For. Sci. 63(2):173–183
http://dx.doi.org/10.5849/forsci.15-156
Copyright © 2016 Society of American Foresters

forest ecology

Characterization of *Nothofagus pumilio* (Lenga) Understory in Managed and Unmanaged Forests of Central Patagonia, Argentina

Patricia V. Silva, Claudia P. Quinteros, Alina G. Greslebin, José O. Bava, and Guillermo E. Defossé

In managed forests, biodiversity conservation is crucial for the sustainable use of ecosystem resources. In the Patagonian-Andes forests of Argentina, lenga (*Nothofagus pumilio*) is the most important native tree because of its ecological functions and economic importance as a timber provider. In this study, we determined how the shelterwood-cut system impacts understory vegetation attributes in three sites representing typical lenga forests of central Andean-Patagonia. In each site, two 250-m^2 treatment plots (managed and unmanaged) were established, and canopy cover, soil temperature, and moisture were determined. Within plots in 10 randomly placed 0.25-m^2 microplots, we determined plant cover, from which we calculated diversity attributes. Canopy cover and soil moisture were higher in unmanaged treatments, whereas the reverse was true for soil temperature. The Shannon-Wiener index showed similar values (~1), whereas species richness was slightly higher in unmanaged (4.8 ± 0.5) than in managed treatments (3.8 ± 0.3). Generally, native plants dominated the understory (~40%), whereas exotic species were rare (~1%). Shrub cover was higher in managed (24.1 ± 4.2) than in unmanaged (9.5 ± 1.7) treatments, whereas herbaceous species dominated unmanaged forests. These results confirm that the shelterwood-cut system may be used for diversity conservation in Patagonian lenga forests.

Keywords: forest harvesting, diversity, lenga, shelterwood-cut system, understory vegetation

The continued increases in the human population and per capita consumption have led to a nonsustainable use of the Earth's biological diversity, whose effective conservation is essential for human survival and ecosystem maintenance processes. However, despite some conservation successes (especially at local scales) and the increasing interest of governments and the public at large to live in a sustainable way, biodiversity continues to decrease at the global level (Rands et al. 2010).

Forests in general are environments rich in species diversity and have a wide range of taxa (Noble and Dirzo 1997), from birds and canopy arthropods to soil microorganisms. Long-term maintenance of such biological diversity represents an important challenge for forest management (Lindenmayer 1999).

The understory is an essential component of forest ecosystems, because it provides nutrients and protects the soil from erosion; it is the basis of food chains and the habitat for many life forms. Forest understory also regulates many ecosystem functions and contains the largest part of the forest species richness (Kerns and Ohmann 2004, Ellum 2009, Duguid and Ashton 2013). In general, species of the forest understory may present heterogeneous distribution patterns associated with tree canopy structure and composition (Veblen et al. 1978, Damascos and Rapoport 2002) and also with microenvironmental characteristics and site conditions (Huebner and Randolph 1995, Lencinas et al. 2008). Anthropogenic and natural disturbances affect various components of the forest ecosystem and especially the specific composition of the understory (Echeverría

Manuscript received October 26, 2015; accepted August 2, 2016; published online November 24, 2016.

Affiliations: *Patricia V. Silva (vsilva@correociefap.org.ar), Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Secretaréa de Ciencia, Tecnología e Innovación Productiva, Chubut. Claudia P. Quinteros (pquinteros@correociefap.org.ar), CIEFAP, CONICET. Alina G. Greslebin (agreslebin@gmail.com), Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB), CONICET. José O. Bava (jbava@correociefap.org.ar), CIEFAP, UNPSJB. Guillermo E. Defossé (gdefosse@correociefap.org.ar), CIEFAP, CONICET, UNPSJB. The authors P.V. Silva and C.P. Quinteros contributed equally to this work..*

Acknowledgments: *This study was funded by Agencia Nacional de Promoción Científica y Tecnológica, Argentina (ANPCyT-FONCyT 2010–1229). We thank L. Leveau for helping with the statistical analyses, D. Mohr Bell for providing the lenga map, and M.L. Besio for reviewing the English grammar. We also acknowledge the suggestions given by two anonymous reviewers for improving this article.*

This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.394 in.; hectares (ha): 1 ha = 2.471 ac; meters (m): 1 m = 3.28 ft; square meters (m^2): 1 m^2 = 10.76 ft^2; kilometers (km): 1 km = 0.621 mi; square meters per hectare (m^2/ha): 1 m^2/ha = 4.356 ft^2/ac.

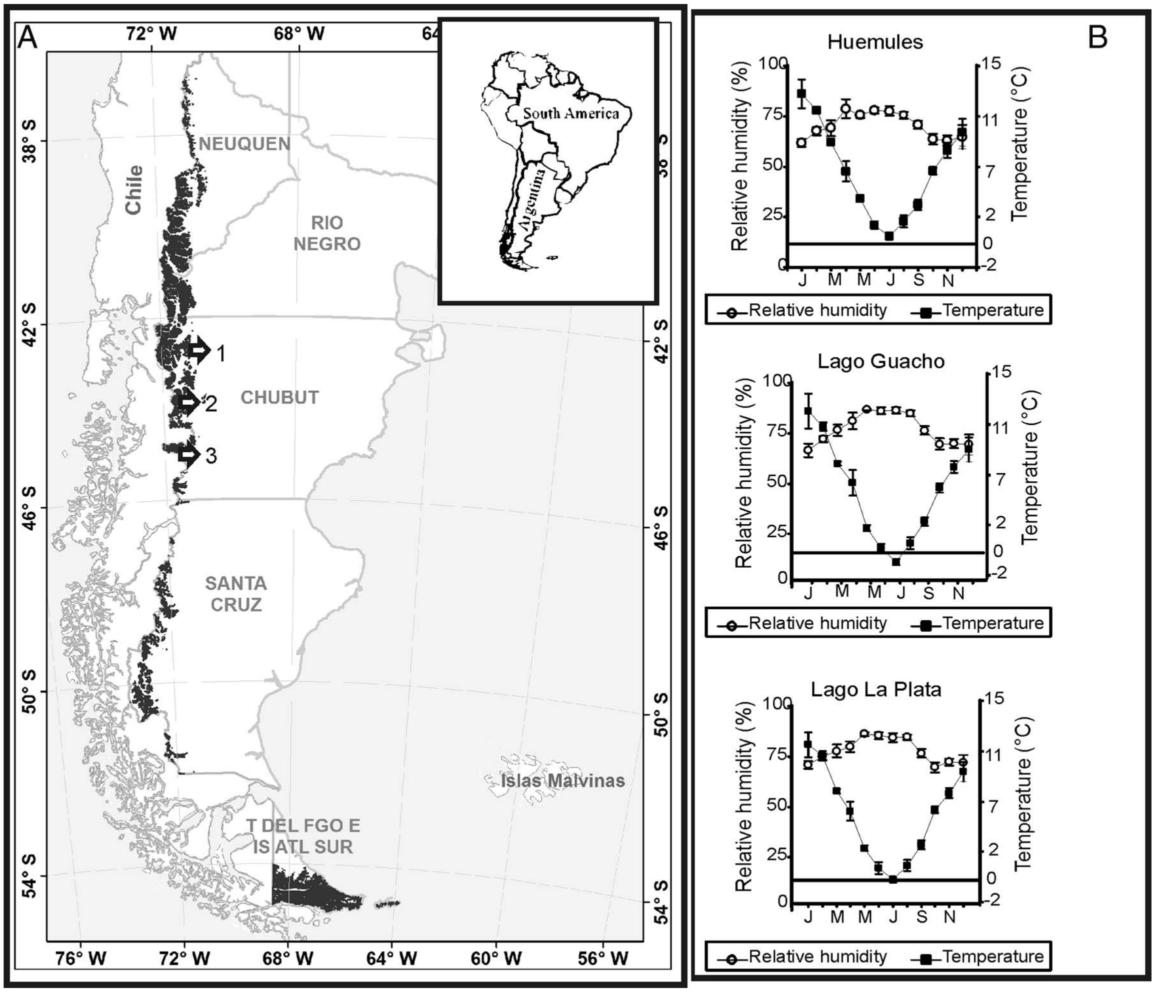

Figure 1. A. Lenga distribution along the Andes in Patagonia, Argentina, showing the three study sites located in the west of Chubut province in Central Patagonia (1, Huemules; 2, Lago Guacho; and 3, Lago La Plata). B. Monthly air temperatures and relative humidity of the three study sites in central Patagonia. Values are means ± 1 SE. Data were taken from 2012 to 2014.

et al. 2007). Forest harvesting causes changes in the microenvironmental conditions below the canopy. Canopy openings increase solar radiation within the forest, alter wind speed, and also redistribute incoming rainfall (Caldentey et al. 2000). These factors may change soil microenvironmental variables such as understory air temperature and moisture. Changes in microclimatic conditions affect the regeneration process and sometimes alter understory species composition (Oliver and Larson 1996, Landsberg and Gower 1997). However, studies carried out in temperate forests of North America and Europe have shown that, in general, appropriate timber harvesting techniques may cause only slight modifications in understory plant composition and diversity (Paillet et al. 2010, Duguid and Ashton 2013, Brockway and Outcalt 2015). These modifications depend on the silvicultural treatment applied and on vegetation successional stage. In temperate ecosystems, understory plant communities are diverse, and their dynamics rapidly respond to fine-scale disturbances and site conditions (Ellum 2009). Site-specific factors such as resource availability and microenvironmental heterogeneity also influence understory plant composition (Ellum 2009, Duguid and Ashton 2013).

Lenga (*Nothofagus pumilio* [Poepp. & Endl.] Krasser) forests are of great ecological and economic importance on both slopes of Patagonian Andes in Argentina and Chile (Ramírez et al. 1997, Bava and Rechene 2004). On the eastern slopes of the Andes in Argentina, these forests are distributed in a narrow strip (30–50 km wide and 2,000-km long) from 35°35′ S in Neuquén province to 55°S in Tierra del Fuego (Figure 1A). Within this latitudinal range, lenga forests develop in very diverse sites and environmental conditions, mainly determined by differences in rainfall patterns, altitude, temperatures, and soil quality conditions (Veblen et al. 1996, González et al. 2006). In Argentina, there are approximately 1.2 million ha of pure lenga forests (Secretaría de Ambiente y Desarrollo Sustentable 2006); 360,000 ha of them form production forests (i.e., those able to produce raw materials for the timber industry) (Dirección General de Bosques y Parques de la Provincia del Chubut 1997, Bava 1999, Collado et al. 2008). These production forests have an average height of 14 m or taller and grow on slopes of less than 60%. These characteristics allow for developing economic timber activities (López Bernal 2010).

In Chubut Province, in central Argentinean Patagonia, there are 109,281 ha of lenga forests identified as production forests (Bava et al. 2006). However, since the mid-1990s, Chubut Province Forest administration requires approved management plans as a condition for harvesting (López Bernal et al. 2003, Carabelli and Ferrando 2004). One of the aims of this enforcement was to promote the replacement of the traditional practice of timber extraction, represented by the selective cutting of the best specimens (high grading), by the shelterwood-cut, or successive cut system. In general, the shelterwood-cut system simulates the natural gap dynamics typical of many forests by gradually extracting selected trees throughout successive partial cuttings. The gaps of different sizes created by these extractions allow germination and establishment of seedlings of the species of interest, and advanced regeneration is later released by moderating the light environment in the gap (Smith et al. 1997). This method has been adapted by Schmidt and Urzúa (1982) for lenga forests. These authors proposed three phases for the application of this system. In the first phase, termed "preparatory intervention," about 50% of trees in a particular stand should be harvested. This intervention increases crown sizes of remaining trees, providing better ecological conditions for growth and favoring seed production. In the second phase, termed "dissemination intervention," trees are cut to allow the formation of gaps, which will provide suitable environmental conditions for germination and development of new lenga seedling cohorts. The third phase "final cut" starts when lenga regeneration is already established. At this moment or afterward, the protective canopy could be removed in one or several successive cuttings until the final cut. As a result, even-aged stands are created, simulating the natural dynamics of the species in the region (Schmidt and Urzúa 1982).

The effects of the shelterwood-cut system on lenga regeneration and its forthcoming stand structure along different growing cycles have been widely studied (Martínez Pastur et al. 2000, Caldentey et al. 2009). Changes in environmental variables between primary and harvested lenga forests have also been described (Caldentey et al. 2000, Promis et al. 2010). Changes in canopy cover, density, and forest structure under the shelterwood-cut system increase understory radiation levels, modify air and surface soil temperature as well as wind speed, and reduce air relative moisture (Caldentey et al. 2000, Promis et al. 2010, Mansilla 2012). The effects of these microenvironmental changes on the lenga understory, as a consequence of different forest interventions, have only been studied in the southern part of lenga distribution in Tierra del Fuego, where lenga grows under an Oceanic Subpolar Climate, with no moisture deficit throughout the year (Lencinas et al. 2011, Gallo et al. 2013). The effects of similar microenvironmental changes on the lenga understory of Chubut forests, which grow under a typical Mediterranean Climate with a marked summer water deficit (Veblen et al. 1996), have not been studied yet. Apart from different climate conditions, the understories of most lenga forests in central Patagonia (either virgin or managed) are subjected to seasonal cattle grazing (i.e., only used as summer pastures). Conversely, in Tierra del Fuego, because of the locations of lenga forests at lower altitudes, their understories are mostly grazed yearlong.

Grazing by large and small herbivores is a common disturbance in many managed and virgin forests around the world (Zamorano-Elgueta et al. 2012, Thompson et al. 2013). These disturbances not only impact understory vegetation by selective browsing or grazing but also through trampling and dung and urine depositions. Like any other forest management practice, grazing disturbance may also induce changes in the species composition of the understory, which generally shifts toward herbaceous, exotic, and/or grazing/browsing-tolerant species. In the lenga forests of central Patagonia, grazing is banned for 35 years after any forest cutting intervention. However, despite this prohibition, it is not unusual to find lenga forest areas in which timber and grazing activities coexist (Vázquez 2002, Raffaele et al. 2011, Quinteros et al. 2012, 2013).

The shelterwood-cut system has proved to satisfactorily mimic natural dynamics in pure lenga forests, mainly by opening gaps in which regeneration establishes (Schmidt and Urzúa 1982, Smith et al. 1997); however, its effects on diversity, soil moisture, temperature, and other attributes of the understory in the lenga forests of central Patagonia are still unknown. Thus, the objectives of this study were to evaluate, in three lenga sites representative of its distribution in central Patagonia, Argentina, the effects of one harvest management technique (the shelterwood-cut system) compared with those of unmanaged (control) sites on the following three attributes: soil temperature and moisture and percentage of lenga canopy cover; composition of the understory vegetation; and most common plant community attributes found. Knowledge of the effects of shelterwood-cut on these attributes will be helpful in developing sustainable forest management schemes that consider local diversity conservation. It will also be a contribution to the worldwide knowledge on how appropriate timber harvesting techniques (in this case the shelterwood-cut system) may be used for conserving diversity in managed forest stands.

Methods

Study Area and Forest Characteristics

The three lenga forest sites, managed and unmanaged, studied in Chubut Province were located in the eastern Andean area of central Patagonia, Argentina, in Huemules (42°46′44.4″ S; 71°27′50.4″ W and 42°46′52.8″ S; 71°28′12.0″ W, 1175 m above sea level [asl]; site 1), Lago Guacho (43°50′00.2″ S; 71°29′3.6″ W and 43°49′49.6″ S; 71°27′57.7″ W, 1265 m asl; site 2), and Lago La Plata (44°49′57.4″ S; 71°43′34.7″ W and 44°50′2.9″ S; 71°43′38.5″ W, 947 m asl; site 3) (Figure 1A). They were chosen because (1) they are representative of the wide range of pure lenga forests distributed in central Patagonia (Figure 1A), (2) all forest sites had been intervened using the same silvicultural technique (shelterwood-cut system) and had an unmanaged (control) area nearby (Berón 1996, Davel and Bava 1999, Antequera 2002), (3) the managed areas did not present any other significant human intervention, and (4) they share similar environmental conditions (mean air temperature and relative humidity, Figure 1B) and also similar uneven-aged forest structures.

In spring 2014 (when most plant species flourish), a 50 × 50-m plot was established in each managed lenga stand in all sites (under the shelterwood-cut system), and a similar one was set in a nearby area (<1 km away) with no forest management and with little or no anthropogenic impact. Before intervention, lenga stands in the three sites showed the following structural data: 59.2, 75.2, and 47.8 $m^2 \cdot ha^{-1}$ of basal area and densities of 376, 477, and 482 stems $\cdot$ ha^{-1} in Huemules, Lago Guacho, and Lago La Plata, respectively (Berón 1996, Davel and Bava 1999, Antequera 2002). On these three sites, the shelterwood-cut intervention was performed about 16 to 18 years before treatment establishment. At the time of establishment, treatment and control plots presented the structural and stand characteristics given in Table 1. Because cattle grazing was excluded since intervention, we rechecked that by surveying the presence of cattle dung depositions on treatment and control plots in each site (von Müller 2013).

Study of Microenvironmental Variables

In each plot, 10 points were randomly selected, and soil temperature and moisture were recorded. Soil temperature below the litter mantle (mineral soil, at 10 cm soil depth) was taken with a digital

Table 1. Characterization of lenga managed and unmanaged plots for the three study sites in central Patagonia.

Site	Treatment	Time from last intervention (yr)	Basal area ($m^2 \cdot ha^{-1}$)	Stem density ($n \cdot ha^{-1}$)	Lenga seedlings ($n \cdot m^{-2}$)	Cattle dung depositions (%)
1: Huemules	Managed	16	20.8	104	4.2 ± 1.2	0
	Unmanaged		49.5	304	3.2 ± 0.9	0
2: Lago Guacho	Managed	18	35.1	168	13.9 ± 4.3	0
	Unmanaged		74.6	560	16.3 ± 6.2	0
3: Lago La Plata	Managed	16	20.4	68	3 ± 0.5	0
	Unmanaged		42.5	324	6.9 ± 1.9	0

For lenga seedling numbers, the values represent means ± 1 SE.

thermometer (265Astem133; Luft Germany). Cylindrical (5 cm in diameter and 10 cm in depth) soil core samples ($n = 10$) were also taken to determine soil moisture in the 0 to 10 cm soil depth by the gravimetric method (International Organization for Standardization 1993). In each of the 10 points, a photograph of the tree canopy cover was taken (18-mm f/3.5–5.66G lens, Nikon D5100), from which a percentage of lenga canopy cover was visually estimated.

Vegetation Survey

Within each plot, 10 points were randomly selected, at each of which a 50 × 50-cm square microplot was placed for surveying lower strata vegetation up to 1-m height, since taller vegetation strata are rare in these forests (Bava and Rechene 1998, Bertolin et al. 2015). The survey included lenga seedlings shorter than 1 m, whereas advanced lenga regeneration (seedlings and saplings taller than 1 m) was not considered. In each microplot, the presence of all vascular plant species was recorded, and their cover was visually estimated. The size of the microplots was considered satisfactory for total plant species determination, after construction of the species-accumulation curves for each treatment in all three sites, to capture as much species diversity as possible with the lowest sampling effort. Unknown individuals were collected for later identification in the laboratory. Species were determined according to Correa (1969–1988) and Zuloaga et al. (2008). In addition, each plot was surveyed to identify the presence of any species not recorded in the microplots. The species recorded outside the microplots were considered in the overall species richness.

Data Analyses

To validate the sampling effort to cover the whole range of vascular species present in the plots, species accumulation curves were constructed based on the presence/absence of superior vascular plant species by using richness and Chao2 in the free EstimateS 9.1 software (Colwell 2013). Species richness (S) and the Shannon-Wiener diversity index (H′) were used as measures of diversity because of their simplicity and wide use in ecological (Magurran 2004) and forest studies (Kimmins 1997). Alpha diversity was estimated as the number of the different plant species found in each microplot; beta diversity was analyzed through ordination (Bray-Curtis distance), and gamma diversity was estimated based on the number of the different plant species found in each plot (Moreno 2001). For classification and ordination, all plant cover data were $\log(x + 1)$ transformed. To compare plant communities (beta diversity), the mean plant cover per treatment in each site was used to construct a matrix based on the Bray-Curtis distance. The resulting matrix was used to perform a nonmetric multidimensional scaling (nMDS) analysis. Permutational multivariate analyses of variance (PERMANOVA) (bifactorial) (McCune et al. 2002) were used to test differences in plant communities between treatments and among sites. To analyze how communities vary according to the treatment at the same location, a test of dissimilarities percentage (SIMPER) (Clarke and Warwick 2001) was applied to determine which plant species contributed the most to the differences observed between groups. nMDS ordinations were used to compare plants species composition in managed and unmanaged treatments, and for different sites, we used the vegan package in R statistical software (Oksanen et al. 2010).

Linear mixed-effect models were used to analyze the effects of treatments (managed and unmanaged) on the following microenvironmental variables (soil temperature and moisture and canopy cover) and understory variables (total understory cover, cover by life form and by origin, S, and H′). Treatments (managed and unmanaged) were considered as a fixed effect, and the variable site was considered as a block (random effect). The amount of the model variance that was explained by differences among sites was calculated by dividing the random effect variance by the total variance. The data were analyzed using the lme function (Pinheiro et al. 2013) and lme4 algorithms (Bates et al. 2013) in the R package (R Development Core Team 2013) interfaced by InfoStat statistical software version 2012 (Di Rienzo et al. 2011).

Results

Microenvironmental Variables

Even though the three sites were located far apart one from each other, they showed strong similarities in soil moisture, soil temperatures, and canopy cover percentages. However, these variables significantly differed between managed and unmanaged treatments within sites. Soil temperature was significantly higher in managed (8.8 ± 0.2° C) than in unmanaged treatments (7.7 ± 0.2° C). Unmanaged plots showed significantly higher values of soil moisture (73.4 ± 3.9%) and canopy cover (85.7 ± 3.8%) than managed plots (60.4 ± 3.9% and 63.9 ± 3.8%, respectively) (Figure 2).

Composition of the Understory Vegetation

The species-accumulation curves (Figure 3) showed that each one reached, or was close to reaching, the asymptote in the two treatments of the three sites analyzed. This indicated that the assembly of understory species was satisfactorily sampled. In addition, as was expected, the cattle dung survey showed that neither treatments nor control plots on any site presented evidence of cattle grazing from the cutting intervention and until treatments were set (Table 1).

Plant Species Composition

A total of 32 species were recorded in the three sites. Of them, 29 (91%) were native and only 3 (9%) were exotic herbs (Table 2). Only one individual (Poaceae 1) could not be identified to the level of genus or species. Lenga seedlings represented the only tree life

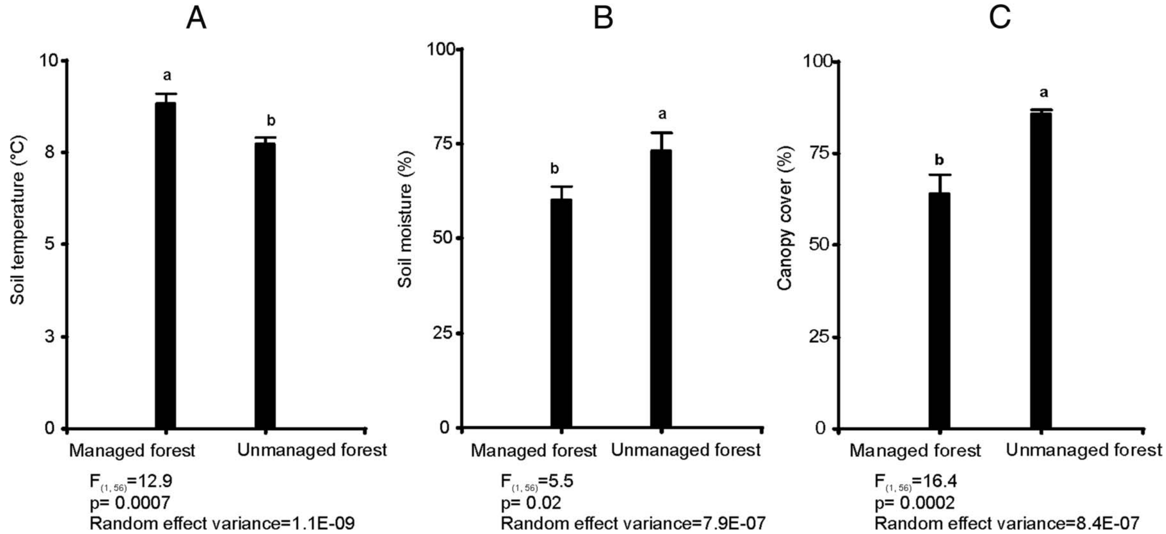

Figure 2. Soil temperature and moisture and canopy cover averages for managed and unmanaged treatments in lenga forests of Patagonia in Argentina. Bars and lines represent means ± 1 SE, respectively.

form found in the understory; 10 species were shrubs and the remaining 21 were perennial herbs and grasses. Even though the sampling was carried out when most species flourished, no annual herbs or grasses were recorded (Table 2). The majority of the species recorded showed cover values of less than 3%, and total understory cover was 39 ± 3.7%.

Related to treatments, 26 species were recorded in managed plots and 28 in the control plots. In managed plots, 7.7% of understory species corresponded to exotic species, and this percentage diminished to 3.6% in control plots. Some species (*Phacelia secunda*, *Bromus coloratus, Calceolaria biflora, Valeriana laxiflora,* and *Viola maculata*) were only found in control plots, whereas others (*Rumex acetosella, Senecio neaei,* and *Lathyrus magellanicus*) were only found in managed plots (Table 2).

The species that showed average cover values higher than 3% were *Osmorhiza chilensis*, *Maytenus disticha*, *Chiliotrichum diffusum, N. pumilio,* and *Maytenus chubutensis.* They also showed differences between treatments. *O. chilensis* showed higher cover percentage in unmanaged (7.8 ± 1.7%) than in managed treatments (4.8 ± 1.1%). *M. disticha* showed higher cover in managed (7.2 ± 3%) than in unmanaged treatment (0.2 ± 0.1%), although it appeared in only one site (Lago La Plata). *C. diffusum* presented an average cover of 6.3 ± 2.5% in managed compared with 1.2 ± 0.6% in unmanaged treatments. *N. pumilio* and *M. chubutensis* showed no variation between treatments (Table 2).

Changes in Plant Composition

Understory plant communities were significantly different between treatments ($F_{1,58} = 3.01$, $R^2 = 0.04$, $P = 0.004$). The nMDS ordination identified two groups (managed and unmanaged) with a stress value of 0.177 (Figure 4A). In addition, plant communities were significantly different among sites ($F_{2,58} = 8.55$, $R^2 = 0.23$, $P = 0.004$). The nMDS ordination identified three groups (sites 1, 2, and 3) with a stress value of 0.178 (Figure 4B). Although some differences were recorded among plant communities at the treatment or site levels, the R^2 value indicated that dissimilarities were higher at site levels than at treatment levels. The results of SIMPER analysis that compared the two groups (treatments) showed that the only species that contributed to the dissimilarity between forest treatments with a value higher than 1 was *O. chilensis*. This species showed significantly higher abundance in unmanaged than in managed treatments. The results of SIMPER analysis that compared the two sites (1 to 3 and 2 to 3) indicated that the species which contributed to dissimilarities were *O. chilensis* and *C. diffusum.* These two species were more abundant in site 3 than in the other sites. Between sites 1 and 2, the species contributing the most to dissimilarities were *M. chubutensis* and *O. chilensis*, which presented higher cover in site 1.

Variations in the Attributes of Understory Plant Community

Total plant cover showed no variations between managed and unmanaged treatments (Table 3). Related to H′, similar values were found between managed and unmanaged forests (Table 3). However, the S values were significantly higher in unmanaged treatments than in managed ones (Table 3). When species origin was evaluated, native species showed no differences between treatments. Cover of exotic species was low (<2%) and did not show significant differences between treatments (Table 3).

Regarding plant life form, herbs showed significantly higher values in unmanaged than in managed treatments. Shrub cover was higher in managed than in unmanaged treatments. Tree cover (represented only by lenga seedlings) presented similar values between managed and unmanaged forests (Table 3).

Discussion

Microenvironmental Variables

Lenga forests in Argentinean Patagonia are distributed in a long and narrow strip (30–50 km wide and 2,000 km long) along the eastern side of the Andean cordillera, ranging from near 2,000 m of altitude in the northern province of Neuquén up to sea level in Tierra del Fuego (Veblen et al. 1996, González et al. 2006). In central Patagonia, the study sites, located at altitudes from about 950 to 1,250 m asl and 200 km apart one from each other, showed strong similarities in the environmental variables (air temperatures and relative humidity). Microenvironmental variables, however, significantly differed between treatments. Despite the time that had

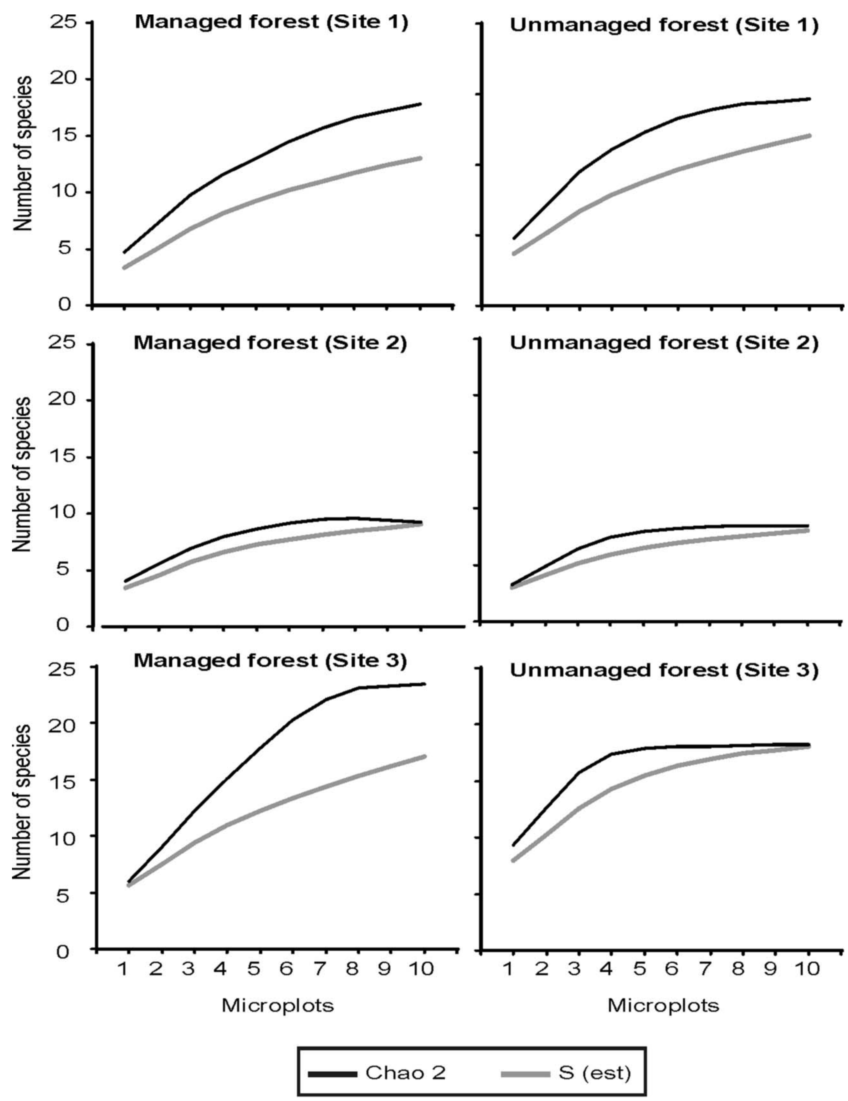

Figure 3. Species accumulation curves of estimated species (S) and of the richness estimator (Chao2) in the understory of managed and unmanaged lenga forests in Andean Patagonia, Argentina.

passed since the last interventions (16–18 years), the typical microenvironmental conditions found in unmanaged forest were altered in the managed forest when the shelterwood-cut treatment was applied. These results coincided with studies carried out in other lenga forests, which showed that this cut system increases incoming light and soil temperature compared with those in unmanaged forest (Veblen et al. 1978, Heinemann et al. 2000, Promis et al. 2010). The magnitude of these micro environmental variations appears to be related to the extent of the disturbance, especially to the size of the opened gap, and the time that has passed since the gap was created (Lencinas et al. 2011, Duguid and Ashton 2013, Gallo et al. 2013). In this study, managed forests showed lower canopy cover and topsoil moisture, and higher soil temperatures and light availability than unmanaged forests. Even though the extent of the cutting intervention was different in each of the three sites (as observed in the number of remaining trees after these interventions (Table 1), it seems that its impact on total understory composition was minimal. This may be due to the fact that the different plant species and life forms found in the understory of managed lenga forests are tolerant to small variations in physical and micro-environmental changes produced by low-impact forest interventions (Reader and Bricker 1992, Ellum 2009, Duguid and Ashton 2013), produced in this case by the shelterwood-cut system. The microenvironmental changes, however, may have particular effects, by either increasing or decreasing cover of certain particular species, when virgin or unmanaged lenga forests are converted to managed forests. These small changes in understory species composition and cover induced by modifications in microenvironmental conditions produced by the shelterwood-cut system may have also been favored by the lack of cattle grazing since the cutting intervention and until the sampling was performed. This assertion is based on the fact that cattle grazing in lenga forests may produce abrupt changes in the structure of its understory vegetation (Vázquez 2002, Collado et al. 2008, Raffaele et al. 2011, Quinteros et al. 2012, 2013, Zamorano-Elgueta et al. 2012).

Composition of the Understory Vegetation

The species composition found was somewhat similar to that reported in other studies describing understory vegetation of unmanaged lenga forests in both its northern (Río Negro [Damascos and Rapoport 2002]) and southern (Tierra del Fuego [Martínez Pastur et al. 2002, Bastías Fuentes 2005]) distribution range. Most

Table 2. Plant species, recorded in the three sites, sorted according to botanical families.

Family	Species	LF	Site 1		Site 2		Site 3	
			M	UM	M	UM	M	UM
Apiaceae	*Osmorhiza chilensis* Hook. & Arn.	PH	4 ± 2.5	9.9 ± 4.4	5 ± 1.5	1.5 ± 0.7	5.5 ± 1.5	12 ± 1.3
	Adenocaulon chilense Less.	PH	2.9 ± 2	2 ± 1	1 ± 0.7			2.5 ± 1
	Chiliotrichum diffusum (G. Forst.) Kuntze	S			1 ± 0.7		18 ± 6.3	3.7 ± 1.4
Asteraceae	*Senecio neaei* DC.	S	0.11 ± 0.1					–
	Leucheria thermarum Phil. (Phil.)	PH	0.2 ± 0.1	3.7 ± 2.3				–
	Macrachaenium gracile Hook.f.	PH	0.1 ± 0.1					–
Berberidaceae	*Berberis microphylla* G. Forst.	S		X			0.5 ± 0.5	–
	Berberis serratodentata Lechl.	S	0.5 ± 0.3		4.5 ± 1.9	1.6 ± 1.1	1.7 ± 1.5	X
Caryophyllaceae	*Cerastium arvense* L.*	PH					0.2 ± 0.2	0.1 ± 0.1
Celastraceae	*Maytenus chubutensis* (Speg.) Lourteig, O´Donell & Sleumer	S	10.2 ± 5.2	1.8 ± 1.8	1.5 ± 1.1	7.5 ± 1.4	0.2 ± 0.2	–
	Maytenus disticha (Hook. F.) Urb.	S					21.6 ± 7.3	0.7 ± 0.4
Ericaceae	*Gaultheria mucronata* (L. f.) Hook. & Arn.	S			5.5 ± 1.4			0.4 ± 0.4
Fabaceae	*Lathyrus magellanicus* Lam.	PH					0.1 ± 0.1	–
Hydrophyllaceae	*Phacelia secunda* J.F. Gmel.	PH		1.5 ± 1.5				–
Nothofagaceae	*Nothofagus pumilio* (Poepp. & Endl.) Krasser	T		X	9.5 ± 5.2	5.3 ± 2.6	3.2 ± 2.9	3.8 ± 2.9
Orchidaceae	*Gavilea lutea* (Pers.) M.N. Correa	PH					0.5 ± 0.5	1 ± 1
	Codonorchis lessonii (Brongn.) Lindl.	PH	0.2 ± 0.2	X	0.5 ± 0.5	1.4 ± 0.7	X	0.5 ± 0.2
Poaceae	*Poa pratensis* L.*	PH	2.5 ± 2.5	5 ± 5				–
	Poa alopecurus (Gaudich. ex Mirb.) Kunth	PH					3.6 ± 1.6	0.1 ± 0.1
	Poaceae 1	PH				X		–
	Elymus angulatus J. Presl	PH		1.5 ± 1.5			4.5 ± 2.1	–
	Bromus coloratus Steud.	PH						15.8 ± 7.3
	Festuca magellanica Lam.	PH					0.1 ± 0.1	0.4 ± 0.3
Polygonaceae	*Rumex acetosella* L.*	PH	X					–
Rosaceae	*Acaena ovalifolia* Ruiz & Pav.	PH	3.9 ± 3.5	10.7 ± 4.7			0.3 ± 0.3	2 ± 1.5
Rubiaceae	*Galium hypocarpium* (L.) Endl. ex Griseb.	PH					0.2 ± 0.1	X
Santalaceae	*Myoschilos oblongum* Ruiz & Pav.	S				0.5 ± 0.5	2 ± 1.47	1.4 ± 1
Saxifragaceae	*Ribes cucullatum* Hook. & Arn.	S	0.5 ± 0.5	7.3 ± 4.1	0.5 ± 0.5			–
	Ribes magellanicum Poir.	S	4 ± 4	4 ± 2.8				–
Scrophulariaceae	*Calceolaria biflora* Lam.	PH		1.5 ± 1.5				–
Valerianaceae	*Valeriana laxiflora* DC.	PH		1 ± 1				0.5 ± 0.3
Violaceae	*Viola maculata* Cav.	PH				1.5 ± 1.1		0.8 ± 0.5
S			13	15	9	8	17	18
H′			1.87	2.21	1.8	1.61	1.84	1.97

Life form (LF) is indicated (PH, perennial herbs and grasses; SH, shrubs; T, tree seedlings). From each species, average cover values (% ± 1 SE) for each site (1, 2, and 3) and forest treatment (M, managed; UM, unmanaged) are shown. Plant cover with an average lower than 0.1% is indicated with an X. Species richness (S) and Shannon-Wiener index (H′) are also shown.
* Exotic species.

of the species recorded were also found in floristic surveys carried out in various understories of lenga forests of Chubut, previously subjected to different forest harvesting techniques (Puig and Troncoso 1993, Bertolin et al. 2015). These species could be classified as generalists and seemed to be well adapted to living below lenga canopies and in adjacent canopy gaps opened by tree fall disturbances (Damascos and Rapoport 2002).

It is interesting to note that although more than 100 exotic species have been identified in the whole Patagonian Andean forests (Dimitri 1972), only a few were registered in pure lenga forests, and most of them were associated with grazing disturbance (Domínguez et al. 2006, Quinteros et al. 2012). In all study sites, although no actual grazing was detected, the exotic species *Poa pratensis, Rumex acetosella,* and *Cerastium arvense* were recorded. These European species, however, have been cited as invaders elsewhere (Pysek et al. 2004).

When species composition was compared between managed and unmanaged forests, a low similitude was found. This low similitude value could be explained because understory plant communities in temperate forests are diverse and dynamic. Shorter plant species turnover times and greater environmental sensitivity and specificity mean that the understory plant community responds faster and at finer scales to disturbance and site variation (Ellum 2009). The species that contributed the most to this dissimilarity between managed and unmanaged forest were the most abundant (*O. chilensis*, *M. disticha*, and *C. diffusum*). In agreement with other studies carried out in typical lenga forests of central Patagonia, the herb *O. chilensis* was the most abundant in unmanaged forest (Puig and Troncoso 1993, Bertolin et al. 2015) and the shrubs *M. disticha* and *C. diffusum* were the most abundant in managed forests, which showed a more open canopy (Arroyo et al. 1996).

Variations in the Attributes of Understory Plant Community

The total cover of the understory showed an average value of 40%. This value is within the range reported by Bastías Fuentes (2005) for other *N. pumilio* forests in Chile. It is interesting to note that herbs were the dominant species in all sites, which coincides with what was reported for lenga forests in Tierra del Fuego by Moore (1983) and Lencinas et al. (2008). Besides different lenga forests, the S and H′ documented in this study are similar to those found for other temperate forest ecosystems in Canada (Reader and Bricker 1992) and the United States (Ellum 2009, Duguid and Ashton 2013). In all of these cases, after 15 years of forest intervention, managed forests showed similar S in the understory as the

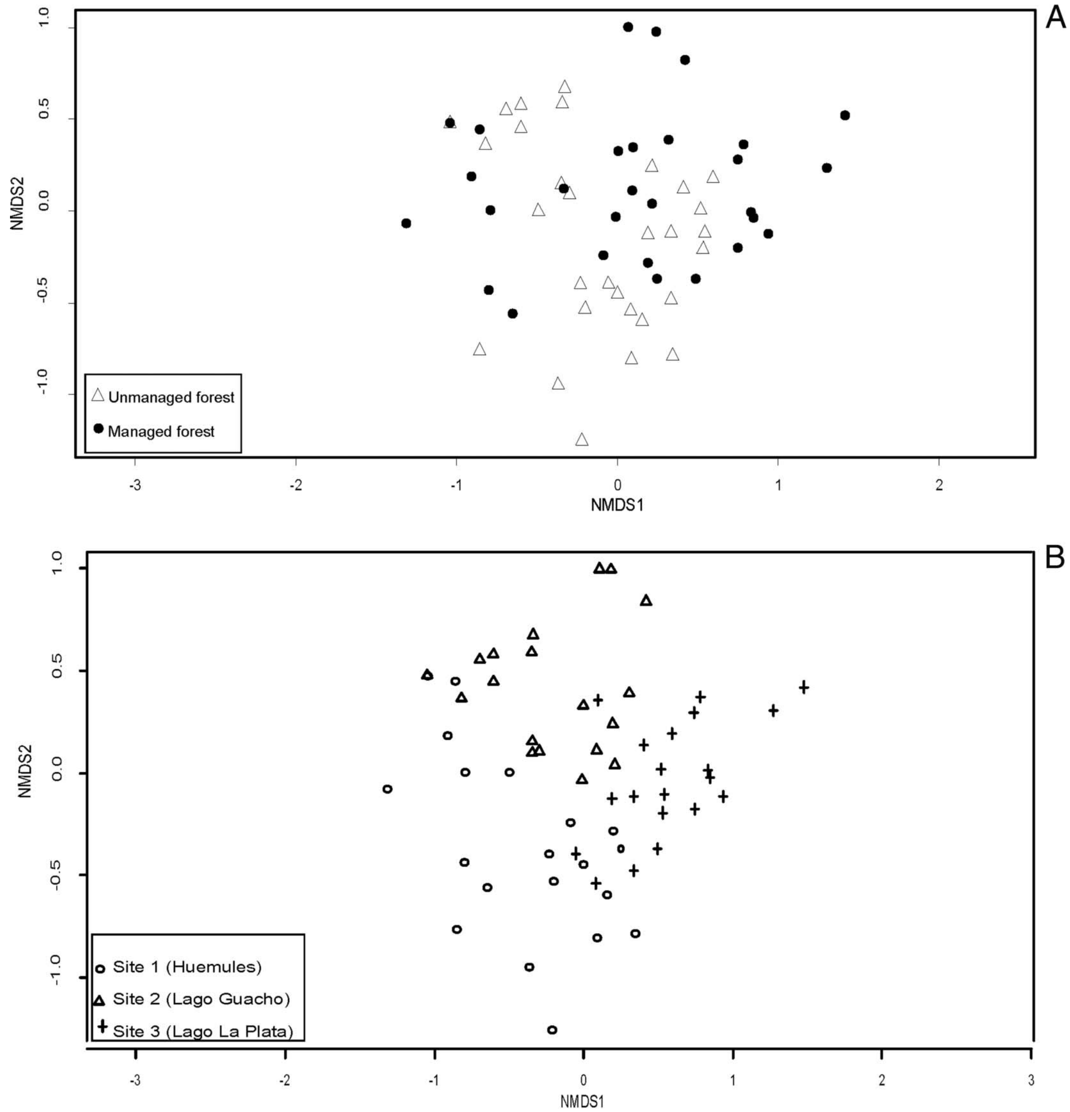

Figure 4. Nonmetric multidimensional scaling ordinations according to species dissimilitude between forest type (managed and unmanaged) (A) and sites (B) in lenga forests of Patagonia in Argentina.

Table 3. Mixed ANOVA model for understory cover, on the lenga forests studied, considering treatment (managed and unmanaged) as a fixed effect and site as a random effect.

		Diversity		Origin		Life form		
Factor: treatment	Total cover	Species richness	H Index	Native	Exotic	Herbs	Shrubs	Seedling trees
Managed forest	40.1 ± 5.3	3.8 ± 0.3	0.9 ± 0.1	39.2 ± 5.5	0.9 ± 0.8	11.7 ± 2	24.1 ± 4.2	4.2 ± 2.1
Unmanaged forest	38.2 ± 5.1	4.8 ± 0.5	1 ± 0.1	36.5 ± 4.9	1.7 ± 1.7	25.9 ± 4.7	9.5 ± 1.7	3.0 ± 1.3
$F_{(1, 56)}$, P	0.07, 0.78	4.40, 0.04	1.03, 0.3	0.16, 0.69	0.19, 0.66	3,12, 0.003	11.4, 0.001	0.25, 0.61
Random effect variance (site)	188.6	3.1	0.6	189	2	115.8	38.3	9.7

Means ± 1 SE are shown.

adjacent nondisturbed forest. In our study, slightly higher S values were recorded in unmanaged than in managed forests, whereas H′ was similar for the two treatments. Similar H′ values indicate a relatively even distribution of species cover between treatments, whereas the higher richness in unmanaged forests could be due to the presence of some species that were exclusive to this treatment.

The reduced cover (<2%) and low species richness (8%) of exotic species found in our study could in part be associated with the time that had passed since the last cutting (16–18 years) and also with the lack of other disturbances such as cattle grazing. In similar lenga forests but having evidence of grazing disturbance, Quinteros et al. (2012) registered higher richness (~19%) and cover of exotic species in the understory than in this study. Similar results with regard to increases in exotic species were recorded in cattle-grazed lenga forest of the nearby Aysén region in the western Andean slopes of Chile (Sánchez-Jardón et al. 2010). In the southern area of lenga distribution, an important increase in frequency and cover of exotic species was registered in forests during the first 6 years after the shelterwood-cut intervention (Fernández et al. 1998). After that time, when lenga seedlings started to establish and branches of remaining lenga trees began to close the canopy, these exotic species started to disappear from the forest understory, probably because after a shelterwood-cut intervention, lenga tree branches grow about 20 cm year^{-1} (López Bernal et al. 2012). Paillet et al. (2010) suggested that 15 to 20 years after the shelterwood-cut intervention, canopy openings and also the plant community that developed below the canopy understory would return to the previous conditions of unmanaged forest. Our results suggest that for long-lived lenga forests growing in Patagonia, more time than suggested by Paillet et al. (2010) would be necessary for the forest to return to the previous unmanaged conditions after the shelterwood-cut intervention.

Herbs showed the highest cover in unmanaged forests, the most abundant in the lenga understory being *O. chilensis*; this may have been due to the fact that it is a shade-tolerant species, and its cover drastically diminishes after a forest intervention, when incoming light increases in the understory (Sánchez-Jardón et al. 2010). In managed forests, in contrast, shrubs showed their highest cover. Their abundance in these forests may be due to the higher levels of light that reach the understory than in unmanaged forests, which showed a more closed canopy and lower light levels (Arroyo et al. 1996).

Finally, lenga seedling regeneration occurred in all unmanaged forests. This species, however, was also present in managed forests, although the saplings were not tallied in our study because they surpassed the established 1-m recording height.

Conclusions

To put into practice the sustainable use of forest resources, a tight link between research and management is needed. Lenga is the most harvested forest species in Chubut province in Patagonia, Argentina. The Argentine legislation, Federal Law 26,331 on Native Forests Protection, promotes the sustainable use of forest resources. The forest management of lenga forests based on the shelterwood-cut system appears to be an appropriate method to attain sustainability, since it does not significantly changes in understory vegetation structure and species diversity compared with pristine vegetation. However, careful consideration should be given to some unexpected increase in shrub cover in managed forests. Further studies, however, should focus on the effects of forest management combined with other disturbances (i.e., grazing) on understory vegetation structure and functioning. These results allow for recommending the shelterwood-cut system as a silvicultural tool for sustainable harvests in lenga forests of central Patagonia for diversity conservation. These recommendations could be used as a reference for other forests with structural and climatic characteristics similar to those presented in this study.

Literature Cited

ANTEQUERA, S.H. 2002. *Efecto del tipo de corta sobre el rendimiento en madera rolliza y la regeneración natural de un bosque de lenga (Nothofagus pumilio) de calidad media en la provincia del Chubut, Argentina* [Effect of cutting type on yield in roundwood and natural regeneration of a medium lenga forest (*Nothofagus pumilio*) in the province of Chubut, Argentina]. MSc thesis, Univ. de Götingen, Götingen, Alemania. 102 p.

ARROYO, M.T.K., M. RIVEROS, A. PEÑALOZA, L. CAVIERES, AND A.M. FAGGI. 1996. Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of southern South America. P. 134–172 in *High-latitude rainforests and associated ecosystems of the West Coast of the Americas*, Lawford R.G., P.B. Alaback, and E. Fuentes (eds.). Springer, New York.

BASTÍAS FUENTES, M.A. 2005. *Composición de especies y cobertura del sotobosque en bosques vírgenes de lenga (Nothofagus pumilio (Poepp. Et Endl.) Krasser) en Monte Alto, XII Región* [Species composition and understory cover in virgin forests of lenga (*Nothofagus pumilio* (Poepp. Et Endl.) Krasser) in Monte Alto, XII Region]. Ingeniero Forestal, Univ. de Chile, Santiago, Santiago, Chile. 83 p.

BATES, D., M. MAECHLER, AND B. BOLKER. 2013. *lme4: Linear mixed-effects models using "Eigen" and S4*. R package version 0.999999-2. Available online at CRAN.R-project.org/package=lme4; last accessed Jan 27, 2016.

BAVA, J.O. 1999. *Aportes ecológicos y silviculturales a la transformación de bosques vírgenes de lenga en bosques manejados en el sector argentino de Tierra del Fuego* [Ecological and silvicultural contributions to the transformation of virgin forests of lenga in managed forests in the Argentinean sector of Tierra del Fuego]. Tech. Publ. No. 29, CIEFAP, Esquel, Argentina. 138 p.

BAVA, J.O., J.D. LENCINAS, AND A. HAAG. 2006. Determinación de la materia prima disponible para proyectos de inversión forestal en la provincia del Chubut [Determination of raw material available for forestry investment projects in the province of Chubut]. P. 117 in *Informe final.* Consejo Federal de Inversiones, San Martín, Argentina.

BAVA, J.O., AND D.C. RECHENE. 1998. Alternativas para el manejo de lenga (*Nothofagus pumilio* (Poepp. et Endl.) *Krasser*) en base a la dinámica de su regeneración, en la provincia de Tierra del Fuego, Argentina [Alternatives for the handling of lenga (*Nothofagus pumilio* (Poepp. Et Endl.) *Krasser*) based on the dynamics of its regeneration, in the province of Tierra del Fuego, Argentina]. Presented at the *First Congreso Latinoamericano IUFRO, 1998 November 22–28, Valdivia, Chile*. 15 p.

BAVA, J.O., AND D.C. RECHENE. 2004. Dinámica de la regeneración de lenga (*Nothofagus pumilio* (Poepp. et Endl) Krasser) como base para la aplicación de sistemas silvícolas [Dynamic regeneration Lenga (*Nothofagus pumilio* (Poepp. Et Endl) Krasser) as a basis for the application of systems silvícolas]. P. 1–22 in *Ecología y Manejo de los Bosques de Argentina*, Arturi M.F., J.L. Frangi, and J.F. Goya (eds.). Editorial de la Univ. Nacional de La Plata, La Plata, Argentina.

BERÓN, F. 1996. *Plan de Manejo Forestal Lago Guacho Sur. Esquel* [Forest Stewardship Plan Lago Guacho Sur Esquel]. Administration of National Parks, Beunos Aires, Argentina. 26 p.

BERTOLIN, M.L., M.F. URRETAVIZCAYA, AND G. DEFOSSÉ. 2015. Fire emissions and carbon uptake in severely burned lenga beech (*Nothofagus pumilio*) forests of Patagonia, Argentina. *Fire Ecol.* 11:32–54.

BROCKWAY, D.G., AND K.W. OUTCALT. 2015. Influence of selection systems and shelterwood methods on understory plant communities of longleaf pine forests in flatwoods and uplands. *For. Ecol. Manage.* 357:138–150.

CALDENTEY, J., H. MAYER, M. IBARRA, AND A. PROMIS. 2009. The effects of a regeneration felling on photosynthetic photon flux density and regeneration growth in a *Nothofagus pumilio* forest. *Eur. J. For. Res.* 128:75–84.

CALDENTEY, J., A.A. PROMIS BAEZA, H. SCHMIDT, AND M. IBARRA. 2000. Variación microclimática causada por una corta de protección en un bosque de lenga (*Nothofagus pumilio*) [Microclimatic variation caused by a protection cut in a lenga forest (*Nothofagus pumilio*)]. *Cienc. For.* 14:51–59.

CARABELLI, F.A., AND J.J. FERRANDO. 2004. Análisis de la eficacia de los planes de manejo de bosque nativo en la provincia de Chubut, Argentina [Analysis of the effectiveness of native forest management plans in Chubut Province, Patagonia, Argentina]. *Bosque* 25:3–13.

CLARKE, K., AND R. WARWICK. 2001. *Change in marine communities: An* *approach to statistical analysis and interpretation*, 2nd ed. PRIMER-E Ltd., Plymouth, UK. 176 p.

Colwell, R.K. 2013. *EstimateS: Statistical estimation of species richness and shared species from samples. User's guide and application*. Available online from http://viceroy.eeb.uconn.edu/EstimateS/EstimateSPages/EstSUsersGuide/EstimateSUsersGuide.htm; last accessed Nov. 18, 2016.

Collado, L., S. Farina, F. Jaras, and H. Vargas. 2008. Monitoreo del estado de intervención y de la regeneración de *Nothofagus pumilio* en un plan de manejo forestal en el ecotono estepa-bosque de Tierra del Fuego, Argentina [Monitoring of harvesting and regeneration state of a *Nothofagus pumilio* forestry management plan located near the forest-steppe border in Tierra del Fuego, Argentina]. *Bosque* 29:85–90.

Correa, M.N. 1969–1988. Flora patagónica (scientific collection). Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina. 193p.

Damascos, M.A., and E.H. Rapoport. 2002. Diferencias en la flora herbácea y arbustiva entre claros y áreas bajo dosel en un bosque de *Nothofagus pumilio* en Argentina [Differences in the herb and shrub flora growing under canopy gaps and under closed canopies in a *Nothofagus pumilio* forest of Argentina]. *Rev. Chil. Hist. Nat.* 75:465–472.

Davel, M., and J.O. Bava. 1999. *Estudio comparativo de distintos tratamientos silvícolas en bosques de lenga (Nothofagus pumilio (Poep. et Endl.) Krasser)* [Comparative study of different silvicultural treatments in lenga forests (*Nothofagus pumilio* (Poep. Et Endl.) Krasser)]. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina. 36 p.

Di Rienzo, J.A., R.E. Macchiavelli, and F. Casanoves. 2011. *Modelos lineales mixtos: Aplicaciones en InfoStat* [Mixed linear models: Applications in InfoStat]. Grupo Infostat, Córdoba, Argentina. 193 p.

Dimitri, M.J. 1972. *La región de los bosques Andino-Patagónicos. Sinopsis general* [The region of the Andean-Patagonian forests. General synopsis]. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina. 381 p.

Dirección General de Bosques y Parques de la Provincia del Chubut. 1997. *Inventario forestal del bosque nativo de la provincia del Chubut* [*Native forest inventory of Chubut province*]. Subsecretaría de Desarrollo Económico, Ministerio de la Producción y Turismo, Gobierno del Chubut, Argentina. 11 p.

Domínguez, E., A. Elvebakk, C. Marticorena, and A. Pauchard. 2006. Plantas introducidas en el Parque Nacional Torres del Paine, Chile [Alien plants in Torres del Paine National Park, Chile]. *Gayana Bot.* 63:131–141.

Duguid, M.C.D., and M.S. Ashton. 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *For. Ecol. Manage.* 303:81–90.

Echeverría, C., A.C. Newton, A. Lara, J.M.R. Benayas, and D.A. Coomes. 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecol. Biogeogr.* 16:426–439.

Ellum, D.S. 2009. Floristic diversity in managed forests: Demography and physiology of understory plants following disturbance in southern New England forests. *J. Sustain. For.* 28:132–151.

Fernández, M.C., G. Staffieri, G. Martinez Pastur, and P.L. Peri. 1998. Cambios en la biodiversidad del sotobosque a lo largo del ciclo del manejo forestal de la lenga [Changes in undergrowth biodiversity throughout the lenga forest management cycle]. Presented at the *First Congreso Latinoamericano IUFRO 1998 November 22-28, Valdivia, Chile*. 10 p.

Gallo, E.A., M.V. Lencinas, and G.J. Martinez-Pastur. 2013. Site quality influence over understory plant diversity in old-growth and harvested *Nothofagus pumilio* forests. *For. Syst.* 22:25–38.

González, M.E., Z.C. Donoso, P. Ovalle, and G. Martínez Pastur. 2006. *Nothofagus pumilio* (Poep. et End) Krasser. Lenga, roble blanco, leñar, roble de Tierra del Fuego. P. 486–500 in *Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología* [The arboreal species of the temperate forests of Chile and Argentina. Autoecology], Donoso, Z.C. (ed.). María Cuneo Ediciones, Santiago, Chile.

Heinemann, K., T. Kitzberger, and T.T. Veblen. 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. *Can. J. For. Res.* 30:25–31.

Huebner, C.D., and C. Randolph. 1995. Environmental factors affecting understory diversity in second-growth deciduous forests. *Am. Midl. Nat.* 134:155–165.

International Organization for Standardization. *Soil quality. Determination of dry matter and water content on a mass basis—Gravimetric method*. ISO 11465:1993(E). International Organization for Standardization, Geneva, Switzerland.

Kerns, B.K., and J.L. Ohmann. 2004. Evaluation and prediction of shrubs cover in coastal Oregon forest (USA). *Ecol. Indicat.* 4:83–98.

Kimmins, J.P 1997. *Forest ecology. A foundation for sustainable management*, 2nd ed. Prentice Hall, Upper Saddle River, NJ. 596 p.

Landsberg, J.J., and S.T. Gower. 1997. *Applications of physiological ecology of forest management*. Academic Press, San Diego, CA. 354 p.

Lencinas, M., G. Martínez Pastur, P. Rivero, and C. Busso. 2008. Conservation value of timber quality versus associated non-timber quality stands for understory diversity in *Nothofagus* forests. *Biodivers. Conserv.* 17:2579–2597.

Lencinas, M.V., G. Martinez Pastur, E.A. Gallo, and J.M. Cellini. 2011. Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests. *For. Ecol. Manage.* 262:1236–1250.

Lindenmayer, D.B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *For. Ecol. Manage.* 115:277–287.

López Bernal, P. 2010. *Balance de las interacciones entre el dosel y la regeneración avanzada en bosques productivos de Nothofagus pumilio* [Balance of the interactions between the canopy and the advanced regeneration in productive forests of *Nothofagus pumilio*]. PhD dissertation, Univ. Nacional del Comahue, Bariloche, Argentina. 150 p.

López Bernal, P.M., J.O. Bava, and S.H. Antequera. 2003. Regeneración en un bosque de lenga (*Nothofagus pumilio* (Poepp. et Endl.) *Krasser*) sometido a un manejo de selección en grupos [Natural regeneration in a lenga forest (*Nothofagus pumilio* (Poepp. Et Endl.) Krasser) submitted to selection management in groups]. *Bosque* 24:13–21.

López Bernal, P.M., G. Defossé, C.P. Quinteros, and J.O. Bava. 2012. Sapling growth and crown expansion in canopy gaps of *Nothofagus pumilio* (lenga) forests in Chubut, Patagonia, Argentina. *For. Syst.* 21:489–497.

Magurran, A.E. 2004. *Measuring biological diversity*. Malden, MA. 264 p.

Mansilla, P.R. 2012. *Evaluación de la alteración y restauración de los ciclos biogeoquímicos en bosques de Nothofagus pumilio de Tierra del Fuego afectados por prácticas de manejo forestal* [Evaluation of the impact and restoration of the biogeochemical cycles in *Nothofagus pumilio* forests in Tierra del Fuego affected by forest management practices]. PhD dissertation, Univ. Buenos Aires, Buenos Aires, Argentina. 151 p.

Martínez Pastur, G., J.M. Cellini, P.L. Peri, R.F. Vukasovic, and M.C. Fernández. 2000. Timber production of *Nothofagus pumilio* forests by a shelterwood system in Tierra del Fuego (Argentina). *For. Ecol. Manage.* 134:153–162.

Martínez Pastur, G., P. Peri, M. Fernandez, G. Staffieri, and M.V. Lencinas. 2002. Changes in understory species diversity during the *Nothofagus pumilio* forest management cycle. *J. For. Res.* 7:165–174.

McCune, B., J.B. Grace, and D.L. Urban. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR. 300 p.

Moore, D.M. 1983. *Flora of Tierra del Fuego*. Missouri Botanical Garden and Anthony Nelson, St. Louis, MO. 296 p.

Moreno, C.E. 2001. *Métodos para medir la biodiversidad* [Methods to

measure biodiversity]. M&T Manuales y Tesis SEA. Sociedad Aragonesa de Entomología (SEA), Zaragoza, Spain. 83 p.
NOBLE, I.R., AND D. DIRZO. 1997. Forests as human-dominated ecosystems. *Science* 277:522–525.
OKSANEN, J., F.G. BLANCHET, R. KINDT, P. LEGENDRE, P.R. MINCHIN, R.B. O'HARA, G.L. SIMPSON, ET AL. 2010. *Vegan: Community ecology package*, R package version 1.17–4. R Foundation for Statistical Computing, Vienna, Austria.
OLIVER, C.D., AND B.C. LARSON. 1996. *Forest stand dynamics*, update ed. John Wiley & Sons, New York. 544 p.
PAILLET, Y., L. BERGÈS, J. HJÄLTÉN, P. ÓDOR, C. AVON, M. BERNHARDT-RÖMERMANN, R. BIJLSMA, ET AL. 2010. Does biodiversity differ between managed and unmanaged forests? A meta-analysis on species richness in Europe. *Conserv. Biol.* 24:101–112.
PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, AND R DEVELOPMENT CORE TEAM. 2013. *nlme: Linear and nonlinear mixed effects models*. R Foundation for Statistical Computing, Vienna, Austria.
PROMIS, A., J. CALDENTEY, AND M. IBARRA. 2010. Microclima en el interior de un bosque de *Nothofagus pumilio* y el efecto de una corta de regeneración [Microclimate within a *Nothofagus pumilio* forest and the effects of a regeneration felling]. *Bosque (Valdivia)* 31:129–139.
PUIG, C.J., AND O. TRONCOSO. 1993. *Identificación y clasificación de las especies que conforman el sotobosque de lenga* [Identification and classification of the species that make up the understory of lenga]. Ingeniero Forestal, Univ. Nacional de la Patagonia San Juan Bosco, Esquel, Chubut, Argentina. 16 p.
PYSEK, P., D.M. RICHARDSON, M. REJMÁNEK, G. WEBSTER, M. WILLIAMSON, AND J. KIRSCHNER. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53:131–143.
QUINTEROS, C., P. LÓPEZ BERNAL, M. GOBBI, AND J. BAVA. 2012. Distance to flood meadows as a predictor of use of *Nothofagus pumilio* forest by livestock and resulting impact, in Patagonia, Argentina. *Agrofor. Syst.* 84:261–272.
QUINTEROS, C.P., M.S. FEIJÓO, N. ARIAS, P. LÓPEZ BERNAL, AND J. BAVA. 2013. Dieta de verano de bovinos pastoreando en bosques de lenga (*Nothofagus pumilio*) y mallines de Chubut, Argentina [Summer diet of cattle grazing in lenga forests (*Nothofagus pumilio*) and flood meadows of Chubut, Argentina]. *Rev. Fac. Cienc. Agri. Univ. Nacl. Cuyo* 45:285–292.
R DEVELOPMENT CORE TEAM 2015. *R package*. Version 3.2.3. R Foundation for Statistical Computing, Vienna, Austria.
RAFFAELE, E., T.T. VEBLEN, M. BLACKHALL, AND N. TERCERO-BUCARDO. 2011. Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *J. Veg. Sci.* 22:59–71.
RAMÍREZ, C., C. SAN MARTÍN, A. OYARZÚN, AND H. FIGUEROA. 1997. Morpho-ecological study on the South American species of the genus *Nothofagus*. *Plant Ecol.* 130:101–109.
RANDS, M.R.W., W.M. ADAMS, L. BENNUN, S.H.M. BUTCHART, A. CLEMENTS, D.A. COOMES, A. ENTWISTLE, ET AL. 2010. Biodiversity conservation: Challenges beyond 2010. *Science* 329:1298–3003.
READER, R.J., AND B.D. BRICKER. 1992. Values of selectively cut deciduous forest for understory herb conservation: An experiment assessment. *For. Ecol. Manage.* 51:317–327.
SÁNCHEZ-JARDÓN, L., B. ACOSTA, A. DEL POZO, M.A. CASADO, C. OVALLE, H.F. ELIZALDE, C. HEPP, AND J.M. DE MIGUEL. 2010. Grassland productivity and diversity on a tree cover gradient in *Nothofagus pumilio* in NW Patagonia. *Agri. Ecosyst. Environ.* 137:213–218.
SECRETARÍA DE AMBIENTE Y DESARROLLO SUSTENTABLE. 2006. *Primer Inventario Nacional de Bosques Nativos. Informe regional bosque andino-patagónico* [First national inventory of native forests. Andinopatagonico forest regional report]. Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires, Argentina. 104 p.
SCHMIDT, H., AND A. URZÚA. 1982. *Transformación y manejo de los bosques de lenga de Magallanes* [Transformation and management of lenga forests of Magellan]. Facultad de Ciencias Agrarias, Veterinarias y Forestales, Corporación Nacional Forestal, Santiago, Chile. 62 p.
SMITH, D.M., B.C. LARSON, M.J. KELTY, AND P.M.S. ASHTON. 1997. *The practice of silviculture. Applied forest ecology*, 9th ed. John Wiley & Sons, New York. 560 p.
THOMPSON, I.D., M.R. GUARIGUATA, K. OKABE, C. BAHAMONDEZ, N. ROBERT, V. HEYMELL, AND C. SABOGAL. 2013. An operational framework for defining and monitoring forest degradation. *Ecol. Soc.* 18:20.
VÁZQUEZ, D.P. 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. *Biol. Invas.* 4:175–191.
VEBLEN, T.T., D.H. ASHTON, F.M. SCHLEGEL, AND A.T. VEBLEN. 1978. Influencia del estrato arboreo sobre los estratos inferiores en un bosque mixto perenni-caducifolio de Antillanca, Osorno, Chile [Influence of the arboreal stratum on the lower strata in a perennial-deciduous mixed forest of Antillanca, Osorno, Chile]. *Bosque* 2(2):88–104.
VEBLEN, T.T., C. DONOSO, Z., T. KITZBERGER, AND A.J. REBERTUS. 1996. Ecology of southern Chilean and Argentinian *Nothofagus* forests. P. 293–353 in *The ecology and biogeography of Nothofagus forests*, Veblen, T.T., R.S. Hill, and J. Read (eds.). Yale Univ. Press, New Haven, CT.
VON MÜLLER, A.R. 2013. Adecuación de la carga ganadera para asegurar la conservación de la estructura y los servicios ecosistémicos en el bosque andino patagónico [Adaptation of livestock load to ensure the conservation of ecosystem structure and services in the Patagonian Andean forest]. Presented at the *II Jornadas Forestales de Patagonia Sur 2nd Congreso Internacional Agroforestal Patagónico, 2013 May 16–17, El Calafate, Santa Cruz, Argentina*. 119 p.
ZAMORANO-ELGUETA, C., L. CAYUELA, M. GONZÁLEZ-ESPINOSA, A. LARA, AND M.R. PARRA-VÁZQUEZ. 2012. Impacts of cattle on the South American temperate forests: Challenges for the conservation of the endangered monkey puzzle tree (*Araucaria araucana*) in Chile. *Biol. Conserv.* 152:110–118.
ZULOAGA, F., O. MORRONE, AND M. BELGRANO. 2008. *Catálogo de las plantas vasculares del Cono Sur* [Catalog of vascular plants of the Southern Cone]. Missouri Botanical Garden, St. Louis, MO. 3888 p.