand level (e.g., gaps). For example, the spatial configuration of

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overstorey trees switches from dense and closed canopy forests within the stem exclusion phase of development, to mature forests where self-thinning and gap-scale disturbances create and maintain canopy openings (Fig. 1). Moreover, human impacts such as timber harvesting or thinning for agroforestry purposes, can substantially alter microhabitat and microclimatic conditions by tree removal (Fig. 1), and thereby influence the distribution and abundance of canopy organisms (Nadkarni et al., 2004). In *Nothofagus antarctica* forests, thinning practices in silvopastoral systems modify the overstorey to increase understorey forage production by increasing available photosynthetic active radiation through reduction of tree density. Several studies have provided valuable information on changes in environmental parameters (e.g., solar radiation, temperature), tree physiological performance (e.g., photosynthetic response) and many other ecological processes (e.g., nutrient cycling) at the stand level (Peri, 2009; Bahamonde et al., 2012, 2013). However, little is known about how canopy communities are affected by forest practices. A recent study (Soler et al., 2013) has shown that harvesting with variable retention in *Nothofagus pumilio* forests reduces epiphytic lichen biomass, but increases mistletoe biomass according to the level of canopy retention ($30 \text{ m}^2 \text{ ha}^{-1}$ basal area retained in one circular aggregate per hectare, and $10\text{--}15 \text{ m}^2 \text{ ha}^{-1}$ basal area of the most dominant trees distributed between the aggregates). Based on regional inventories in Santa Cruz (the mainland of Southern Patagonia), Peri and Ormaechea (2013) reported the percentage of trees affected by *Misodendrum punctulatum* have similar abundances of *Usnea barbata* (15–40%) in the canopy of *N. antarctica*, with higher values in disturbed forests.

In Patagonian forests, mistletoes (*Misodendrum* sp.) and epiphytic lichens (*Usnea* sp.) are two common components of the canopy of *Nothofagus* trees. *Misodendrum* (Misodendraceae) is a genus of eight species that is endemic in *Nothofagus* Sub-antarctic forests (Rossow, 1982; Mathiasen et al., 2008). *M. punctulatum* is the most abundant mistletoe in Patagonian forests (Orfila, 1978; Tercero-Bucardo and Rovere, 2010), primarily parasitic on *N. antarctica* and *N. pumilio* through colonization of small branches

and stems (Tercero-Bucardo and Rovere, 2010). The epiphytic lichen *Usnea* (Parmeliaceae), generally grows hanging from tree branches in moist upland areas throughout the world (Clerc, 1998), including *Nothofagus* forests. *U. barbata* is the most abundant species of lichen in Tierra del Fuego growing epiphytically on *Nothofagus* trees (Hawksworth and Moore, 1969). Both mistletoe and lichens are ecologically important as food, shelter and nesting materials for wildlife (Calvelo et al., 2006; Díaz and Kitzberger, 2006; Díaz and Peris, 2011). For example, the austral parakeet (*Enicognathus ferrugineus*) feeds heavily on buds, flowers and foliage of mistletoes during winter (Díaz and Kitzberger, 2006), and guanacos (*Lama guanicoe*) consume mistletoes year round, but consumption increases in winter (Soler et al., 2012) when the tree branches are more accessible due to accumulation of snow.

There is a growing recognition of the importance of arboreal plant communities in forest ecosystem functioning. Recent studies have found that litter input from parasitic plants enhance the ground litter mass and plant productivity of the understorey (March and Watson, 2007; Fisher et al., 2013), while fruticose lichen litter increases nutrient availability, especially nitrogen and phosphorus, in forests soil (Li et al., 2014). There are many gaps in our understanding of the role of arboreal plant communities, particularly in regards to human-induced disturbances such as logging. The objectives of this study were to investigate: (i) how mistletoes (*Misodendrum* sp.) and epiphytic lichens (*Usnea* sp.) contribute to litterfall in *N. antarctica* forests (unmanaged mature and second-growth); (ii) how thinning for silvopastoral purposes affects these litterfall patterns; and (iii) seasonal and annual variation in litterfall.

2. Materials and methods

2.1. Study area

The southernmost forested ecosystems are found at the austral extreme of South America, Tierra del Fuego Island, which is shared between Chile and Argentina. *N. antarctica* is one of the main tree species in the central portion of the island. Trees can grow up to 14 m height in high-quality sites, or as shrubs of 1–3 m height in xeric sites (Ivancich et al., 2011). These forests are mainly used for agroforestry purposes (silvopastoral systems) where private ranches have been established in a transition zone with the Fuegian steppe. Wind-throw is the primary natural disturbance in these forests (Rebertus and Veblen, 1993).

The study was conducted using permanent plots established as part of PEBANPA network of INTA-CADIC-UNPA: Biodiversity and Ecological long-term plots in Southern Patagonia at Los Cerros Ranch ($54^{\circ}18' \text{ S}$, $67^{\circ}49' \text{ W}$). Plots were located within a large area of pure (monospecific) *N. antarctica* forests in the central zone of Tierra del Fuego Island (Argentina). Some areas were subject to burning in the 1960s to increase grasslands extension for livestock, which led to formation of patches of second-growth dense forests. These patches are interspersed with unmanaged old-growth forests and other types of vegetation (e.g., grasslands and peatlands). Since 2005, thinning in mature forests has been applied as part of implementation of silvopastoral strategies in the region (Peri, 2009). As a result of this practice, part of the original canopy is retained as well as other natural components (e.g., stumps, coarse woody debris) after thinning.

The climate of the central zone of Tierra del Fuego Island is cold with a strong Antarctic influence and is characterized by short summers and long, cold winters. Mean monthly air temperatures range from -3 to 9 °C (minimum temperature in July and maximum in February) with only 3 months per year with mean daily temperatures greater than 0 °C. The growing season of these

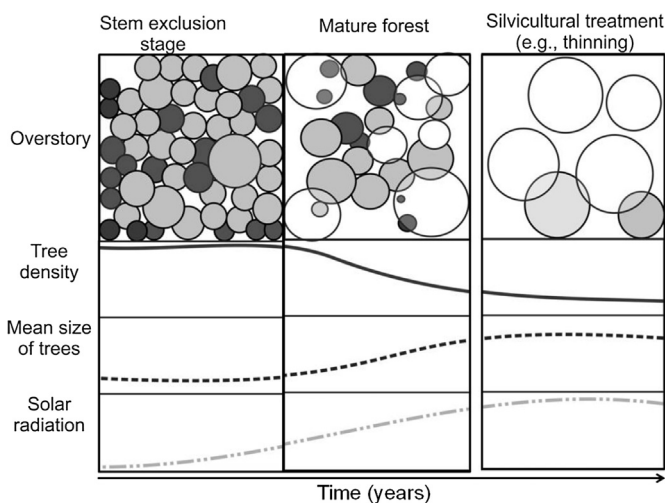


Fig. 1. Theoretical overview of canopy patterns and changes in *Nothofagus* forest structure which occur naturally over time and artificially under silviculture. Circles represent individual tree crowns, circle size corresponds to crown (and tree) size, and the color corresponds to the position in the canopy (white: dominant tree, light gray: co-dominant tree, dark gray: intermediate or suppressed tree) associated with a specific range of tree density, mean tree size and amount of solar radiation reaching the forest floor. The time scale between the stem exclusion stage and mature forest can be taken as continuous; silvicultural treatment, however, initially involves dramatic changes over a smaller time scale.

forests is approximately 5 months (Barrera et al., 2000). Precipitation reaches up to 600 mm yr⁻¹ and 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), which occur mainly during the summer season (December–February). Areas occupied by forests are mostly of glacial origin, consisting of loess and alluvial sediments in the foothills that formed acid brown soils (Frederiksen, 1988).

2.2. Forest structure characterization

Nothofagus forests with three different management histories (forest type) were selected within a 1500 ha area, with four replicates per forest type (12 sampling sites): (i) 50% thinned mature forests (100–150 years old) with silvopastoral use, (ii) second-growth forests, and (iii) unmanaged mature forests without previous harvesting (control sites). The structure of each forest was characterized using the point sampling method (Bitterlich, 1984, Basal Area Factor = 6). We measured the diameter at breast height (DBH) (trees > 5 cm) in all trees to estimate basal area (m² ha⁻¹) (BA), quadratic mean diameter (cm) (QMD), stem density (n ha⁻¹) (D), and total over bark volume (m³ ha⁻¹) (TOBV) of each site. The dominant height (maximum height within the general canopy level, m) was measured for three dominant trees per site by using a TruPulse 200 laser rangefinder (Laser Technology, USA). To further characterize canopy structure and solar radiation transmission, hemispherical photographs of the forest canopy were taken with an 8-mm fish-eye lens (Sigma, Japan) mounted on a 35-mm digital camera (Nikon, Japan), and analyzed with Gap Light Analyzer software v.2.0 (Frazer et al., 2001). We obtained crown cover (%) as a percentage of open sky relative to forest canopy, effective leaf area index, and global radiation (W m⁻²) at the understorey level as the amount of direct and diffuse radiation transmitted through the canopy along the growing season (November–March) (for equations and methodologies see Martínez Pastur et al., 2011).

2.3. Litter collection

We sampled litterfall production for three consecutive years (2008–2010) starting at three years post-thinning (2005) in the managed stands. The litterfall sampling method has been used in previous studies (Sillett, 1994; March and Watson, 2007; Soler et al., 2013) to adequately assess biomass production of epiphytic plants in the canopy at the stand level. Thus, high litter production was interpreted as an increase of mistletoe and lichen biomass in the canopy (c.f. March and Watson, 2007), while a decline in litter reflected the opposite. At each site, 10 circular traps were installed systematically along a 50 m transect (separated 1 m from each other, and at 1.8 m above the ground), to represent the whole plot and not only the dominant tree species. The litter traps were plastic buckets (27.5 cm in diameter and 30.0 cm depth) with several small holes in the base to allow water to escape. Litterfall biomass was collected monthly and manually classified into three groups: (i) *N. antarctica* litter (leaves, fine branches and reproductive structures), (ii) mistletoe (leaves, fine branches and reproductive structures), and (iii) epiphytic lichen (alive and dead thallus). The material collected was oven-dried at 70 °C until constant weight was reached, and weighed with a precision balance (accuracy ± 0.0001 g). Mistletoe and epiphytic components were identified at the genus level as *Misodendrum* sp. and *Usnea* sp. Annual litterfall (tree, mistletoes, and epiphytic lichens) were expressed as kg dry matter (DM) ha⁻¹ year⁻¹. In this study, one year of study corresponded to a calendar year.

2.4. Data analysis

Univariate tests were conducted using one-way ANOVA to determine differences in structure of each forest type (unmanaged mature, second-growth and thinned forests with silvopastoral use). Litterfall patterns from trees, mistletoes and lichens were analyzed using repeated measure ANOVA, using the forest type (unmanaged mature, second-growth and thinned forests for silvopastoral use) and sampling year as the main factors. Regarding the sampling years, we refer to the years post-thinning applied in managed forests, but unmanaged mature and second-growth forests were unaffected and hence, any temporal variation here should be considered a natural pattern (unmanaged mature sites were used as a control to determine natural variability). The years after harvesting were 2008 = 3, 2009 = 4, and 2010 = 5. The response variables were: (i) litterfall from *N. antarctica* (tree), *Misodendrum* sp. (mistletoe) and *Usnea* sp. (lichen) (kg DM ha⁻¹ year⁻¹); (ii) ratios of mistletoe/tree and lichen/tree; and (iii) ratios of mistletoe/BA and lichen/BA (kg DM m⁻² BA⁻¹). When the sphericity test was significant, the Greenhouse and Geisser (1959) univariate adjustment was applied to evaluate within-subjects effects. A post-hoc Tukey's HSD test was used for mean comparisons (p < 0.05). To gain greater insight into the temporal dynamics of litterfall, repeated measure ANOVA was also used to test monthly differences, with month and sampling year as the main factors for each forest type.

3. Results

As expected, forest structure showed significant differences depending on management (Table 1). Unmanaged mature forests represent the control situation with a high total over bark volume and basal area, although this last variable did not show significant differences when compared with second-growth forests. The structure of second-growth forests was reflected in higher stem density and reduced mean quadratic diameter of trees compared to mature stands. Thinning practices reduced basal area, total over bark volume and crown cover. Dominant height was the only variable that was similar among the three forest types (Table 1).

High stem density in second-growth forests resulted in greater canopy closure and consequently a high leaf area index causing a low level of solar radiation reaching 1 m over the understorey (Table 2). Not surprisingly, the silvopastoral sites had the lowest leaf area index and the highest percentage of solar radiation compared to unmanaged mature forests.

Tree litterfall was correlated with crown cover (Table 2). The greatest litterfall was recorded in second-growth forests with 3398 ± 245 kg DM ha⁻¹ year⁻¹ (average ± standard error), followed by unmanaged mature forests with 1954 ± 124 kg DM ha⁻¹ year⁻¹, and silvopastoral sites with the lowest value of 1485 ± 127 kg DM ha⁻¹ year⁻¹. There were small annual variations in tree litter, with higher amounts of litter during 2009 (4 years post-thinning in the managed stands) (Table 2).

Litterfall biomass of mistletoes was similar among forest types, and ranged between 307 and 333 kg DM ha⁻¹ year⁻¹ (Table 2). It is important to note that there was high within-factor variability (forest type) which was due to substantial variation among stands mainly in second-growth forests (from 30 to 475 kg DM ha⁻¹ year⁻¹) and silvopastoral sites (from 150 to 422 kg DM ha⁻¹ year⁻¹). Mistletoe/tree and mistletoe/BA ratios did not vary among forest types (Table 2). There was also considerable inter-annual variation with mistletoe litterfall being significantly lower in 2008 (3 years post-thinning in the managed forests) than in the subsequent years.

Litterfall of epiphytic lichen ranged between 11 and

Table 1
Forest structure of unmanaged mature, second-growth, and silvopastoral sites of *Nothofagus antarctica* forest. Values are means (\pm SD) of basal area (BA) ($\text{m}^2 \text{ha}^{-1}$), dominant height (DH) (m), quadratic mean diameter (QMD) (cm), tree density (TD) (n ha^{-1}), and total over bark volume (TOBV) ($\text{m}^3 \text{ha}^{-1}$).

Forest type	BA	DH	QMD	TD	TOBV	Crown cover	Leaf area index	Solar radiation
Unmanaged mature	51.4 (7.6)b	13.6 (1.3)	49.2 (9.6)b	476 (270)a	351.7 (66.2)b	78.9 (2.7)b	1.6 (0.1)b	10.6 (1.6)b
Second-growth	46.8 (9.1)b	10.2 (0.8)	17.4 (4.8)a	3406 (1023)b	245.5 (86.3)a	85.5 (2.1)c	2.3 (0.2)c	7.7 (5.1)a
Silvopastoral sites	33.3 (5.5)a	12.4 (2.8)	46.9 (12.7)b	364 (181)a	252.5 (104.5)a	66.1 (9.1)a	1.3 (0.4)a	16.8 (3.9)c
F	5.97	3.48	117.29	41.24	4.67	61.51	71.99	73.43
p	0.004	0.076	<0.001	<0.001	0.040	<0.001	0.015	<0.001

F = ANOVA F-values, p = probability. Different letters in each column indicates differences by post-hoc Tukey's HSD test ($p < 0.05$).

40 $\text{kg DM ha}^{-1} \text{ year}^{-1}$ (Table 2). Mature forests, both unmanaged and thinned, had greater values of lichen biomass than second-growth forests, even when lichen/tree ratio was considered. However, litterfall from lichens related to the basal area of stands (lichen/BA ratio) did not vary among forest types. Inter-annual differences among years were not detected for litterfall from lichens (Table 2). While we also detected within-factor variability it was not as great as found for mistletoes.

The monthly sequence of litterfall biomass varied among forest types, collection date (months), and litter type (trees, mistletoes, or epiphytic lichens) (Fig. 2). Most tree litterfall occurred in April in all forest types ($792.5 \text{ kg DM ha}^{-1} \text{ month}^{-1}$). Mistletoe litterfall showed two peaks during October and February (52.5 and $48.8 \text{ kg DM ha}^{-1} \text{ month}^{-1}$, respectively) in all forest types compared to other months (10.3 – $44.6 \text{ kg DM ha}^{-1} \text{ month}^{-1}$). During these months, mistletoe litter represented 26–43% of the total litter input in unmanaged mature forests, 21–35% in second-growth forests, and 31–45% in the silvopastoral sites (Fig. 3).

Lichen litterfall was more homogeneously distributed among months, but significantly higher biomass was detected during October, November and December (4.2 , 4.1 , and $3.9 \text{ kg DM ha}^{-1} \text{ month}^{-1}$, respectively) in all forest types compared to other months (1.4 – $2.8 \text{ kg DM ha}^{-1} \text{ month}^{-1}$). During these months, litterfall from epiphytic lichens represented 2–5% of the total litter input in unmanaged mature forests, 0.5–1.3% in second-growth forests, and 2–3% in silvopastoral sites (Fig. 3).

The amount of tree litterfall per month was reduced ($F_v = 52.8$; $p < 0.001$) in silvopastoral sites in comparison to unmanaged mature and second-growth forests (165.4 , 217.1 , and $377.6 \text{ kg DM ha}^{-1} \text{ month}^{-1}$, respectively). While lichen litterfall was reduced in second-growth forests in comparison to unmanaged mature forests and silvopastoral sites (0.95 , 3.49 and $3.47 \text{ kg DM ha}^{-1} \text{ month}^{-1}$, respectively), no significant differences were detected for mistletoe litterfall among forests types (28.95 – $32.40 \text{ kg DM ha}^{-1} \text{ month}^{-1}$).

4. Discussion

Nothofagus antarctica forests had considerable quantities of *Misodendrum* sp. and *Usnea* sp. litterfall in natural conditions in the forests types studied. It has been assumed that a high-level of infection of mistletoe and occupancy of epiphytic lichen occurs in less vigorous and more open *N. antarctica* forests of Tierra del Fuego (Peri, 2009). Our results suggest that while silvopastoral practices reduce canopy cover it does not alter biomass production of mistletoe and lichen litter. The unmanaged forests and forests thinned for silvopastoral purposes differed by only 14% of stand crown cover. Both mature forests types produced higher biomass of litterfall from epiphytic lichens than second-growth forests. This could be related to (i) solar radiation as a key factor for development of epiphytic lichens (Hawksworth and Moore, 1969), (ii) less crown surface allowing better interception of local precipitation and bark furrows which could channel stemflow (Hauck and Spribille, 2005), and (iii) increased roughness of tree bark (surface adsorption) enabling greater element concentrations in the substrate (Esseen et al., 1996). For example, epiphytic *Usnea* sp. growing on mountain beech trees (*Nothofagus solandri*) in New Zealand prefers thicker and textured bark in high-light environments (Denta et al., 2013). However, the response of epiphytic lichens to certain factors can vary widely with forest type and canopy openness. Soler et al. (2013) reported that 45% of openness resulting from harvesting *N. pumilio* forests strongly reduced the epiphytic lichen biomass compared to unmanaged areas. Similarly, many studies in forests in Europe and North America have shown that young forests (managed stands) have lower abundance of epiphytic lichens (e.g., *Usnea* sp.) compared to old natural stands (Esseen et al., 1996; Storaunet et al., 2008). It is important to consider the period of time required for colonization and dispersion of these lichens. Once a tree is colonized, the lichen spreads more rapidly due to vegetative propagation (e.g., thallus fragments) such that lichen biomass increases not only with tree size but also with age. Based on this idea, production of lichen litter is higher in

Table 2
Annual litterfall ($\text{kg DM ha}^{-1} \text{ year}^{-1}$) of tree (*Nothofagus antarctica*), mistletoe (*Misodendrum* sp.) and epiphytic lichen (*Usnea* sp.) from 3 to 5 years post-thinning; and the ratios mistletoe/tree, lichen/tree, mistletoe/BA and lichen/BA ($\text{kg DM m}^{-2} \text{ year}^{-1}$), where BA is the basal area ($\text{m}^2 \text{ha}^{-1}$) of each forest type. Values are means (\pm SD).

Factor		Tree	Mistletoe	Mistletoe/tree	Mistletoe/BA	Lichen	Lichen/tree	Lichen/BA
Forest type	Unmanaged mature	1954 (787)ab	333 (138)	17.8 (9.4)	6.7 (3.3)	40.5 (23.0)b	2.1 (1.5)b	0.9 (0.4)
	Second-growth	3398 (920)b	317 (211)	14.9 (7.9)	5.9 (4.1)	10.9 (7.8)a	0.4 (0.2)a	0.4 (0.1)
	Silvopastoral sites	1486 (807)a	307 (204)	17.2 (13.2)	7.7 (6.5)	35.4 (15.0)ab	2.3 (1.3)b	0.6 (0.4)
	F	14.60	0.03	0.06	0.30	6.41	15.45	0.84
	p	0.001	0.965	0.936	0.748	0.018	0.001	0.469
Year	2008	2260 (1226)ab	276 (102)a	13.9 (9.5)a	5.5 (3.1)a	32.5 (17.9)	1.7 (1.0)	0.5 (0.8)
	2009	2505 (1203)b	359 (95)b	18.0 (11.8)b	7.9 (2.1)b	28.7 (14.5)	1.5 (1.0)	0.6 (0.5)
	2010	2073 (951)a	322 (136)ab	17.4 (11.7)b	7.0 (1.9)b	25.7 (20.5)	1.5 (0.8)	0.6 (0.5)
	F	5.11	4.10	7.31	9.21	0.54	0.44	0.08
	p	0.017	0.034	0.006	0.003	0.594	0.647	0.919
Interaction	F	0.46	0.85	1.55	0.05	0.93	1.18	2.55
	p	0.759	0.508	0.242	0.990	0.469	0.350	0.085

F = ANOVA F-values, p = probability. Different letters in each column indicates differences by post-hoc Tukey's HSD test ($p < 0.05$).

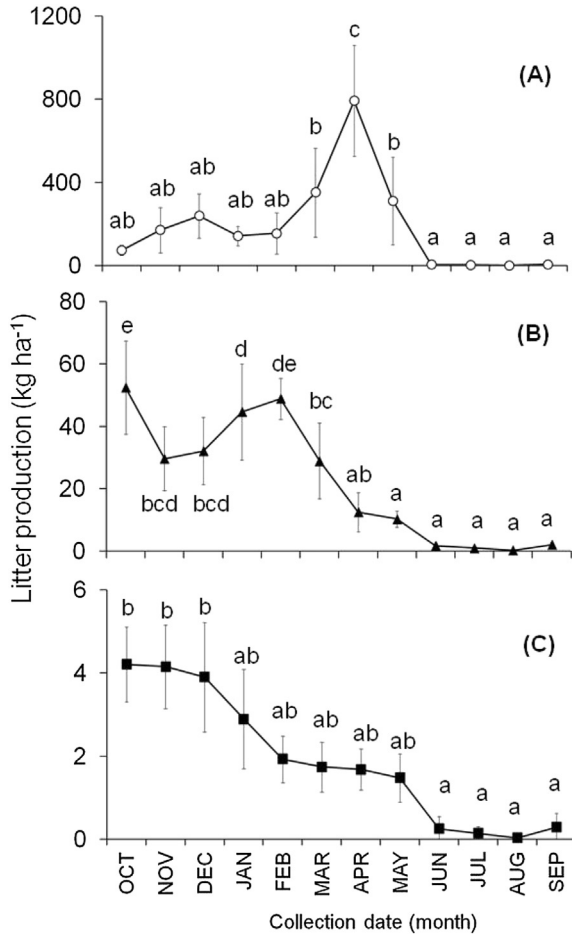


Fig. 2. Monthly litterfall ($\text{kg DM ha}^{-1} \text{ month}^{-1}$) from (A) trees, (B) mistletoes and (C) lichens in all forest types. Values are means (over a 3-year period) \pm SD. Letters indicate significant differences detected by repeated measure ANOVA and post-hoc Tukey's HSD test ($p < 0.05$).

mature forests where both processes (dispersion and colonization) take longer but are not affected by management practices.

We found little effect of canopy cover on biomass production of mistletoe and litterfall did not vary among forest types (net, per tree unit, or per basal area unit). Noetzli et al. (2003) and Henríquez-Velásquez et al., 2012 suggested that stand-level factors (e.g., tree density) determined the rate of spread and infection by mistletoes. However, and contrary to what we expected, the

structural characteristics and solar radiation of second-growth or thinned forests for silvopastoral use did not reduce or increase mistletoe litter production compared to unmanaged mature forests. In dense stands, mistletoes develop mainly on taller trees (dominant and co-dominant) that receive adequate light. Individuals grow very slowly after initial infection, but after a few years they start to grow exponentially (Noetzli et al., 2003; Barbu et al., 2012). Furthermore, since species of *Misodendrum* have very short dispersal distances (<10 m) (Tercero-Bucardo and Rovere, 2010), colonization could increase among close individuals and thereby increase biomass produced per unit area. In mature forests the processes of infection and colonization takes longer and *Misodendrum* can live over 100 years when set in the main trunks of the host (Tercero-Bucardo and Rovere, 2010). This might be one of the reasons why the reduction of canopy cover was not an important factor in this study.

The architecture of *N. antarctica* trees changes with age. The structure of young trees competing for light is characterized by a single main trunk devoid of live branches and small-diameter crown, while mature trees are characterized by a shorter main trunk (as a result of the death of upper branches and distal terminals of lower main branches) and a larger and wider crown than young trees (Steconni et al., 2000). It is likely that mistletoe biomass production and distribution may vary according to the spatial crown configuration without differences between forest types. To confirm this, the distribution of mistletoe needs to be assessed at the individual tree level.

Compared with other *Nothofagus* forests in the area (e.g., *N. pumilio*), our results indicate much greater mistletoe litterfall (Barrera et al., 2000; Soler et al., 2013). This difference may be related to increased canopy density in forest dominated by *N. pumilio* and taller individuals than forest dominated by *N. antarctica* and other differences in tree morphology and architecture (Steconni et al., 2010). It may also occur because *Nothofagus antarctica* is considered more susceptible to attack by fungus (e.g., *Cyttaria* sp.) or mistletoe infections than other species of *Nothofagus* (Alvarado Ojeda, 2006).

According to our results, mistletoes and lichens significantly increased the spatial and temporal complexity of litterfall components. *N. antarctica* litter had a large input during autumn (March–May), which is typical of deciduous species of *Nothofagus* in the Southern hemisphere (Alley et al., 1998). In contrast, the peak of mistletoe and lichen litterfall occurred during spring and summer seasons, thus displaying a complementary relationship with tree litterfall. However, variation of litterfall occurs at individual tree level, among trees with comparable mistletoe loads, among trees with differing mistletoe loads, and among stands with differing mistletoe densities (March and Watson, 2007). In this

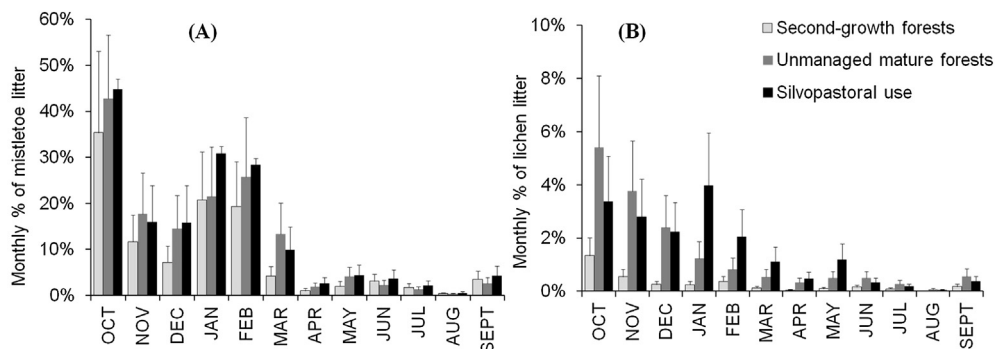


Fig. 3. Monthly percentage of (A) mistletoe and (B) lichen litter relative to total annual litterfall in unmanaged mature forests, second-growth forests, and silvopastoral sites. Values are means (over a 3-year period) \pm SD.

study, substantial variation in the litter components within and between stands of the same treatment was detected, although not deeply explored. Consequently, the amount and quality of litter input to the ecosystem is determined by compositional elements of the forest canopy (epiphytic lichens, mistletoes). Moreover, the period of high litterfall was extended a couple of months, mainly in October when seedling recruitment occurs (Martínez Pastur et al., 2011). This input could represent an important nutrient source for natural regeneration, since litter is the major source of mineral nitrogen availability for *Nothofagus* seedlings in the forest soil (Bahamonde et al., 2012). Several studies support the idea that lichen and mistletoe play an important role as sources of nutrient-rich litter input in temperate forests (March and Watson, 2007; Fisher et al., 2013). In addition, many species of *Usnea* have the capacity to fix atmospheric nitrogen making them a functionally important element in boreal and temperate forests and also their litter of disproportional significance (Li et al., 2014). For this reason, and among other ecological functions, these organisms have been described as a keystone resource in many forest ecosystems (Watson, 2001).

Canopy communities and their relevance in forests ecosystems are becoming increasingly recognized around the world (March and Watson, 2007; Storaunet et al., 2008; Rawat et al., 2011; Fisher et al., 2013; Soler et al., 2013; Li et al., 2014). During the last decade, forest managers have incorporated new strategies (e.g., variable retention) to preserve the original composition and function of forests as a whole system. We recommend that *Usnea* sp. and *Misodendrum* sp. are maintained at the stand level in managed *N. antarctica* forest (low-intensity thinning) at a level similar to unmanaged mature forests. For management planning, a better understanding of the habitat requirements of *Usnea* sp. and *Misodendrum* sp. is required. Consistent with our findings, Soler et al. (2013) suggested that these organisms also survive after logging in *N. pumilio* forests, mainly within patches of original forest that has been retained (aggregated retention). It is possible that analysis at the stand level is not fine enough to detect the natural variations of mistletoe and lichen litter input in *Nothofagus* forests. Open mature stands or a particular spatial crown configuration of individual trees may provide suitable habitat for epiphytic lichens and mistletoes in *Nothofagus* forests. Further comparative studies investigating the relationship among canopy organisms and microhabitat variations are clearly needed and would offer valuable insights into their ecological role at the canopy level.

Author contributions

R.S. and G.M.P. conceived the idea and conducted the field work, M.V.L. carried out the statistical analyzes. P.P. provided editorial advice. Also, all authors analyzed the bibliography and contributed to the discussion of the results and wrote the manuscript, which was led by R.S.

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