



Variable retention effects on vascular plants and beetles along a regional gradient in *Nothofagus pumilio* forests



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ABSTRACT

Variable retention mitigates harmful effects of traditional practices on biodiversity of forest ecosystems, preserving habitats for species affiliated with closed forests and providing habitats for early-seral species. In *Nothofagus pumilio* forests variable retention effects on several taxa have been actively monitored in short- and medium-terms. However, these have rarely been investigated further than six years since harvesting, seldom considering multiple taxonomic groups in the same research. Furthermore, there is a lack of information about responses along the regional gradient of a forest natural distribution. We evaluated the effect of variable retention on plant and beetle assemblages, seven to eleven years after harvesting, in three locations along a regional gradient of the natural distribution of *N. pumilio* forest in Tierra del Fuego, Argentina.

We surveyed three silvicultural treatments (aggregated retention-AR, dispersed retention-DR, old growth forests-OGF) at three localities, where we characterized understory vascular plant and beetle communities during mid-summer by species richness, abundance, Shannon-Wiener diversity and Pielou evenness indices, as well as community structure. We found 58 plants and 45 species of beetles. Assemblages of old growth forests showed differences among the three locations along the studied regional gradient, with only 25% of plants and one beetle shared among them. Plant distribution may be driven by microclimatic and geographical conditions, while availability of food resources or habitat structural complexity could influence beetles. Likewise, variable retention modified original assemblages with greater effects in DR than in AR. However, this trend was not uniform for each taxa or locality, and seems to be related to the composition of original assemblages and the influx of species from surrounding environments. The specialist vs. generalist quantities in the original assemblage could influence the resistance/resilience of the community, since old growth assemblages with a greater proportion of generalist and/or non-sensitive species could maintain more similarity between aggregates and old growth forest. The influx of species (mainly generalists or exploiters) occurred mainly in DR, generating higher dissimilarities between DR and OGF. The correlation between taxa was not so clear for all locations; therefore, retention effects cannot be generalized among taxa and localities. Finally, the utility of potential bioindicators in the whole region could differ for a particular locality, and vice versa. Particularities in the biotic assemblages of different taxa in a regional gradient are important for management and conservation planning, and support variable retention as a useful strategy to combine conservation and production objectives in a managed landscape.

1. Introduction

Variable retention is a silvicultural approach to forest timber management implemented worldwide, which consists of a regeneration treatment with different degrees and patterns of stand retention (Kohm and Franklin, 1997; Gustafsson et al., 2012; Lindenmayer et al., 2012). The major objectives of variable retention are: to provide refuge for species and processes over the regeneration phase; to increase structural variation in managed stands; and to enhance connectivity at the

landscape level (Franklin et al., 1997; Gustafsson et al., 2012). This approach emerged as an alternative management proposal to mitigate harmful effects of traditional practices on biodiversity of forest ecosystems, like those generated by clear-cuts and shelterwood cuts (e.g. on vascular plants: Duffy and Meier, 1992; Jenkins and Parker, 1999; Nagaike et al., 1999; Quinby, 2000; Martínez Pastur et al., 2002; e.g. on insects: Michaels and McQuillan, 1995; Lewis and Whitfield, 1999; Werner and Raffa, 2000; Huber and Baumgarten, 2005; Baker et al., 2004). Complementarily, retention forestry could be considered as an

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analogous concept to the idea of land sharing (Lindenmayer et al., 2012), which integrates different (and often conflicting) objectives of both biodiversity conservation and commodity demands on the same land (Fischer et al., 2008). Changes across regional landscapes make off-reserve conservation strategies necessary, since national, provincial or private natural reserves usually are not so numerous and widely distributed to cover all natural forest variations along a regional gradient. Therefore, the retention approach complements the provision of reserves. Both principles of land-sharing and land-sparing can thus ensure multiple ecosystem services sourced from forest ecosystems (Mori and Kitagawa, 2014).

Variable retention has been implemented in North American, northern European and Australian temperate forests, and their benefits for vascular plant and insect conservation have been reported on by several studies (e.g. North et al., 1996; Vanha-Majamaa and Jalonen, 2001; Aubry et al., 2004; Lemieux and Lindgren, 2004; Hyvärinen et al., 2005, 2006; Nelson and Halpern, 2005; Martikainen et al., 2006; Matveinen-Huju et al., 2006; Craig and Macdonald, 2009; Halpern et al., 2012; Baker et al., 2015). Similarly, variable retention has been implemented in Argentinean South Patagonian forests (Martínez Pastur et al., 2009), where the effects on biodiversity of several taxa have been actively monitored in short- and medium-term studies (Lencinas et al., 2007, 2008a, 2009, 2011, 2014; Martínez Pastur et al., 2011; Peri et al., 2016). In contrast to traditional practices, retention maintains habitat for species affiliated with closed forests, mitigating the negative effects of timber harvesting, while also providing habitat for early-seral species (Fredowitz et al., 2014). Therefore, retention practices can potentially contribute to biodiversity conservation, by preserving species richness equivalent to that of primary forests at different world regions or economic development levels (Mori and Kitagawa, 2014). However, biotic responses to variable retention have rarely been investigated at more than six years since harvesting (e.g., Halpern et al., 2012), and seldom considering multiple taxonomic groups in the same research (e.g., Baker et al., 2015).

Argentinean South Patagonia comprises two provinces: Santa Cruz, in the extreme of the South American continent, and Tierra del Fuego, an archipelago separated from the continent by the Magellan Strait. The landscape of South Patagonia hosts several semi-natural environments, varying from *Nothofagus* forests to arid steppes. *Nothofagus pumilio* (Poepfig & Endl.) Krasser forests are the predominant forest type in the main island of Tierra del Fuego, shared between Chile and Argentina. This island hosts the world's most southern and extensive forest ecosystems and, due to their large-scale use is recent (since the 1950s), can be considered one of the least disturbed habitats on the planet (Mittermeier et al., 2003). *Nothofagus pumilio* is a deciduous tree with an extensive natural distribution, from 36°50' to 55°02'S. It comprises monospecific forests in central and southern Tierra del Fuego, covering approximately 400 km by 150 km, with a wide variety of soils, topography, regional macroclimate influences and particular microclimatic conditions. In the Argentinean portion of Tierra del Fuego, these forests are mainly used for timber production, livestock and tourism, strongly prioritising economic aspects over ecosystem conservation. Furthermore, silvicultural management has produced an anthropogenic matrix of forests with varying degrees of succession and intensity of intervention (Luque et al., 2010; Martínez Pastur et al., 2011). The understory of *N. pumilio* timber stands usually contains low vascular plant diversity (Lencinas et al., 2008b), while their arthropofauna include several endemics, unique, rare and relictual species (Lanfranco, 1977; McQuillan, 1993) of great importance to define biogeographic regions (Niemelä, 1990). Exotic plant and insect species are also present, deliberately or accidentally introduced (Moore and Goodall, 1977; Collantes and Anchorena, 1993; Sola et al., 2015).

In previous works on the effects of variable retention on understory vascular plants of *N. pumilio* forests, we found: (a) richness, cover and biomass are directly related to site quality of the stands; (b) understory composition and relative abundance remains similar to old growth

forests inside the aggregates; (c) a combination of aggregated and dispersed retention better limits exotic species introduction and protects sensitive species, improving conservation in harvested stands; and (d) changes in understory diversity start in the first year after harvesting and these are greater in the harvested areas than in aggregates, trending to stabilization at the fourth year after harvesting (Lencinas et al., 2011). In contrast, when evaluating effects of variable retention on insects of *N. pumilio* forest (Lencinas et al., 2014), we found: (a) richness is not related to site quality of the stands; (b) both richness and abundance are negatively affected by variable retention harvesting in the short term with ingress of other species to the system increasing with time; (c) diversity also fluctuates annually in old growth primary forests; and (d) fewer changes in insect richness and relative abundance occur inside aggregates. Nevertheless, these results for *N. pumilio* forests were obtained from a single ranch in Tierra del Fuego, with particular biotic and abiotic characteristics; therefore, we cannot discard possible differences within the regional gradient of distribution of these forests. Other studies also highlight biodiversity benefits generated by the retention approach can vary by region, silvicultural system and taxonomic and functional group (Rosenvald and Löhmus, 2008; Baker et al., 2015). Likewise, the correlation between insect and plant diversity under harvesting impacts is largely unknown, which could be useful for defining monitoring strategies. Coincidental sampling of taxa in time and space makes it possible to evaluate more fully the ecological consequences of forest management (Baker et al., 2015).

With these unknowns in mind, we evaluated the effect of the variable retention silvicultural approach on vascular plant and beetle assemblages, seven to eleven years after harvesting, in three locations along a regional gradient of *N. pumilio* forest in Tierra del Fuego. We selected vascular plants and beetles due to availability of taxonomic knowledge of these two groups. We hypothesized that: (i) plant and beetle assemblages in old growth forests varied in different locations along a regional gradient, according to the influence of the regional climate despite the same forest type; (ii) variable retention effects on plants and beetles depend on the composition of their initial assemblages; (iii) plant and beetle responses to variable retention are correlated, independently of their initial assemblages or regional gradient location. We also discussed the potential utility of some plant and beetle species as bioindicators, and whether these indicators for a particular locality are also useful for the whole natural distribution of the forest type. Finally, we argued the importance of considering particularities in the biotic assemblages of different taxa in a regional gradient for management and conservation planning, in addition to incorporating variable retention as a useful strategy to combine conservation and productive objectives in a managed landscape.

2. Materials & methods

2.1. Study site and forest structure description

The study sites were selected at three different locations (Fig. 1) in Tierra del Fuego (Argentina) along a regional gradient, which include differences in latitude, longitude, elevation and influence of regional climate over local climate (Martínez Pastur et al., 2011; Henn et al., 2014). These locations were associated with three localities: San Justo Ranch (SJ) at 54°7'22.39"S, 68°36'2.80"W; Los Cerros Ranch (LC) at 54°22'20.14"S, 67°52'0.47"W; and Río Irigoyen (RI) at 54°37'7.78"S, 66°36'24.5"W, which are included in the PEBANPA network (Biodiversity and Ecological long-term plots in Southern Patagonia; Peri et al., 2016). In SJ, the northern and westernmost locality, local climate has a strong influence of north and west winds and storms (mainly Pacific Ocean influence), due to the low height of the Andes Mountains to the west (less than 600 m.a.s.l.) not acting as barriers. On the contrary, at RI, the southern and easternmost locality, local climate is mainly controlled by east wind and storms (Atlantic Ocean influence), due to the proximity to the sea shores (approximately 18 km) and lack of high



Fig. 1. Location of the study sites (black dots) at three localities distributed in the regional gradient of the natural distribution of *Nothofagus pumilio* forests in Tierra del Fuego (Argentina). Main cities are marked with empty squares; capital city of the province is underlined.

barriers to the north and east. Finally, LC is the more wind and storm protected locality compared to SJ and RI, relatively close to middle height mountain chains (900 m.a.s.l. at the highest) in the central part of the island, furthest from sea shores (more than 50 km).

The study was conducted summer (January–February) 2012 in natural *N. pumilio* forests, which were harvested between 2001 and 2005 following the variable retention approach proposed by Martínez Pastur et al. (2009). In this proposal, variable retention is applied in forests that have not been disturbed by forestry practices before silvicultural regeneration systems were in place. Variable retention combines aggregated and dispersed retention, with one circular aggregate of 30 m radius per ha (representing 30% of the area) plus several dominant single trees evenly distributed among the aggregates (adding 10–15 m² ha⁻¹ of retained basal area), totaling 30–45 m² ha⁻¹ of remnant overstory after harvesting, depending on the original basal area on each site. The studied stand presented a middle-to-high site quality according to Martínez Pastur et al. (1997), with a total overbark volume of 700–900 m³ ha⁻¹ and total dominant height between 20.5 and 27.5 m. Surrounding harvested stands, unharvested old-growth forests remained and continued under the influence of natural disturbances without human intervention, with a similar structure (uneven aged structure with some large trees more than 200 years-old, multilayered canopy, and large coarse woody debris) to those stands where harvesting was applied. Biophysical description of localities, including characteristics of forest structure and general ground cover for old-growth forests and harvested sectors (aggregated and dispersed retention), are summarized in Table 1. The climatic variables were obtained from WorldClim (Hijmans et al., 2005).

In Tierra del Fuego, weather is generally characterized by short, cool summers and long, snowy and frozen winters (Martínez Pastur et al., 2011). In the old-growth forests, mean monthly temperatures (measured 2 m above the floor) usually vary annually from 0 °C to 10 °C (extreme minimum and maximum from –10 °C in July to 25 °C in February), while in harvested stands temperature varies from

Table 1
Biophysical description of three localities studied along the regional gradient of the natural distribution of *Nothofagus pumilio* forest type in Tierra del Fuego (Argentina).

Biophysical variables	San Justo (SJ)	Los Cerros (LC)	Río Irigoyen (RI)
<i>Geographical characterization</i>			
Latitude	54°7'22.39"S	54°22'20.14"S	54°37'7.78"S
Longitude	68°36'2.80"W	67°52'0.47"	66°36'24.5"W
Elevation	215 m.a.s.l.	160 m.a.s.l.	258 m.a.s.l.
<i>Climatic characterization</i>			
Mean annual temperature	5.0 °C	5.1 °C	4.0 °C
Mean diurnal range	7.5 °C	7.9 °C	8.2 °C
Max temperature warmest month	13.5 °C	13.9 °C	12.6 °C
Min temperature coldest month	–1.9 °C	–2.1 °C	–3.3 °C
Temperature annual range	15.4 °C	16.0 °C	15.9 °C
Mean total annual precipitation	473 mm	432 mm	450 mm
<i>Forest structure in old growth forests</i>			
Basal area	63 m ² ha ⁻¹	72 m ² ha ⁻¹	76 m ² ha ⁻¹
Canopy cover	98%	98%	99%
<i>Forest structure in aggregated retention</i>			
Basal area	19 m ² ha ⁻¹	22 m ² ha ⁻¹	23 m ² ha ⁻¹
Canopy cover	94%	94%	96%
<i>Forest structure in dispersed retention</i>			
Basal area	18 m ² ha ⁻¹	9 m ² ha ⁻¹	11 m ² ha ⁻¹
Canopy cover	10%	18%	11%
<i>Ground cover in old-growth forests</i>			
Litter or bare soil without vegetation	34%	50%	19%
Debris	25%	11%	30%
Tree regeneration	2%	2%	9%
Shrubs/subshrubs	2%	< 1%	3%
Forbs	9%	20%	13%
Graminoids	16%	12%	8%
Bryophytes	13%	5%	16%
Ferns	< 1%	< 1%	2%
<i>Ground cover in aggregated retention</i>			
Litter or bare soil without vegetation	28%	32%	41%
Debris	28%	29%	29%
Tree regeneration	4%	4%	4%
Shrubs/subshrubs	< 1%	< 1%	< 1%
Forbs	7%	15%	10%
Graminoids	22%	14%	4%
Bryophytes	11%	4%	10%
Ferns	1%	3%	3%
<i>Ground cover in dispersed retention</i>			
Litter or bare soil without vegetation	10%	7%	9%
Debris	25%	29%	33%
Tree regeneration	10%	3%	8%
Shrubs/subshrubs	4%	2%	< 1%
Forbs	22%	21%	29%
Graminoids	25%	38%	11%
Bryophytes	1%	1%	3%
Ferns	2%	< 1%	7%

–1 °C to 10 °C (extremes from –11 °C in July to 26 °C in February). Only three months per year have mean monthly temperatures over 0 °C, and the growing season is approximately five months. Soil temperatures at 30 cm deep are usually never below freezing in old-growth forests, but soil freezing can be observed in harvested stands (0 to –1 °C during June–July). Effective precipitation that reaches the forest floor inside old-growth forests, including snowfall, is usually a 60–70% of that recorded in the harvested stands, and 45–50% of that recorded in open areas. Annual average wind speed outside forests was 8 km h⁻¹, reaching up to 100 km h⁻¹ during storms.

2.2. Sampling design

In this work, we followed a two-factor random design, with regional gradient and silvicultural management as the main factors. The regional gradient factor had three levels, which were the three localities previously presented (SJ, LC and RI). The silvicultural management factor also had three levels, which were aggregated retention (AR), dispersed retention (DR), and old growth forests (OGF). We assume OGF is a good representation of the original biodiversity assemblages before harvesting, as well as the comparable state if harvesting would not have been applied at all. At each locality, four replicates of each silvicultural management were selected ($N = 3$ localities at the regional gradient \times 3 silvicultural management \times 4 replicates = 36 plots). Each replicate in AR and DR was located in different aggregates and at least 20 m apart from the edge of each structure, while in OGF replicates were at least 200 m apart one from each other, and at least 50 m from the edge of this structure.

2.3. Understory vascular plant characterization

Vegetation surveys were carried out in a circular plot of approximately 30 m radius centred in each sampling site. Vascular plants (Dicotyledonae, Monocotyledonae and Pteridophytae) were taxonomically identified to the species level, following Moore (1983) and Correa (1969–1998). We estimated ground cover (Pauchard et al., 2000) for each vascular plant species separately, and then they were added to obtain family and total vascular plant cover. The complementary covers (average data for old growth forests in Table 1; AR and DR data not shown) to reach 100% ground cover were: bryophytes (mosses and liverworts), debris (woody material up to 3 cm diameter), and bare soil without vegetation (including litter). Species richness was calculated as the total number of vascular plant species identified in each locality at the regional gradient and silvicultural management. Information was collected for each vascular plant species about its life form (tree, shrub, subshrub, graminoid, forb, fern), origin (native, endemic, exotic) and preferred habitat (old growth *N. pumilio* forests, other *Nothofagus* forests, and non-forested habitats as grasslands and peatlands) was extracted from published literature and previous works (Martínez Pastur et al., 2002; Lencinas et al., 2008b, 2009; Gallo et al., 2013). Voucher specimens were deposited in the Herbarium of Tierra del Fuego at Centro Austral de Investigaciones Científicas (CADIC-CONICET) in Ushuaia, Argentina. A vascular plant species list is presented in Table A1.

2.4. Arthropod sampling

Beetle samples were taken using pitfall traps in February 2012, a thermally relevant period for insect activity in South Patagonia (Niemiälä, 1990). Traps consisted of buried plastic containers (12 cm diameter and 14 cm height), filled to a third of their volume with soapy water (300 ml) to trap and kill arthropods which fell in.

Based on previous experience (unpublished data) and other works in South Patagonia (Cheli and Corley, 2010), contents of individual traps would have resulted in low catch counts, given low arthropod density under extreme local climatic conditions. Therefore, we used pitfall traps in sets of five in each plot, and contents of the five traps in a plot were pooled and used as a single sample in order to raise total capture per sample (Cheli and Corley, 2010). Traps were arranged placing one at the center and the remaining four at 5 meters from the first, and at 90 degrees from each other, left open at ground level for one week before being collected.

We obtained four samples for each silvicultural treatment (OG, AR, DR) in each locality at the regional gradient (SJ, LC, RI), totaling 36 samples from 180 pitfall traps.

All samples were taken to the laboratory for specimen identification and quantification. Identifications were performed under a binocular

dissecting microscope to genus or species level when possible (Roig-Juñent and Domínguez, 2001; Marvaldi and Lanteri, 2005; Posadas, 2012). Due to a lack of complete taxonomic data on Patagonian beetles, some specimens could not be determined to the species level. We employed the recognizable taxonomic unit or morphospecies concept (Oliver and Beattie, 1993; Gerlach et al., 2013) when the former could not be determined (hereafter, “species”). Morphospecies may be sufficiently close to estimate species richness with average errors below 15% in assessment of biodiversity inventories, monitoring or preliminary ecological studies (Oliver and Beattie, 1993). Moreover, it has been demonstrated to be a good tool for insect diversity studies in Patagonian ecosystems, such as *Nothofagus* forests (Spagarino et al., 2001; Lencinas et al., 2008c, 2014; Sola et al., 2016). Voucher specimens were deposited in the permanent reference collection at Centro Austral de Investigaciones Científicas (CADIC-CONICET) in Ushuaia, Argentina.

Different functional groups may respond differently to the presence of residual trees (Matveinen-Huju et al., 2006); therefore, complementary analyses were carried out by sorting and quantifying species according to pre-defined functional groups, based on their response to environmental change (in this case, silvicultural management). Two main response types could be identified: detectors, which are sensitive to environmental change and decrease with added environmental stress, and exploiters, which increase in abundance in response to environmental stress (Gerlach et al., 2013).

For more detailed analyses, a sub-classification was utilized, by which detectors were sub-classified as (i) R-OGF: old growth forest species sensitive to any kind of harvesting; (ii) R-AR: old growth forest species better conserved in aggregated retention; (iii) R-DR: old growth forest species better conserved in dispersed retention; (iv) S-AR: species exclusively sensitive to aggregated retention; (v) S-DR: species exclusively sensitive to dispersed retention. Likewise, exploiters were sub-classified as (vi) H: species equally favored by both harvesting; (vii) H-AR: species mainly favored by aggregated retention; (viii) H-DR: species mainly favored by dispersed retention. Last, another category was considered: (xi) NS: non-sensitive species to environmental changes. R-OGF, R-AR, R-DR, S-AR and S-DR corresponded to species affiliated with mature forest structures, while H-AR, H-DR and H corresponded to species affiliated with disturbed areas. The assignment of each species to each category was defined by their average abundance in the silvicultural treatments, standardized by the maximum observed abundance, following the rules described in the Table 2. A beetle species list is presented in Table A2.

Table 2

Assignment rules of response type and category for beetle species, according to their abundance in the silvicultural treatments (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention) standardized by the maximum observed abundance.

Response type	Category	Standardized abundance
<i>Detectors</i>	R-OGF	Greater than 50% and maximum in OGF
	R-AR	Least 2-fold greater in DR than in OGF, and lesser than 50% in the other treatments
	R-DR	At least 2-fold greater in DR than in OGF, and lesser than 50% in the other treatments
	S-AR	Lesser than 50% in AR and greater than 75% jointly in the other treatments
	S-DR	Lesser than 50% in DR and greater than 75% jointly in the other treatments
<i>Exploiters</i>	H	Lesser than 50% in OGF and greater than 75% jointly in the harvesting treatments
	H-AR	Lesser than 50% in OGF and higher than 75% in AR
	H-DR	Lesser than 50% in OGF and higher than 75% in DR
	NS	Lesser than 50% in OGF and lesser than 75% jointly in the harvesting treatments

Table 3

Understory vascular plant species richness (S) and abundance (A) for the whole sampling, by regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen) and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention), taxonomically classified by family. Abundance is the vascular plant ground cover (%).

Family	Whole sampling S (A)	Regional gradient			Silvicultural management		
		SJ S (A)	LC S (A)	RI S (A)	OGF S (A)	AR S (A)	DR S (A)
Apiaceae	4 (7.3)	3 (5.9)	3 (5.9)	2 (10.1)	2 (7.7)	3 (5.5)	4 (8.7)
Orchidaceae	1 (< 0.1)			1 (0.1)	1 (0.1)		
Asteraceae	8 (4.7)	3 (3.8)	4 (5.3)	5 (5.2)	6 (3.1)	5 (2.0)	7 (9.1)
Brassicaceae	1 (0.2)	1 (0.3)	1 (0.1)	1 (0.3)	1 (0.2)	1 (0.2)	1 (0.2)
Caryophyllaceae	5 (1.3)	1 (0.6)	5 (1.3)	3 (1.9)	2 (0.2)	2 (1.5)	3 (2.1)
Cyperaceae	4 (2.5)	1 (2.4)	4 (2.2)	1 (3.0)	1 (2.1)	1 (2.5)	4 (2.9)
Ericaceae	1 (0.1)			1 (0.2)	1 (0.2)		
Nothofagaceae	1 (5.1)	1 (5.4)	1 (2.8)	1 (7.2)	1 (4.4)	1 (4.0)	1 (7.0)
Rubiaceae	2 (1.1)	1 (1.0)	2 (2.4)		1 (2.3)	2 (0.8)	1 (0.3)
Gunneraceae	1 (< 0.1)			1 (< 0.1)	1 (< 0.1)		
Plantaginaceae	1 (0.1)	1 (0.1)	1 (0.3)				1 (0.3)
Lycopodiaceae	1 (0.8)			1 (2.3)	1 (0.1)	1 (0.3)	1 (2.0)
Euphorbiaceae	1 (0.3)		1 (0.4)	1 (0.5)	1 (0.4)	1 (0.5)	1 (0.1)
Poaceae	15 (11.0)	7 (14.8)	11 (15.7)	9 (2.9)	5 (8.1)	6 (9.0)	15 (16.0)
Polygonaceae	1 (1.6)	1 (1.4)	1 (3.3)		1 (< 0.1)	1 (0.2)	1 (4.5)
Athyriaceae	1 (0.1)	1 (0.3)	1 (0.1)	1 (< 0.1)	1 (< 0.1)	1 (0.2)	1 (0.2)
Blechnaceae	1 (0.2)		1 (0.2)	1 (0.3)	1 (0.2)	1 (0.3)	1 (< 0.1)
Berberidaceae	1 (0.1)	1 (0.2)	1 (< 0.1)	1 (0.1)	1 (0.3)		
Ranunculaceae	2 (0.1)	1 (< 0.1)		2 (0.2)	1 (0.1)		2 (0.1)
Grossulariaceae	1 (0.3)	1 (0.3)	1 (0.5)				1 (0.8)
Rosaceae	4 (3.7)	3 (5.8)	3 (3.2)	4 (2.1)	4 (2.4)	3 (2.4)	4 (6.3)
Violaceae	1 (0.5)		1 (0.6)	1 (0.9)	1 (0.7)	1 (0.7)	1 (0.1)
Total = 22	58 (41.0)	27 (42.1)	42 (44.1)	37 (36.9)	32 (32.7)	30 (29.7)	50 (60.8)

2.5. Data analyses

We estimated species richness (S), abundance, occurrence frequency, Shannon-Wiener diversity (H') and Pielou evenness (J) indices for the general characterization of understory vascular plant and beetle diversity. Richness calculations were made per plot, per each level of regional gradient and silvicultural management, and for the whole study, while abundance was calculated per plot only. Abundance was cover (%) for understory vascular plants, while it was the number of adult individuals per trap set and sampling period for beetles. Occurrence frequency for each species was obtained as a proportion of the occurrence in each plot relative to the total plots, for each level of regional gradient and silvicultural management, and for the whole study. Shannon-Wiener diversity index was obtained as $H' = -\sum p_i \ln p_i$, where p_i is relative abundance of i species at each plot; Pielou evenness index was obtained as $J = H'/H'_{\max}$, where $H'_{\max} = \ln(S)$, where S is from each plot (Pielou, 1975).

To evaluate species richness, abundance, Shannon-Wiener diversity and Pielou evenness indices of understory vascular plants and beetles, we used two-way ANOVAs after statistical assumptions (homocedasticity, normality) were met, analyzing regional gradient (SJ, LC and RI) and silvicultural management (OGF, AR and DR) as main factors. Interaction terms (regional gradient x silvicultural management) were also analyzed, for which differences among levels of one main factor for each level of the other main factor were evaluated by one-way ANOVAs. Averages were tested for significant differences using Tukey *a posteriori* comparisons ($p < 0.05$). Statgraphics (Statistical Graphics Corp., USA) software was used for these analyses.

Relationships among levels of regional gradient and silvicultural management for vascular plant and beetle community structures were examined by two multivariate methods:

(1) Non Metrical Multidimensional Scaling (NMDS) ordination method (Minchin, 1987) by manual methodology, with Bray-Curtis distance and 250 iterations. A Monte Carlo test was used to evaluate stress in randomized data; probability was presented for each axis. This methodology is widely used to graphically analyze arthropod

assemblages and composition (e.g., Grove and Forster, 2011; Baker et al., 2015; Sola et al., 2016). Points represent plots, and distances between plots are proportional to the dissimilarity of their community structures. This analysis was performed globally (for the total plots), classifying them by locations in the regional gradient, and by silvicultural treatments.

(2) Permutation-based nonparametric MANOVA (PerMANOVA, Anderson, 2001), with Bray-Curtis distance, 4999 randomizations, and Monte Carlo test for pair-wise comparisons. This analysis was performed globally (for the total plots, with one and two-factor designs), or partially (one-factor design), where regional gradient and silvicultural management were main factors. When PerMANOVA was conducted partially, it compared levels of one main factor for each level of the other main factor.

Finally, we used Indicator Species Analysis (Dufrene and Legendre, 1997) to explore possible associations (in specificity and fidelity) of understory vascular plants and beetles with silvicultural treatments (e.g. Grove and Forster, 2011). These analyses included a random re-allocation procedure with 4999 permutations (Monte Carlo test) to evaluate the significance of the maximum indicator values (IndVal) provided ($p < .05$). Following Tejeda-Cruz et al. (2008), we considered as “indicator species” those species with IndVal greater than 50 and p values lower than .05. Indicator Species Analysis was performed for the whole regional gradient (all samplings from different location together), and by location. We used the software PC-ORD (McCune and Mefford, 1999) to conduct NMDS, MRPP and Indicator Species Analysis.

3. Results

3.1. General description of vascular plant and beetle communities

Understory vegetation included 58 vascular plant species overall with a total average ground cover of approximately 40%. The species found belonged to 22 families, being Poaceae (15 spp.) and Asteraceae (8 spp.) the richest ones (Table 3). Among these, there were only one

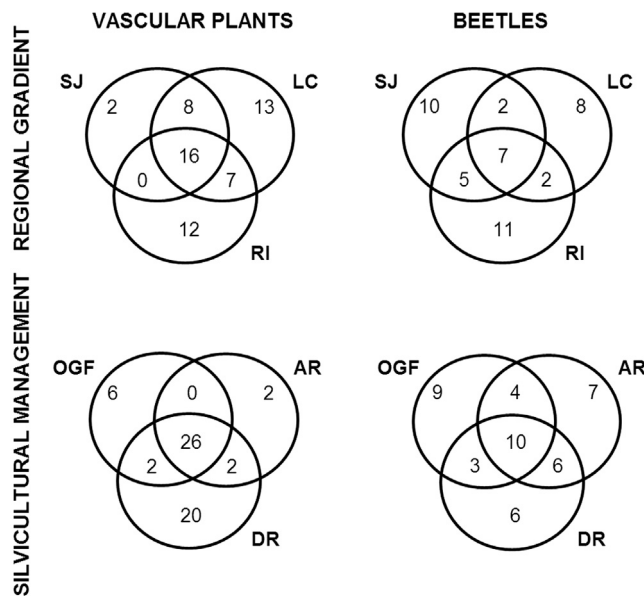


Fig. 2. Overlapping representation of shared and exclusive species richness of understory vascular plants and beetles in *Nothofagus pumilio* forests, among regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen) and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention).

tree, two shrubs and two subshrubs, 19 graminoids, 31 forbs and three ferns, of which 19 species were associated with old growth *N. pumilio* forests according to published studies, 14 were more associated with other *Nothofagus* forests, and 25 preferred grassland and peatlands (Table A1). The most frequent species in the whole sampling were the regeneration of the tree species, *N. pumilio* (100%), the forb *Osmorhiza depauperata* (97%) and the graminoids *Phleum alpinum* (89%), *Uncinia lechleriana* (81%), *Festuca magellanica* and *Trisetum spicatum* (both with 78% occurrence frequency). Regarding regional gradient, the overall richness of each locality varied from 42 to 26 vascular plant species following the order LC > RI > SJ, while cover fluctuated from 44% to 37%, with LC > SJ > RI (Table 3). Shared richness among all localities were 16 spp. (28%), while 7–8 spp. (12–14%) were shared only between two localities (except SJ and RI, which did not share any species), and 2–13 spp. (3–22%) were exclusive of one of them (Fig. 2). Under silvicultural management, overall richness at each treatment varied from 50 to 30 vascular plant species, while cover varied from 61% to 30%, following both variables the order DR > OGF > AR (Table 3). Shared richness among all silvicultural treatments were 26 spp. (45%), while two spp. (3%) were shared only between two treatments (except OGF and AR, which did not share any species), and 2–20 spp. (3–34%) were exclusive of one of them (Fig. 2).

In our beetle sampling we collected 1437 individuals, classified in 45 species and 16 families (Table 4), of which 15 species were singletons and seven, doubletons. Most species belonged to Curculionidae (11 spp.), Carabidae and Staphylinidae (eight spp. each), while Perimylopidae was the most caught (919 ind.), followed by Carabidae (257 ind.). Among these, there were 24 detector species (12 R-OGF, four R-AR, three R-DR, two S-AR and three S-DR) and 21 exploiter species (four H, eight H-AR, seven H-DR and two NS) (Table A2). The most frequent species in the whole sampling were *Migadops latus* and a rove beetle (Staphylinidae 8; both with 61% occurrence frequency), and *Hydromedion anomocerum* (50%). Regarding regional gradient, the overall richness of each locality varied from 25 to 19 beetle species, following the order RI > SJ > LC, while abundance fluctuated from 749 to 165 ind., being SJ > RI > LC (Table 4). Shared richness among all localities were seven spp. (16%), while 2–5 spp. (4–11%) were shared only between two localities, and 8–11 spp. (18–24%) were exclusive to one of them (Fig. 2). Under silvicultural management, overall

richness varied from 29 to 25 species while abundance varied from 943 to 191 ind., following the order OGF > AR > DR for both variables (Table 4). Shared richness among all silvicultural treatments were 10 spp. (22%), while 3–6 spp. (7–13%) were shared only between two treatments, and 6–9 spp. (13–20%) were exclusive of one of them (Fig. 2).

3.2. Comparisons by regional gradient and silvicultural management

Locations in the regional gradient as well as silvicultural treatments generated significant differences in understory vascular plant and beetle richness, abundance and indices (Table 5). For plants, mean richness significantly differed in regional gradient ($F = 15.09$, $p < 0.001$) and silvicultural management ($F = 18.23$, $p < 0.001$), following the previously described overall pattern (LC > RI > SJ and DR > OGF > AR). However, although vascular plant mean abundance showed significant differences among silvicultural treatments ($F = 24.77$, $p < 0.001$), being DR > OGF and AR, these differences were not detected among localities. Shannon-Wiener diversity and Pielou evenness indices presented significant interactions between the main factors (Fig. 3). For Shannon-Wiener index, interaction occurred by significant lower values in OGF compared to AR and DR in LC, and significantly lower values in AR compared to DR in RI (OGF with intermediate values), while no differences were detected among silvicultural management for SJ. Likewise, RI presented significantly lower values for both AR and DR compared to LC (without differences with SJ), but differences were not found among locations for OGF. For Pielou evenness index, interaction occurred due to significantly lower values observed in OGF compared to AR and DR in LC, but differences were not detected among silvicultural treatments for other localities. Moreover, localities did not differ when compared for each silvicultural management (Fig. 3).

For beetles, mean richness significantly differed in the regional gradient ($F = 3.72$, $p = 0.037$), being RI > LC while SJ did not significantly differ from either; moreover, differences were not detected for silvicultural management (Table 5). However, Shannon-Wiener diversity index did not show significant differences for regional gradient, but they were found for silvicultural management ($F = 11.92$, $p < 0.001$), with AR and DR > OGF. Finally, Pielou evenness index presented significant differences for both main factors, with LC > SJ (RI with intermediate values) and AR and DR > OGF. Beetle abundance showed significant interaction between main factors (Fig. 3), which was explained by low abundances in all silvicultural treatments in LC, while OGF presented significantly higher values in SJ and RI compared to AR and DR in these localities. Likewise, LC had significantly lower beetle abundance compared to RI and SJ in OGF, but no significant differences were found among the regional gradient in AR and DR (Fig. 3).

Community structure similarities in understory vascular plants and beetles for regional gradient and silvicultural management were graphically represented in NMDS ordination analyses (Fig. 4). For plant NMDS (14.690 final stress for 3-dimensional solution and 0.005 final instability), Axis 1 ($p = 0.008$) and Axis 3 ($p = 0.004$) were presented; while for beetle NMDS (15.706 final stress for 2-dimensional solution and 0.001 final instability), Axis 1 and Axis 2 were used (both with $p = 0.004$). Locality grouping had strong cohesion and clear split for both plant and beetle NMDS (Fig. 4). Significant differences among centroids of “locality groups” were detected by one-factor PerMANOVA ($F = 5.39$, $p < 0.001$ for plants; $F = 5.71$, $p < .001$ for beetles), being all comparisons between localities significant for both taxa ($t > 1.54$, $P < 0.029$), except RI vs. SJ for beetles ($t = 1.34$, $P = 0.085$). Similarly, significant differences among centroids of “silvicultural management group” were found by one-factor PerMANOVA ($F = 1.76$, $p = 0.029$ for plants; $F = 3.10$, $p = 0.001$ for beetles), being all comparisons between silvicultural treatments significant for both taxa ($t > 1.54$, $P < 0.029$), except OGF vs. AR and OGF vs. DR

Table 4

Beetle species richness (S) and abundance (A) for the whole sampling, by regional gradient (RI = Río Irigoyen; SJ = San Justo; LC = Los Cerros) and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention), taxonomically classified by family. Abundance is the number of individuals per trap set and sampling period.

Family	Whole sampling S (A)	Regional gradient			Silvicultural management		
		SJ S (A)	LC S (A)	RI S (A)	OGF S (A)	AR S (A)	DR S (A)
Anthribidae	1 (1)	1 (1)				1 (1)	
Brenthidae	1 (6)	1 (2)	1 (2)	1 (2)	1 (3)	1 (2)	1 (1)
Carabidae	8 (257)	6 (72)	5 (84)	3 (101)	4 (92)	6 (79)	5 (86)
Chrysomelidae	2 (2)		2 (2)		2 (2)		
Cryptophagidae	1 (1)			1 (1)		1 (1)	
Curculionidae	11 (99)	3 (32)	4 (19)	9 (48)	8 (31)	8 (42)	8 (26)
Elateridae	1 (1)	1 (1)					1 (1)
Erotylidae	2 (4)	2 (4)			1 (2)	1 (2)	
Mordellidae	1 (1)	1 (1)					1 (1)
Perimylopidae	1 (919)	1 (585)		1 (334)	1 (788)	1 (123)	1 (8)
Pselaphidae	1 (1)	1 (1)				1 (1)	
Ptiliidae	1 (7)	1 (6)		1 (1)	1 (1)	1 (5)	1 (1)
Scaphidiidae	2 (31)	2 (7)	2 (15)	1 (9)	1 (3)	2 (16)	2 (12)
Scolytidae	1 (2)			1 (2)			1 (2)
Staphylinidae	8 (97)	3 (36)	2 (39)	6 (22)	5 (19)	4 (27)	2 (51)
Tenebrionidae	1 (1)		1 (1)		1 (1)		
Not identified	2 (7)	1 (1)	2 (3)	1 (3)	1 (1)	1 (4)	2 (2)
Total = 16	45 (1437)	24 (749)	19 (165)	25 (523)	26 (943)	28 (303)	25 (191)

Table 5

Two-way ANOVA results for species richness, abundance, Shannon-Wiener diversity and Pielou evenness indices of understory vascular plants and beetles, by regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen) and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention) as main factors. For understory vascular plants, abundance is their cover (%); for beetles, abundance is the number of individuals per trap set and sampling period.

Study	Factor	Level	Richness	Abundance	Shannon-Wiener	Pielou	
Understory vascular plants	RG: Regional gradient	SJ	11.6 a	42.1	2.07	0.84	
		LC	16.7 c	44.1	2.24	0.80	
		RI	14.2 b	36.9	2.10	0.80	
		<i>F (p)</i>		15.09 (< 0.001)	1.15 (0.331)	1.41 (0.261)	0.88 (0.426)
	SM: Silvicultural management	OGF	14.0 b	32.7 a	1.89 a	0.72 a	
		AR	11.4 a	26.7 a	2.07 a	0.86 b	
		DR	17.0 c	60.8 b	2.45 b	0.87 b	
		<i>F (p)</i>		18.23 (< 0.001)	24.77 (< 0.001)	12.95 (< 0.001)	8.84 (0.001)
		RG × SM: <i>F (p)</i>		2.19 (0.096)	0.85 (0.508)	4.56 (0.006)	3.75 (0.015)
	Beetles	RG: Regional gradient	SJ	5.5 ab	62.4 b	0.86	0.54 a
LC			4.7 a	13.8 a	1.13	0.78 b	
RI			7.1 b	43.6 b	1.26	0.64 ab	
		<i>F (p)</i>		3.72 (0.037)	23.55 (< 0.001)	2.72 (0.084)	8.00 (0.002)
SM: Silvicultural management		OGF	5.1	78.6 b	0.59 a	0.40 a	
		AR	6.3	25.2 a	1.31 b	0.76 b	
		DR	5.8	15.9 a	1.35 b	0.80 b	
		<i>F (p)</i>		0.98 (0.389)	23.55 (< 0.001)	11.92 (< 0.001)	26.90 (< 0.001)
		RG × SM: <i>F (p)</i>		0.09 (0.983)	6.12 (0.001)	0.76 (0.559)	1.74 (0.171)

F (p) = Fisher test and significance between parenthesis. Different letters in a column indicate significant differences ($p < 0.05$) by Tukey *a posteriori* comparison.

for plants ($t < 1.19$, $P > 0.179$).

Significant differences among centroids for each group of regional gradient and silvicultural management over vascular plant and beetle assemblages were also detected by two-factor PerMANOVA, but with interactions ($F = 2.15$, $p < 0.001$ for plants; $F = 2.41$, $p < 0.001$ for beetles). Therefore, one-factor PerMANOVA was developed for comparisons among centroids of locality groups for each level of silvicultural management, as well as for comparisons among centroids of silvicultural treatment groups for each level of regional gradient. When comparing among localities, these analyses resulted in significant differences for plants in RI vs. SJ and RI vs. LC at all silvicultural

treatments (OGF, AR and DR), and also in SJ vs. LC at DR (Table 6). While for beetles, significant differences were found in RI vs. LC and SJ vs. LC, at all silvicultural treatments (OGF, AR and DR), and also in RI vs. SJ at DR (Table 6). Likewise, for comparisons among silvicultural treatments, these analyses resulted in significant differences for plants in OGF vs. DR at all localities, as well as in AR vs. DR at LC and RI, and in OGF vs. AR at LC (Table 6). For beetles, there were significant differences in OGF vs. DR at all localities, an also in AR vs. DR at SJ and RI, as well as in OGF vs. AR at RI (Table 6).

Indicator Species Analysis (Table 7) to compare silvicultural management for the whole regional gradient only identified two vascular

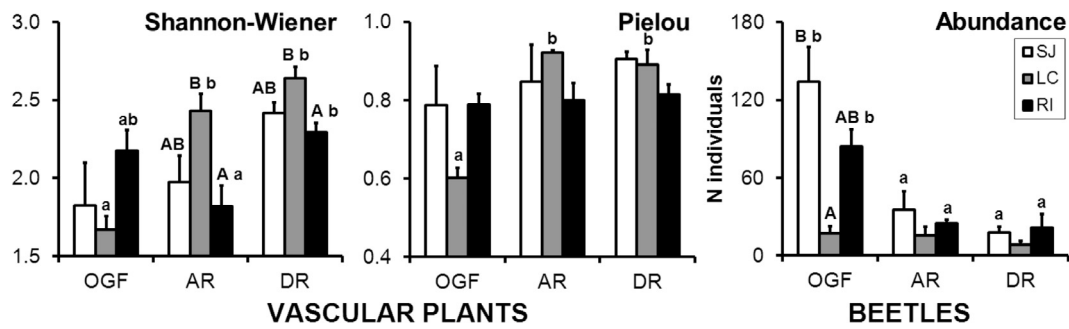


Fig. 3. Graphical representation of interactions between regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen) and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention), for Shannon-Wiener diversity and Pielou evenness indices of understory vascular plant, and for beetle abundance (number of individuals per trap set and sampling period), according to Table 5. Error bars indicate standard deviation. Capital letters in each graphic indicate significant differences among regional gradient for each level of silvicultural management by Tukey comparisons ($p < 0.05$); lower case letters indicate significant differences among silvicultural management for each level of regional gradient by Tukey comparisons ($p < 0.05$). Absence of letters indicates significant differences did not exist.

plant species as indicators of DR, and one beetle as indicator of OGF. However, the analysis by locality showed: (i) three vascular plant species as indicators of DR and two beetles (one of OGF and other of DR) for SJ; (ii) one plant and one beetle for LC, both as indicators of OGF; and (iii) eight plants (three as indicators of OGF and five as indicator of DR) and one beetle (OGF) for RI (Table 7).

4. Discussion

4.1. Plant and beetle old growth assemblages along a regional gradient

Despite forest type being the same (*N. pumilio* forests) at the three studied localities, plant and beetle assemblages of the old growth forests showed differences among them along the studied regional gradient. Similar results were observed by Gossner et al. (2014) when studying arthropods in unmanaged beech forests in Germany, which presented differences in the species composition among three different

regions.

Concerning plant assemblages in *N. pumilio* forests, old growth understories in SJ and in LC were very similar to each other (Fig. 4), and both were extremely different from RI, although richness values were more similar between RI and LC (24 and 23 species, respectively) than with SJ (16 species). This occurred because 33% of RI richness was composed of exclusive species, with very few species shared only with LC (8%) and none only with SJ. While LC and SJ had less exclusive species (14% and 3%, respectively), they had more species shared between them (17%). Notably, only 25% of the total old growth forests understory plant species was shared among the three localities, despite the same forest type.

Plant species composition depends strongly on environmental conditions. Since SJ and LC were located at lower latitudes, farther away from the sea and at lower elevation than RI, these conditions could influence temperature (mean annual temperature, temperature annual range, maximum and minimum annual temperatures) and photoperiod,

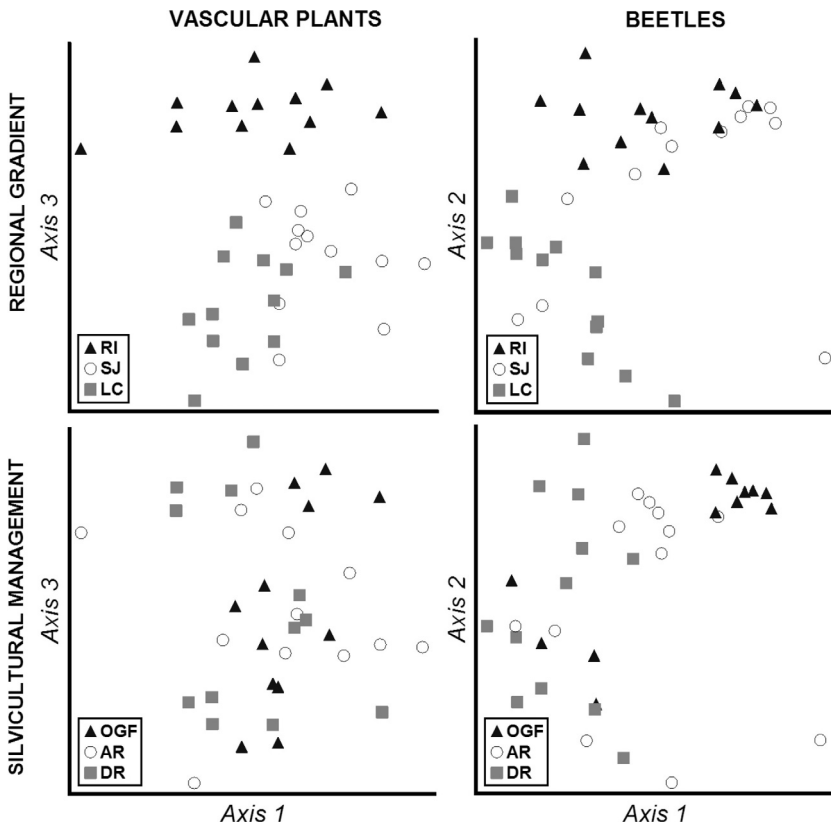


Fig. 4. Non Metric Multidimensional Scaling (NMDS) analysis for understory vascular plant and beetle assemblages in *Nothofagus pumilio* forests of Tierra del Fuego. Points represent sampling plots, according to regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen), or silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention).

Table 6

Monte Carlo P-values from pair-wise comparisons following one-factor PerMANOVA tests conducted for understory vascular plants and beetles, in which regional gradient (RI = Río Irigoyen; SJ = San Justo; LC = Los Cerros) and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention) were the main factors.

Factor	Taxa	Levels	Comparisons		
			RI vs. SJ	RI vs. LC	SJ vs. LC
Regional gradient	Understory vascular plants	OGF	0.0154	0.0040	0.1066
		AR	0.0200	0.0227	0.1156
	Beetles	DR	0.0046	0.0022	0.0314
		OGF	0.1300	0.0010	0.0010
		AR	0.1890	0.0060	0.0290
		DR	0.0310	0.0120	0.0450
		OGF vs. AR	OGF vs. DR	AR vs. DR	
Silvicultural management	Understory vascular plants	SJ	0.1594	0.0249	0.0519
		LC	0.0142	0.0050	0.0351
	Beetles	RI	0.0573	0.0125	0.0161
		SJ	0.0520	0.0040	0.0480
		LC	0.0700	0.0060	0.4500
		RI	0.0020	0.0020	0.0420

enough to modify understory plant distribution. Moreover, dispersion of anemocore species could be facilitated by predominant winds from northwest to southeast direction (from SJ to LC), which could explain that almost all species in SJ are also in LC old growth forests except one (*Taraxacum gillesii*). Then, SJ represented an impoverished understory assemblage of LC (94% of SJ richness shared with LC).

Regarding beetles in *N. pumilio* forests, RI and SJ old growth assemblages were greatly overlapped (Fig. 4), and both had great dissimilarity with the LC old growth assemblage, although richness values were higher in LC and RI (11 and 15 species, respectively), and lower in SJ (8 species). Unlike plants, only one beetle species was shared among the three localities (*Antarctobius hyadesii*), but similarly to plants, SJ showed an impoverished old growth beetle assemblage, but related to RI instead to LC (67% of SJ beetle richness shared with RI). Furthermore, LC had almost the same quantity of exclusive species than RI (eight and seven species, respectively), with only one species shared between these two localities (an undetermined Scaphidiidae species).

Dissimilarities among beetle assemblages of relatively homogeneous sites were also found in Estonian pine forests (Zolotarjova et al., 2016).

Table 7

Values from indicator species analysis (IndVal and probability) for comparisons among silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention), analyzing the whole regional gradient jointly or by location.

Analysis type	Taxa	Species	Silvicultural management			
			OGF	AR	DR	
Whole regional gradient	Understory vascular plants	<i>Taraxacum officinale</i>			62.8 (0.003)	
		<i>Cerastium fontanum</i>			52.0 (0.004)	
	Beetles	<i>Hydromedius anomocerus</i>	57.2 (0.007)			
By locality	San Justo	Understory vascular plants	<i>Rumex acetosella</i>		100 (0.007)	
			<i>Taraxacum officinale</i>		84.8 (0.007)	
			<i>Acaena magellanica</i>		77.6 (0.031)	
	Beetles	<i>Hydromedius anomocerus</i>	83.9 (0.005)			
		<i>Metius malachiticus</i>			100.0 (0.005)	
	Los Cerros	Understory vascular plants	<i>Acaena magellanica</i>	77.0 (0.006)		
		Beetles	<i>Cydrorhinus caudiculatus</i>	75.0 (0.061)		
	Río Irigoyen	Understory vascular plants	<i>Festuca magellanica</i>	90.0 (0.011)		
			<i>Viola magellanica</i>	76.2 (0.007)		
			<i>Berberis buxifolia</i>	75.0 (0.048)		
		Beetles	<i>Taraxacum officinale</i>			100.0 (0.007)
<i>Schizeilema ranunculoides</i>					94.4 (0.002)	
<i>Senecio acanthifolius</i>					86.7 (0.007)	
		<i>Lycopodium magellanicum</i>		85.7 (0.007)		
		<i>Cerastium fontanum</i>		83.3 (0.012)		
		<i>Hydromedius anomocerus</i>	88.9 (0.007)			

Beetles are a heterogeneous group with varied feeding biology. Thus, the availability of resources can explain in part the occurrence of certain species in certain localities more than physical factors alone, which could determine the structure of other arthropod communities, e.g. generalist predators like spiders (Huhta, 1971). Other potentially important factors that influence above ground-active beetle communities include the structural complexity of forests and the abundance of leaf litter, mosses, and coarse woody debris (Peltonen et al., 1997; Halaj et al., 2008). Although the abundance of leaf litter was not assessed in this study, we found more debris and bryophyte cover in SJ and RI, which could generate greater structural heterogeneity inside forests than in LC. Habitat heterogeneity, i.e. the number and proportional distribution of habitat patches with constant habitat variability, also has an effect over ground beetle assemblage diversity, but it may be related to the spatial scale. In this sense, Brose (2003) found a positive correlation on the micro- and meso-scale (0.25 and 500–1000 m², respectively), but it was non-significant on a macro-scale of 10 km².

4.2. Variable retention effects on plant and beetle assemblages

Harvesting by variable retention, including aggregated and dispersed retention, modified original plant and beetle assemblages in Tierra del Fuego *N. pumilio* forests. Some studies have reported that aggregated trees show advantages over dispersed retention for the maintenance of forest biodiversity, whereas other studies have argued that benefits result from dispersed trees (see Baker and Read, 2011; Baker et al., 2013; Rosenvald and Löhmus, 2008). The effects of retention types on biodiversity responses are indeed variable due to several factors, including taxon-specific habitat requirements and dispersal abilities, recovery times of microclimates and biota, and spatial scales of the management unit (Baker et al., 2013). However, changes are attributed to harvesting intensity (proportion of living stand volume removed) on several taxa, as was observed for macroarthropod communities in Finland (e.g. Siira-Pietikäinen et al., 2003), for which the response to harvesting in the retention tree patches is usually parallel but smaller than the responses of the communities in the felled areas. According to previous results (Lencinas et al., 2011, 2014), we also expected greater effects in DR than in AR, as was indeed observed for both plants and beetles in *N. pumilio* forests (e.g., in RI, Fig. 4). However, this trend was not uniform for each taxa or locality in this work (e.g., in SJ for plants and in LC for beetles).

In *N. pumilio* forests, harvesting impacts seem to be related with the composition of original assemblages and the influx of species from surrounding environments. The quantity of specialist vs. generalist species in the original assemblage could have an influence on the resistance/resilience of the community, since assemblages composed by more generalist or non-sensitive species could be able to better adapt to a modified habitat, like those generated by harvesting. Therefore, old growth assemblages with a greater proportion of generalist and/or non-sensitive species could maintain more similarity between harvested areas and old growth forest, specifically in less impacted areas, such as aggregated retention. This occurred with vascular plant assemblages in LC and RI (approximately 60% specialist vs. 40% generalists). In plants, forest generalists and late-seral species usually dominate aggregates (Baker et al., 2015). On the contrary, assemblages with a higher proportion of specialists, as in SJ (75% specialist vs. 25% generalists), are more fragile and usually more impacted by harvesting, even in aggregated retention. A decline in the total number of specialized forest arthropod species after harvesting (as obligatory predators), while more generalist species (using also other food resources) benefited from the harvesting, was reported previously by several authors (e.g., Szujewski, 1971, 1972). The existence of non-sensitive species in the assemblages buffered the effects of harvesting, as occurred in SJ and RI (approximately 90% detector species vs. 10% non-sensitive species), while assemblages without any non-sensitive species, as in LC (100% detector species), responded randomly to harvesting.

The magnitude of spatial and temporal habitat effects, mainly on microclimate and microsite characteristics, determines the effect of variable retention on biotic communities. In some studies, the main factors inducing changes in the above-ground macroarthropod community after harvesting were: changes in understory vegetation, reduction in moss cover, and alterations in litter layer, the habitat where most of the soil macrofauna live (Siira-Pietikäinen et al., 2003). The responses of macroarthropods seemed to be attributed, at least partly, to the feeding biology of the animals, since the numbers of predators, herbivores and soil-dwelling fungivores usually decreased and those of certain detritivores increased on the harvested areas (Siira-Pietikäinen et al., 2003). For example, herbivores decreased because their food resources, roots of living plants, decreased after harvesting. It should be noted that vegetation frequently changed completely (species and root system) after harvesting, as was observed in LC, where grasses (e.g., *Poa pratensis* and *Phleum alpinum*) dominated the herbaceous layer, mainly in DR (more than 35% cover of graminoids), while the moss layer was greatly reduced (1% cover). Because of this, the beetle species composition changed after harvesting, with existing dominant forest species being replaced by others. Despite no animal group of higher taxonomic and functional group level disappears, the relative number of beetles is slightly affected (Siira-Pietikäinen et al., 2003). However, it is important to mention that harvesting has commonly no effect on macroarthropods if soil remains undisturbed (Siira-Pietikäinen et al., 2003).

On the other hand, a greater influx of species from surrounding environments (mainly generalists or exploiters) in the more impacted harvested areas generated higher dissimilarities between DR and OGF assemblages (as was observed in RI-13 sp. and in LC-19 sp. for plants, and in RI-10 sp. and in SJ-15 sp. for beetles). Meanwhile, those localities where lower influx of species occurred (SJ-11 sp. for plants, and LC-8 sp. for beetles), presented lesser dissimilarities between DR and OGF. The scarce influx of species in some localities resulted in their low total richness, which resulted in the effects of variable retention being similar in the richest localities (LC and RI for plants, SJ and RI for beetles), and different in the poorest ones (SJ for plants and LC for beetles).

Dominance of early-seral species in the harvested areas was also observed by other authors (Baker et al., 2015). The ability to colonize disturbed environments is another factor that may influence the possibilities of a species of invading harvested areas: for flying insects, such as most Coleoptera, this can hardly be considered a problem (Huhta,

2002). However, biological responses may vary depending on the history of frequency and intensity of disturbances at landscape level. For taxa poorly dispersed and more common in older than younger landscapes (Ranius, 2006; Hopper, 2009), re-establishment into harvested areas could be delayed.

Although we developed a useful classification of species according to preferred habitat for plants, and response type for beetles, more studies are needed on the autecology of the species to evaluate and predict their response to harvesting or other impacts, and better understand directionality of changes in Tierra del Fuego vascular plant and beetle assemblages.

Finally, some authors have stated that the first three years after treatments are likely to be a transient period and not indicative of long-term effects (Siira-Pietikäinen et al., 2003). This study, conducted 7–11 years after harvesting, seems to be a good approximation to the long-term effect of variable retention on Southern Patagonia *N. pumilio* forests, at least in the stage before canopy closure by regrowth of regenerating forests, when microclimatic differences between aggregated and regenerating forests are much more reduced compared to younger sites (Baker et al., 2015). Moreover, our results reinforce the finding that even small aggregates (approximately 0.3 ha) have the capability to support forest associated species of vascular plants and beetles for at least a decade after harvesting, which was previously found by Lencinas et al. (2011, 2014) in mid-term studies (four years after harvesting), and also reported by Baker et al. (2015).

4.3. Relation between vascular plants and beetles

Conservation planning needs reliable predictors when resources do not permit exhaustive ground surveys (Schaffers et al., 2008). Studies on biological responses to forest management rarely consider multiple taxonomic groups; therefore, natural resource or conservation managers usually assume that responses of forest-dependent or early-seral species in one taxonomic group apply to other taxa.

However, whether some taxa (i.e. plants) serve as surrogates for other taxa remains unresolved. While some studies show surrogacy between plants and arthropods (e.g., Panzer and Schwartz, 1998; Kati et al., 2004; Schaffers et al., 2008), in others there is no clear relationship (e.g., Oliver et al., 1998; Wolters et al., 2006). Moreover, this relation can be time dependent, since it was found in birch woodlands that up to a successional age of 16 months, the taxonomic diversities of plants and insects rose; thereafter, the diversity of the plant species declined far more than that of insect species. The maintenance of a high level of taxonomic diversity of some orders of insects correlated with the rising structural diversity of the green plants in the later successional stages, which virtually compensates for their falling taxonomic diversity (Southwood et al., 1979).

Our hypothesis about the correlation between plant and beetle responses to variable retention as independent of their regional location was rejected. Although responses were similar between plants and beetles for one locality (RI), the correlation was not so clear for the other localities (LC and SJ), which demonstrates the influence of different composition of the original assemblages in the taxa response. Other authors that evaluated plants and invertebrates together suggest the differing responses of both groups highlight the potential danger in generalizing about biodiversity responses to forest influence and to retention forestry in general; therefore, that benefits of retention cannot be generalized among taxa (Baker et al., 2015).

4.4. Potential bioindicator species

Bioindicators are taxa or functional groups that have become increasingly popular as environmental and ecological impact indicators (Niemi, 2001; Underwood and Fisher, 2006; Gerlach et al., 2013). They can reflect the state of the environment, acting as early warning indicators of changes (environmental indicator), monitoring a specific

ecosystem stress (ecological indicator) or indicating levels of taxonomic diversity (biodiversity indicator). The species indicator method developed by Dufrene and Legendre (1997) implies finding a significant association between species and particular habitats, taking into account the relative abundance and occupancy of habitats, and comparing the occupancy of a particular species in different habitats with the occupancy predicted by a null model. The definition of indicator species could help to identify forests with high conservation value, and ideally, such indicators should be the same over large areas (Gossner et al., 2014).

In this work, we found some species as potential bioindicators for the whole studied regional gradient (two vascular plants and one beetle, Table 7). However, when analyses were performed by locality, these three species lost relevance while others appeared as potential bioindicators depending on the particularities of each locality. These differences in bioindicator species between small and large scales reinforce the utility of retention forestry as land sharing strategy, which were also observed by Gossner et al. (2014). This occurs because not all species were present along the whole natural area of the forest type distribution, despite their higher overall abundance (e.g., *H. anomocorum* was not present in LC). Likewise, other species had different habitat preferences in different localities (e.g., *Berberis buxifolia* appeared as typical from OGF in RI, while preferred open habitats more in LC-data not shown). Therefore, the utility of a species identified as potential bioindicator for a region in a particular locality, and vice versa, must be carefully evaluated considering whether this species is present or not in the area, its relative abundance, and whether its habitat preference is the same over the whole regional gradient. Moreover, similarities in the arthropod communities between different forest types and the temporal dynamic nature of the communities themselves do not allow for the identification of arthropod indicators of forest land-use at large spatial scales (Gossner et al., 2014).

5. Conclusions

Plant and beetle assemblages of old growth *N. pumilio* forests show differences along the regional gradient of their natural distribution in

Appendix

Table A1
Occurrence frequency (%) and origin of understory vascular plants in *Nothofagus pumilio* forests, from a regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen), and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention), grouped according to preferred habitat and life form.

Life form	Species names and authors	Origin	Regional gradient			Silvicultural management			Total
			SJ	LC	RI	OGF	AR	DR	
Preferred habitat: <i>Old growth N. pumilio</i> forests									
Tree	<i>Nothofagus pumilio</i> (Poeppig & Endl.) Krasser 1896	Endemic	100	100	100	100	100	100	100
Shrub	<i>Berberis buxifolia</i> Lam. 1792	Endemic	8	8	25	42			14
Graminoid	<i>Deschampsia flexuosa</i> (L.) Trin. 1836	Native	50	42		58	8	25	31
	<i>Festuca magellanica</i> Lam. 1788	Endemic	100	92	42	67	67	67	78
	<i>Phleum alpinum</i> L. 1753	Native	92	92	83	83	92	92	89
	<i>Poa pratensis</i> L. 1753	Exotic	58	100	8	67	42	58	56
	<i>Uncinia lechleriana</i> Steudel 1855	Endemic	83	67	92	67	92	83	81
Forb	<i>Adenocaulon chilense</i> Less. 1831	Endemic		8	92	33	42	25	33
	<i>Cardamine glacialis</i> (Forster f.) DC 1821	Endemic	33	33	8	50	17	8	25
	<i>Codonorchis lessonii</i> (D'Urv.) Lindley 1840	Endemic			17	17			6
	<i>Dysopsis glechomoides</i> (A. Richard) Müller Arg. 1866	Native		50	67	67	33	17	39
	<i>Galium aparine</i> L. 1753	Native	58	50		50	42	17	36
	<i>Macrachaenium gracile</i> Hooker f. 1847	Endemic			58	25	17	17	19
	<i>Osmorhiza depauperata</i> Phil. 1894	Native	92	100	100	100	100	92	97
	<i>Schizeilema ranunculus</i> (D'Urv.) Domin 1908	Endemic	33	8	75	50	25	42	39
	<i>Taraxacum gillesii</i> Hooker & Arn. 1835	Native	17			17			6
	<i>Viola magellanica</i> Forster f. 1789	Exotic		17	58	33	33	8	25

(continued on next page)

Table A1 (continued)

Life form	Species names and authors	Origin	Regional gradient			Silvicultural management			Total
			SJ	LC	RI	OGF	AR	DR	
Ferns	<i>Cystopteris fragilis</i> (L.) Bernh. 1806	Native	17	42	8	33	17	17	22
	<i>Blechnum penna-marina</i> (Poirot) Khun 1868	Native		8	42	25	17	8	17
Preferred habitat: <i>Other Nothofagus forests</i>									
Graminoid	<i>Bromus unioloides</i> Humb., Bonpl. & Kunth 1815	Endemic		42	8		17	33	17
	<i>Trisetum spicatum</i> (L.) K. Richter 1890	Native	75	92	67	50	92	92	78
Forb	<i>Acaena magellanica</i> (Lam.) Vahl 1804	Native	50	83	50	17	50	92	61
	<i>Acaena ovalifolia</i> Ruiz & Pavón 1798	Endemic	42	67	8	25	33	50	39
	<i>Cerastium arvense</i> L. 1753	Native		8	8			8	6
	<i>Cerastium fontanum</i> Baumg. 1816	Exotic	50	83	58	42	58	92	64
	<i>Cotula scariosa</i> (Cass.) Franchet 1889	Endemic	8	50		25	8	25	19
	<i>Galium fuegianum</i> Hooker f. 1847	Endemic		8			8		3
	<i>Geum magellanicum</i> Comm ex Pers. 1806	Endemic	8	17	17	8		33	14
	<i>Gunnera magellanica</i> Lam. 1789	Native			8	8			3
	<i>Osmorhiza chilensis</i> Hooker & Arn 1833	Native		17			8	8	6
	<i>Rubus geoides</i> Sm. 1789	Endemic			75	33	8	33	25
	<i>Stellaria media</i> (L.) Vill. 1789	Exotic		8	17		17		8
	<i>Taraxacum officinale</i> Weber 1780	Exotic	75	100	33	58	50	100	69
	Preferred habitat: <i>Grasslands and peatlands</i>								
Shrub	<i>Ribes magellanicum</i> Poirot 1812	Endemic	17	33				50	17
Subshrub	<i>Azorella trifurcata</i> (Gaertner) Hooker f. 1847	Endemic	8					8	3
	<i>Pernettya pumila</i> (L.F.) Hooker 1837	Endemic			8	8			3
Graminoid	<i>Agrostis magellanica</i> Lam. 1791	Endemic			17			17	6
	<i>Agrostis perennans</i> (Walt.) Tuckerman 1843	Native	8	8				17	6
	<i>Carex curta</i> Gooden. 1794	Native		25				25	8
	<i>Carex decida</i> Boott 1846	Native		8				8	3
	<i>Carex fuscua</i> D'Urv. 1825	Native		8				8	3
	<i>Deschampsia antarctica</i> Desv. 1853	Endemic		25				25	8
	<i>Deschampsia kingii</i> (Hooker f.) Desv. 1853	Endemic			8			8	3
	<i>Elymus agropyroides</i> C. Presl 1830	Native	17	8				25	8
	<i>Holcus lanatus</i> L. 1753	Exotic			8			8	3
	<i>Hordeum comosum</i> C. Presl 1830	Native		25				25	8
	<i>Poa annua</i> L. 1753	Exotic			8			8	3
	<i>Poa scaberula</i> Hooker f. 1847	Native		8				8	3
	Forb	<i>Erigeron myosotis</i> Pers. 1807	Endemic		8				8
<i>Gamochoa spiciformis</i> (Sch. Bip.) Cabrera 1961		Endemic			17			17	6
<i>Ranunculus biternatus</i> Sm. 1814		Endemic			8			8	3
<i>Ranunculus peduncularis</i> Sm. 1814		Endemic	8		8	8		8	6
<i>Rumex acetosella</i> L. 1753		Exotic	33	75			25	67	36
<i>Sagina procumbens</i> L. 1753		Exotic		17				17	6
<i>Senecio acanthifolius</i> Hombron & Jacquinot 1846		Endemic			58	17	8	33	19
<i>Stellaria debilis</i> D'Urv. 1825		Native		8		8			3
<i>Veronica serpyllifolia</i> L. 1753	Exotic	8	17				25	8	
Ferns	<i>Lycopodium magellanicum</i> (P.Beauv.) Swartz 1806	Endemic			58	8	17	33	19

Table A2

Occurrence frequency (%) of coleopteron species in *Nothofagus pumilio* forests, from a regional gradient (SJ = San Justo; LC = Los Cerros; RI = Río Irigoyen), and silvicultural management (OGF = old growth forests; AR = aggregated retention; DR = dispersed retention), grouped according to the response type.

Response type	Family	Species names and authors	Regional gradient			Silvicultural management			Total	
			RI	SJ	LC	OGF	AR	DR		
<i>Detectors</i>										
R-OGF	Brentidae	<i>Apion</i> sp. Herbst 1797	17	17	17	25	17	8	17	
		Carabidae	<i>Cascellius gravesii</i> Curtis 1839		8		8			3
			<i>Trechisibus antarcticus</i> Dejean 1831			50	33	17		17
	Chrysomelidae	Chrysomelidae 1			8	8			3	
		Peltoberum sp.			8	8			3	
	Erotylidae	Erotylidae 2		17		17			6	
	Perimylopidae	<i>Hydromedion anomocerum</i> Fairmaire 1885	83	67		67	58	25	50	
	Staphylinidae	Staphylinidae 1		8		8			3	
		Staphylinidae 2		8		8			3	
		Staphylinidae 5		17	8	25			8	
		Staphylinidae 7			8	8			3	
		Tenebrionidae	<i>Neopraocis reflexicollis</i> Solier 1851			8	8			3

(continued on next page)

Table A2 (continued)

Response type	Family	Species names and authors	Regional gradient			Silvicultural management			Total
			RI	SJ	LC	OGF	AR	DR	
R-AR	Curculionidae	Curculionidae 4	25	25		17	33		17
	Ptiliidae	Ptiliidae 1	8	33		8	25	8	14
	Scaphidiidae	Scaphidiidae 2	50	33	58	17	58	67	47
	Not identified	Morphospecies 2	17	8	17	8	25	8	14
R-DR	Curculionidae	Curculionidae 1	58			8	17	33	19
	Staphylinidae	Staphylinidae 8	50	42	92	33	75	75	61
	Carabidae	<i>Metius malachiticus</i> Dejean 1828		33	8	8		33	14
S-AR	Curculionidae	Curculionidae 6	33			17		17	11
		<i>Dasydema hirtella</i> Blanchard 1851	8		25	17		17	11
S-DR	Curculionidae	Curculionidae 5	25			8	17		8
		Curculionidae 7	17			8	8		6
		<i>Antarctobius hyadesii</i> Fairmaire 1885	17	75	42	42	58	33	44
<i>Exploiters</i>									
H	Carabidae	<i>Metius flavipleuris</i> Straneo 1951	17	8			8	17	8
		Trechini 1			42	17	25	14	
	Curculionidae	Curculionidae 3		17		8	8	6	
	Scaphidiidae	Scaphidiidae 1		8	8	8	8	6	
H-AR	Anthribidae	Anthribidae 1		8			8		3
	Carabidae	<i>Ceroglossus suturalis</i> Fabricius 1775		8			8		3
	Curculionidae	<i>Cylydrorhinus caudiculatus</i> Fairmaire 1889			25	17		8	8
	Cryptophagidae	Cryptophagidae 1	8			8			3
	Erotylidae	Erotylidae 1		17			17		6
	Pselaphidae	Pselaphidae 1		8			8		3
	Staphylinidae	Staphylinidae 3		8			8		3
H-DR	Carabidae	<i>Metius blandus</i> Dejean 1828	33	8	17		17	42	19
	Curculionidae	Curculionidae 2	8					8	3
	Elateridae	Elateridae 1		8				8	3
	Mordellidae	Mordellidae 1		8				8	3
	Scolytidae	Scolytidae 1	8					8	3
	Staphylinidae	Staphylinidae 6	17					17	6
	Not identified	Morphospecies 1			8			8	3
	Carabidae	<i>Migadops latus</i> Guerin-Meneville 1841	100	75	8	67	67	50	61
	Curculionidae	<i>Falklandius antarcticus</i> Stierlin 1903	67		17	25	17	42	28
	NS								

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