

Structure and conservation status of *Araucaria araucana* forest outside the natural reserves of Argentina.

The case of the Chiuquilihuín Mapuche community

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Chiuquilihuín (39° 36' S and 71° 13' W, 5,144 ha) is an area of natural grasslands, shrublands and forests, dwelled by 300 native people of the Mapuche ethnic group devoted to extensive cattle ranging, forestry and edible seed gathering. The structure and conservation status of natural forests (27.1 % of total area), and particularly those composed of the vulnerable conifer *Araucaria araucana* ((Mol.) K. Koch) ("pehuén") (9.5 %), was evaluated as an indicator of sustainable resource use of this area. *Araucaria araucana* formed pure and mixed stands, with *Nothofagus pumilio* ((Poepp. et Endl.) Krasser), "lenga", and exhibited attributes congruent with a strategy based on large longevity, broad ecological amplitude, shade tolerance, continuous regeneration under canopy and resistance to physical and biological mortality factors. Characteristics of *N. pumilio* were those of an early successional, gap-dependant tree species. Forest conservation tended to be satisfactory (negligible or moderate timber extraction, absent or slight erosion and adequate regeneration of *A. araucana*). However, cattle grazing covered 93.3 % of forest land. Though *A. araucana* seedlings and saplings were abundant and vigorous, reflecting efficient mechanisms of defence against herbivores, those of *N. pumilio* were very scarce and injured or dead by domestic livestock. In Chiuquilihuín, long-term preservation of *A. araucana* depends on maintaining healthy ecosystem components and processes, and particularly *N. pumilio* regeneration. Consequently, management actions as land-use planning, productive diversification, environmental training, grazing restrictions and stocking reduction, enclosure and tree planting and agroforestry, should be implemented to improve forest conservation.

Key words: Pehuén, *Nothofagus pumilio*, Natural forests, Conservation indicators, Northwestern Patagonia.

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En Chiuquilihuín (39° 36' S y 71° 13' O, 5.144 ha) viven 300 miembros de la etnia Mapuche, en un ambiente de bosques, matorrales y pastizales naturales donde practican la ganadería extensiva, la actividad maderera y la cosecha de semillas comestibles. En este estudio se analizó la estructura y conservación del bosque natural (27,1 % del área), y en particular, el compuesto por la conífera vulnerable *Araucaria araucana* ((Mol.) K. Koch) ("pehuén") (9,5 %). *Araucaria araucana* conformó bosques puros y mixtos con *Nothofagus pumilio* ((Poepp. et Endl.) Krasser) ("lenga"), y exhibió características consistentes con una estrategia basada en la gran longevidad, la tolerancia a la sombra, la regeneración continua, la extensa amplitud ecológica y la resistencia a factores de mortalidad físicos y biológicos. Las características de *N. pumilio* correspondieron a las de una especie sucesional temprana y dependiente de claros para regenerar. El estado de conservación de estos ecosistemas fue satisfactorio (extracción moderada de madera, erosión muy leve y regeneración adecuada de *A. araucana*). Sin embargo, el pastoreo del ganado doméstico se extendió en el 93,3 % de la superficie boscosa. Este proceso afectó intensamente a *N. pumilio*, cuyos renovales fueron escasos y en una alta proporción estaban dañados o muertos. En Chiuquilihuín, la preservación en el largo plazo de *A. araucana* depende del mantenimiento de los componentes y procesos ecosistémicos, en general y los que involucran a *N. pumilio* en particular. En consecuencia, es necesario implementar acciones de manejo (e.g., planificación del uso de la tierra, diversificación

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productiva, capacitación ambiental, restricción espacial y temporal de pastoreo, sistemas silvoganaderos) para mejorar el estado de conservación del bosque.

Palabras clave: Pehuén, *Nothofagus pumilio*, Bosque natural, Indicadores de conservación, Patagonia noroccidental.

INTRODUCTION

Conifer is a group whose evolutionary dominance decreased, claimed to be caused by climatic change (Retallack & Dilcher, 1981), by the effect of tectonic activity (Kershaw & McGlone, 1995), or by successional displacement of flowering plants (Haig & Westoby, 1991). Conifers exhibit a slower rate of individual and population increase compared to woody perennial angiosperms (Norton et al., 1987). Many conifers have discontinuous age structures indicating regeneration failures beneath established stands (Enright & Odgen, 1995), which have been formerly interpreted as evidence of progressive declining (Schmithüsen, 1960). However, these theories did not incorporate impact-driven dynamics based in gap dependence for tree establishment (Enright & Odgen, 1995). The current diversity and distribution of southern conifers is only a minor fraction of that which occurred in the geological past, and consequently they are regarded as “living fossils” (Enright et al., 1995). Conifers represent a valuable timber resource, permit the existence of continuous forest cover in inhospitable environments and sustain high biodiversity (Farjon & Page, 1999). However, they are exploited at rates that exceed regeneration or are converted to pasture, arable, or urban areas (Oldfield et al., 1998; Newton et al., 2003). *Araucaria araucana* ((Mol.) K. Koch) (“pehuén”, Araucariaceae) is a long-lived, emergent, shade-tolerant and slow-growing conifer, adapted to fire based on the presence of a thick bark, epicormic buds that sprout after burnings and terminal and protected buds. Vegetative propagation can occur, particularly in dry sites, through basal sprouts (Montaldo, 1974; Veblen & Delmastro, 1976; Muñoz, 1984; Drake et al., 2005). However, reproduction is mainly sexual but it tend to be inadequate given intrinsic (short viability, low fertility and poor passive dispersal of seeds) and extrinsic factors (high pre- and post-dispersal seed predation) (Muñoz, 1984; Armesto et al., 1996; Shepherd et al., 2008; Sanguinetti & Kitzberger, 2010). *Araucaria araucana* exhibits a primarily dioecious character, pollination by wind and heavy seeds (“piñón”) dispersed by gravity over short distances. This species shows environmentally triggered and regionally synchronous production of large seed crops, a masting strategy that would be aimed to satiate seed predators or/and to increase pollination efficiency (Sanguinetti & Kitzberger, 2008; Shepherd et al., 2008). *Araucaria araucana* is distributed in Nahuelbuta Coastal Pacific range and the Andes of both, Argentina and Chile. In Argentina, it extends in a narrow fringe from 37° 30' to 40° 03' S, and from the eastern flank of the Andes to 70° 35' W, reaching a maximum altitude at 1,800 m, in areas with annual rainfall ranging from 900 to 2,500 mm, and soils originating from volcanic ash or metamorphic and sedimentary rocks (Montaldo, 1974; Armesto et al., 1996). It forms pure or mixed forests,

mainly with *Nothofagus pumilio* ((Poepp. et Endl.) Krasser), “lenga”), *Nothofagus antarctica* ((G. Forst.) Oerst., “ñire” (Nothofagaceae), and other southern beeches. The combination of natural and anthropogenic perturbations motivated *A. araucana* been categorized as Vulnerable by the International Union for Conservation of Nature (Walter & Gillett, 1998; Farjon & Page, 1999; Newton et al., 2003), and included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2008). In Chile, it was declared National Monument and in Neuquén province, environmental laws prohibit logging of living trees.

The fossil record suggests that during the Tertiary, the species exhibited a much more extended geographic distribution than at present (Kershaw & Wagstaff, 2001). Before the European settlement period of s. XVI, *A. araucana* encompassed 675,000 ha (Pérez et al., 2000) whereas at present it reaches 443,000 ha, from which 44 % are in protected areas (Lara et al., 1999). In Argentina, 67 % of *A. araucana* forests are not included in natural reserves and comprise the most eastern and xeric stands within the forest - steppe ecotone of the extrandean Patagonia, a region highly disturbed by extensive grazing of domestic livestock and fires (Lara et al., 1999; Rusch et al., 2008). The objective of the present study was to analyse the location, structure and conservation status of forest ecosystems, particularly those composed of *A. araucana*, within the Chiuquilihuín Mapuche community. This assessment is an attempt to ascertain whether the Mapuche people are effective stewards of forests in particular and their environment in general, and to contribute to improve the schemes of conservative use of this vulnerable conifer outside the range of natural reserves of Argentina.

MATERIALS AND METHODS

The Chiuquilihuín Mapuche community

Chiuquilihuín (39° 40' S and 70° 15' W, Neuquén province, 5,144 ha) limits with Aucapán and Atreico Mapuche communities, the Lanín National Park and private and provincial properties (Figure 1). The landform is mountainous with valleys, plateaus and hills with altitudes ranging from 900 to 2,116 m (“Tres Picos Mt.”). Climate is humid with cold winters and dry warm summers, winds are very intense and frequent, mean annual temperature is 7.3 °C and annual rainfall varies from east to west from 1,200 to 1,800 mm (Autoridad Interjurisdiccional de Cuencas, pers. com.). The study area belongs to the “Western District of the Patagonia Province” and the “Pehuén District of the Subantarctic Province” (Cabrera, 1971).

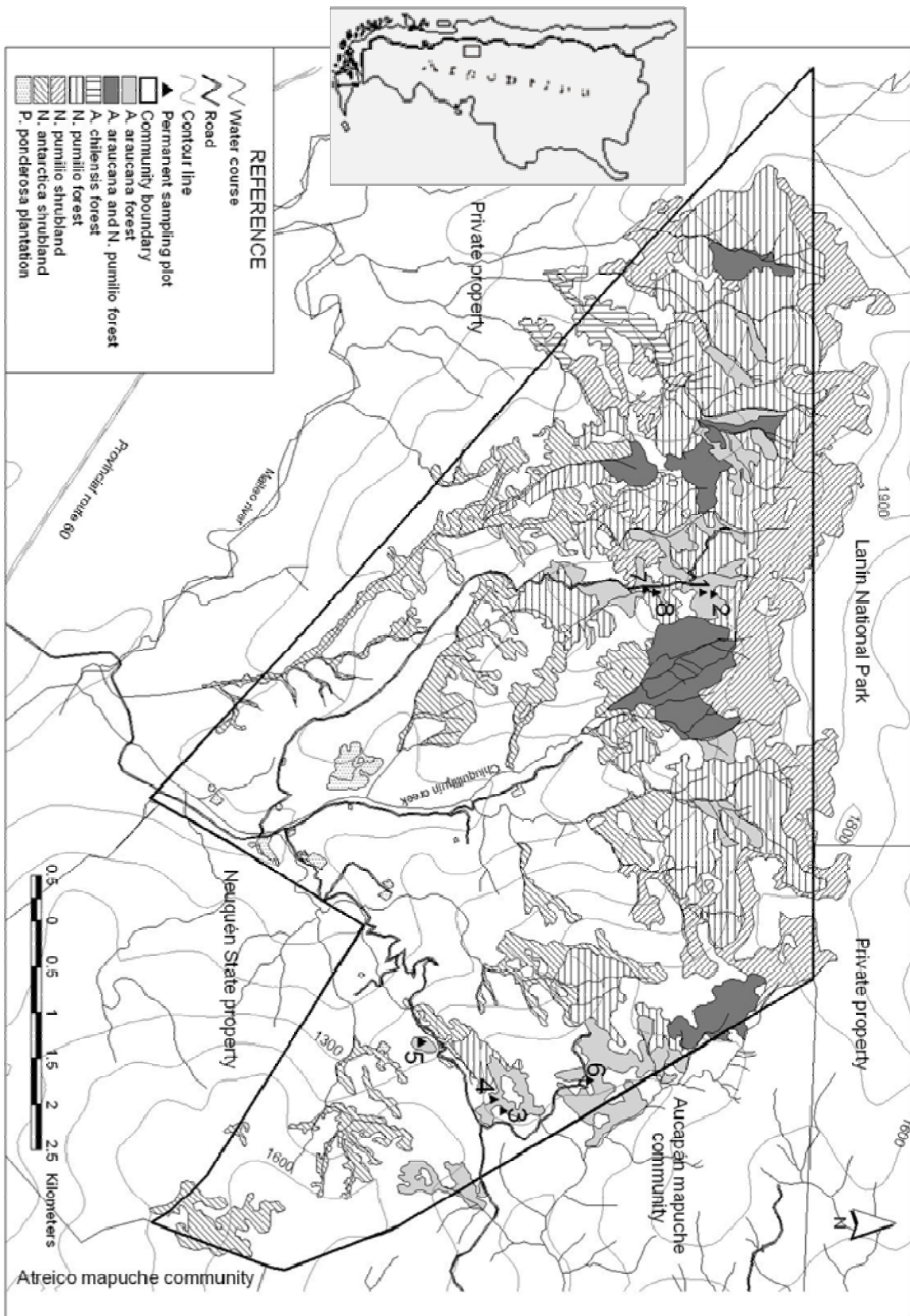


Figure 1: Woody vegetation map of Chiuquilihuín Mapuche community.

In Chiuquilihuín reside a native people of the South American ethnic Mapuche group, composed of around 300 peasants distributed in 60 families. Members of the community are mainly devoted to extensive cattle ranging of goats, sheep, cows and horses in the grasslands of the lowlands (in winter) and in the shrublands and forests of the highlands (in summer). During the 70's, *A. araucana* was exploited by private companies, and at present, Mapuche people collect its firewood, dead timber and seeds. Living *N. pumilio* trees are cut down to obtain timber for construction and handicraft.

Araucaria araucana has an ethnobotanical and economic importance for Mapuche people. The tree is considered sacred and its symbolic and spiritual importance provides a key to the Mapuche's cultural understanding of nature and society (Herrmann, 2006). Seeds constitute a major element of the local economy as they are directly consumed or processed to produce flour and a fermented beverage, fed to livestock and traded in urban centres (Aagesen, 1998; Ladio, 2001). Seed collection is one of the most important activity of the annual social calendar of the community, as they have developed a profound and exact knowledge on the frequency and the degree of seed production and distribution and abundance of female trees (Herrmann, 2006). Traditional measures that encourage sustainable use of *A. araucana* have been reported, which include division of areas into families territories for collecting seeds, digging of seeds into the soil for germination, selective seed harvesting and gathering from the ground, seed harvesting mainly from the proximity of parent trees and tree cultivation and planting in logged areas (Herrmann, 2006). However, other authors have pointed out the direct and indirect detrimental effects of collecting seeds, but also grazing practices, on plant recruitment (Mutarelli & Orfila, 1970; Bragg, 1981; Serret, 1984; Aagesen, 1998).

Methodology

In Chiuquilihuín, water courses, roads and infrastructure were identified in an Aster satellite image (resolution 15 m, coordinates Gauss Krüger band 1, ellipsoid WGS 1984). Woody vegetation was classified as forest of i) *A. araucana* (total BA \geq 80 %), ii) *N. pumilio* (total BA \geq 80 %), iii) *N. pumilio* and *A. araucana*, iv) *Austrocedrus chilensis* ((D. Don.) Pic. Serm. et Biz., "ciprés de la cordillera") and v) *Pinus ponderosa* (Douglas ex C. Lawson, "ponderosa pine") (plantation), and as shrubland of vi) *N. pumilio* and vii) *N. antarctica*. Experimental areas, representative of the intact *A. araucana* forests (pure and mixed with *N. pumilio*), were chosen and 7 permanent sampling plots (PSP 1, 2, 3, 4, 6, 7 and 8) were established for intensive data collection. The criterion for a representative area was the absence of major human influences within the life-span of trees, such as logging, burning, overgrazing or extensive presence of exotic flora. In addition, an area representative of the very open, park-like *A. araucana* woodlands, surrounded by the steppe, was chosen and the PSP 5 was established. All the experimental areas representative of *A. araucana* woodlands showed

overgrazing of domestic livestock. Size of each PSP was 1,600 m² (compass, measuring tape) (Figure 1).

Trees were categorized as seedlings (total height TH < 0.3 m, clinometer), saplings (0.3 m \leq TH < 1.5 m) (regeneration in a broad sense) and adults (TH \geq 1.5 m). Within each plot, all standing adult tree was tagged with a numbered label and measured for diameter at breast height (DBH, 1.3 m above soil) (diameter tape) and evaluated for condition (live or dead) and sociological position, as dominant (receiving direct sunlight at the top and sides), intermediate (receiving direct sunlight through openings of the main canopy) and suppressed (not receiving direct sunlight) (Kraft classification, Daniel et al., 1982). Adults of *A. araucana* with completely visible crowns were measured for TH (clinometer, measuring tape) (n = 84). In order to estimate age (A) of *A. araucana*, cores containing the pith were collected at breast height from a sample of adult trees occurring in PSP 1, 2 and 3 (Pressler type increment borer) (n = 27). The existence of a relatively small database for *A. araucana* is explained by both, the legal restriction of using destructive methods for age estimates and the presence of very large individuals within the PSP. This sampling height for cores was preferred in order to minimize loss of visible tree rings due to stump rot. Cores were mounted in wooden holders and sanded with successively finer grades of sandpaper and annual rings were counted under magnification (30 x), following the procedures of Stokes & Smiley (1968). Chronological tree age was estimated by adding the time needed for individuals to reach core height, and they were calculated averaging their height growth rate from 1.3 m to TH. Trees were grouped according to each sociological class, and a multiple linear model (in the form of $A = a_1 \text{DBH}^2 + a_2 \text{DBH} + a_3$) was developed for each category and selected according to the highest regression coefficient (R²). Then, A was estimated for all trees within the plot.

The relative position of individuals in space and its intensity, as defined by the size of possible tree patches, was assessed using the Morisita's (1959) index of dispersion (I_M). It is given by:

$$I_M = q (\sum n_i (n_i - 1)) / N (N - 1) \quad (1)$$

in which

I_M = Morisita's index of dispersion

q = number of subplots containing the sampling plot

n_i = number of individuals in the i-esim subplot

N = total number of individuals in the whole sampling plot (= $\sum n_i$)

Significance of departure from randomness of I_M was assessed by a Chi-square test (X²) (P < 0.05) (Morisita, 1959). In 7 m²-subplots randomly located within the PSP, *A. araucana* and *N. pumilio* saplings were counted and classified as healthy, infected by pathogens, or browsed by livestock. In each PSP, 32 2 m²-subplots were systematically placed along 40 m-transects separated 5 m each (four transect in each PSP) for seedling counting and condition evaluation (healthy, infected and browsed).

In order to evaluate forest conservation within the study area, 90 sampling stations were homogeneously

established and altitude (altimeter), slope (clinometer), aspect (compass) and composition and basal area (BA) (dendrometer of counting factor = 4) of dominant woody species were recorded. In each sampling station the value of indicators of condition (referred to the quality of the environment) and pressure (referred to the human activities that affect the environment) (ANZEC, 2000) were registered. Indicators were based on the best scientific understanding currently available, so that changes in these simple measures could be related to more complex environmental trends and interpreted accurately. The indicators were abundance and conservation status of tree regeneration and aerial canopy cover (condition), and levels of timber extraction, grazing by domestic livestock and erosion (pressure).

Canopy cover was classified as low (< 30 %, "Woodland"), medium (between 30 and 70 %, "Open forest") and high (> 70 %, "Closed forest"). Regeneration was categorized as adequate (healthy regeneration, homogeneously distributed within the stand), medium (regeneration browsed and grouped in particular areas) and inadequate (regeneration absent or scarce, and intensively browsed) The absence of immature trees of *N. pumilio* does not necessarily imply poor regeneration; this species depends on canopy openings for establishment and therefore on the successional phase of the forest. Level of timber extraction was classified as intense (stand with postharvest gaps $\geq 500 \text{ m}^2$, with past and present stumps and significant soil cover alteration), moderate (postharvest gaps between 100 and 500 m^2 , with past and isolated stumps and no significant soil cover alteration) and negligible (postharvest gaps between < 100 m^2 , with past and isolated stumps and no soil cover alteration).

Cattle browsing was categorized as presence and absence of browsed plants. Soil erosion was classified as present (presence of gullies, ditches, ridges, landslides and stony surface pedestals, and bare soil area $\geq 25 \%$), or slight or absent (bare soil area < 25 %). Conservation status of forest, based on the combination of levels of timber extraction, soil erosion and forest cover was classified as satisfactory, intermediate, or unsatisfactory. Satisfactory level implied negligible timber extraction and very slight or absent erosion, or moderate timber extraction, absent or slight erosion and high canopy cover, or negligible timber extraction, adequate regeneration, slight erosion and high canopy cover. Intermediate level implied moderate timber extraction, present erosion and low or medium canopy cover, or intense timber extraction, present erosion, medium or high canopy cover and medium regeneration. Unsatisfactory level implied intense timber extraction, present erosion and inadequate regeneration.

RESULTS

Forest structure and regeneration

The 8 PSP were localised between 994 (PSP 4) and 1,513 m (PSP 3) and included pure, park-like (PSP 5), open (PSP 4) and closed (PSP 1, 3 and 7) *A. araucana* stands, and mixed, open (PSP 8) and closed stands of

A. araucana and *N. pumilio* (PSP 2 and 6) (Figure 1). Tree density varied between 81 (PSP 5) and 1,194 ind ha^{-1} (PSP 7), and BA between 16 (PSP 5) and 151 $\text{m}^2 \text{ha}^{-1}$ (PSP 3) (Table 1). Diameter-class frequency distribution differed between species. *Araucaria araucana* approached an irregular, reverse "J"-shaped size distribution in which seedling was the largest category (9,637 ind ha^{-1}) and adults was the smallest (537 ind ha^{-1}). *Nothofagus pumilio* approached a regular, normal distribution in which sapling was the most abundant class (1,153 ind ha^{-1}) (Table 2, Figure 2). Average regeneration density was 13,199 ind ha^{-1} (minimum 1,143 ind ha^{-1} in PSP 5 and maximum 24,572 ind ha^{-1} in PSP 7), of which 96 % belonged to *A. araucana* (Table 2).

The proportion of adult living trees of *A. araucana* was equal to or greater than 95 %, while for *N. pumilio* was equal to or greater than 64 % (Table 1). For *A. araucana*, the percentage of healthy seedlings and saplings was very high (92 % and 86 %, respectively), while for *N. pumilio*, this percentage was very low (13 % and 15 %, respectively), and the vast majority of plants were browsed and diseased (Table 2). Potential (TH = a DBH^b) and polynomial (AT = a₁ DBH² + a₂ DBH + a₃) (P < 0.05) models of simple regression for adult trees of *A. araucana* exhibited coefficients of determination (R²) ranging from 0.652 (PSP 2) and 0.957 (PSP 1), while the model for the entire database was TH = 0.7774 DBH^{0.7101} (R² = 0.801, n = 84) (Figure 3). The estimated age for adults of *A. araucana* in PSP 1, 2 and 3 ranged from 41 to 450 years and averaged 229 years (PSP 1, EE = 12.4, n = 108), 287 years (PSP 2, EE = 27.3, n = 25), and 217 years (PSP 3, EE = 10.7, n = 134). The age-class frequency distribution of *A. araucana* in all three plots was irregular (Figure 4).

The tree base maps of *A. araucana* adults (PSP 1 to 8) and saplings (PSP 1) reflected, in general, the presence of a clustered spatial pattern (Im > 1) (Chi-square test, P < 0.05) (Figures 5 and 6). In PSP 3 to 8, two distinct spatial configurations could be seen on the maps: individuals were grouped and groups were placed in particular sectors of the plots. The indices were significant at larger square sizes (e.g., > 20 x 20 m) because the clusters were not evenly distributed in space, and therefore they did not indicate patch size, but patch concentration. In contrast, in PSP 1 individuals were grouped in patches up to 5 x 5 m size and these clusters were distributed randomly within the sampling plot (Chi-square test, P \geq 0.05). The highly intense aggregation pattern at small subplot sizes (< 5 x 5 m) in PSP 5 would result from the presence of a very small number of groups with low quantity of trees, whereas in PSP 6 would be due to the presence of big clusters with large number of trees. The exception to this aggregated general pattern for adults and juveniles was present in PSP 2, where individuals were located in a statistically equidistant configuration forming a regular spatial structure (Im < 1) (Chi-square test, P < 0.05) (Figure 6).

Table 1: Location and structure of *A. araucana* (Aa) and *N. pumilio* (Np) natural forests in Chiuquilihuín Mapuche community. PSP: permanent sampling plot, FT: forest type, CF: closed forest, OF: open forest, WL: woodland, AL: altitude (m), S: slope (°), AS: aspect, D: density (ind ha⁻¹), BA: basal area (m² ha⁻¹), DBH_m: mean diameter at breast height (cm), L: living trees (%), M: male trees (%). Species percentages are indicated in brackets.

PSP	FT	LOCATION	AL S AS	PARAMETER	<i>Araucaria araucana</i>	<i>Nothofagus pumilio</i>	TOTAL
1	Aa CF	39° 36' S 71° 13' W	1,414 12 -	D	644 (97)	19 (3)	663
				BA	142.0 (97)	4.2 (3)	146
				DBH _m	53.0	53.2	-
				L	95	100	-
				M	59	-	-
2	Aa-Np CF	39° 36' S 71° 13' W	1,414 7 WSW	D	150 (57)	113 (43)	263
				BA	50.7 (56)	39.3 (44)	90
				DBH _m	65.6	66.7	-
				L	96	80	-
				M	38	-	-
3	Aa CF	39° 38' S 71° 09' W	1,513 23 E	D	800 (99)	6 (1)	806
				BA	148.6 (99)	2.1 (1)	151
				DBH _m	48.6	65.0	-
				L	100	100	-
				M	70	-	-
4	Aa OF	39° 38' S 71° 09' W	994 15 SSE	D	481 (93)	38 (7)	519
				BA	75.9 (91)	7.3 (9)	83
				DBH _m	44.8	49.8	-
				L	100	90	-
				M	60	-	-
5	Aa WL	39° 38' S 71° 09' W	1,432 24 W	D	81 (100)	-	81
				BA	15.8 (100)	-	16
				DBH _m	49.8	-	-
				L	100	-	-
				M	20	-	-
6	Aa CF	39° 37' S 71° 19' W	1,432 13 WSW	D	319 (31)	694 (69)	1.013
				BA	86.1 (83)	17.6 (17)	104
				DBH _m	58.7	18.0	-
				L	100	100	-
				M	60	-	-
7	Aa-Np CF	39° 37' S 71° 13' W	1,485 8 S	D	1,138 (95)	56 (5)	1.194
				BA	77.4 (77)	22.4 (23)	100
				DBH _m	29.4	71.2	-
				L	98	90	-
				M	57	-	-
8	Aa-Np OF	39° 37' S 71° 13' W	1,485 9 S	D	681 (92)	56 (8)	738
				BA	51.6 (69)	23.7 (31)	75
				DBH _m	31.0	73.2	36.0
				L	98	64	-
				M	46	-	-

Table 2: Conservation level (H: healthy, I: infected and B: browsed) of *A. araucana* (Aa) and *N. pumilio* seedlings and saplings within the eight permanent sampling plots (PSP) in Chiuquilihuín Mapuche community.

PSP	SEEDLING						SAPLING						TOTAL (ind ha ⁻¹)	Aa (%)
	<i>Araucaria araucana</i>			<i>Nothofagus pumilio</i>			<i>Araucaria araucana</i>			<i>Nothofagus pumilio</i>				
	H (%)	H+B (%)	TOTAL (indha ⁻¹)	H (%)	H+B (%)	TOTAL (indha ⁻¹)	H (%)	H+B (%)	TOTAL (indha ⁻¹)	H (%)	H+B (%)	TOTAL (indha ⁻¹)		
1	100	0	10,604	0	0	0	77	23	4,180	0	0	0	14,784	100
2	100	0	7,481	0	0	0	64	36	1,662	20	80	417	9,560	96
3	86	14	2,479	0	0	0	100	0	102	0	0	0	2,581	100
4	87	13	9,601	0	0	0	81	19	1,828	0	0	0	11,429	100
5	100	0	1,043	0	0	0	100	0	100	0	0	0	1,143	100
6	89	11	15,452	100	0	1,223	100	0	1,405	96	4	4,194	22,274	76
7	88	12	14,578	0	0	0	83	17	9,993	0	0	0	24,572	100
8	88	12	15,857	0	100	104	86	14	3,286	0	0	0	19,247	99

Location and status of woody vegetation

Chiuquilihuín was covered by 27.1 % of natural forests and 23.2 % of natural shrublands (Table 3). Forests were composed of coniferous, monospecific, tall and very open (*A. araucana* forests with isolated individuals forming a park-like vegetation surrounded by the steppe) or closed stands (pure forests of *A. araucana* and *A. chilensis*), or of mixed and closed stands with coniferous and broadleaf trees (associations of *A. araucana* and *N. pumilio*). Pine plantation occupied 32 ha (0.6 % of total area) located in the southern sector of the community. The *N. antarctica* shrubland was found from 1,000 to 1,300 m, and occupied 10.9 % of the study area, mainly in canyons, hillsides and valleys of predominantly southern exposure. The pure forest and shrubland of *N. pumilio* was the largest woody vegetation type (28.6 % of total area), and was located above 1,700 m and up to the limit of woody plants at 1,900 m. (Figure 1).

The 93.3 % of forest land showed signs of grazing by domestic livestock on smaller plants (herbs, shrubs and young trees), encompassing likewise pure and mixed forests of *A. araucana* and *N. pumilio* (Table 4). Only 27.1 % of forest area presented adequate regeneration, while the remaining 72.9 % showed a poor or intermediate condition. This phenomenon affected particularly *N. pumilio* stands (57.1 % of the area of this forest type), and this species within the mixed stands with *A. araucana* (100 % of the area of this forest type) (Table 4). The 69.0 % and 10.1 % of the area of natural forest was affected by moderate and intense timber extraction, respectively, and exclusively affected *N. pumilio* trees. The conservation status of 48.8 % of the natural forest area was satisfactory while 12.9 % was unsatisfactory (Table 4, Figure 7).

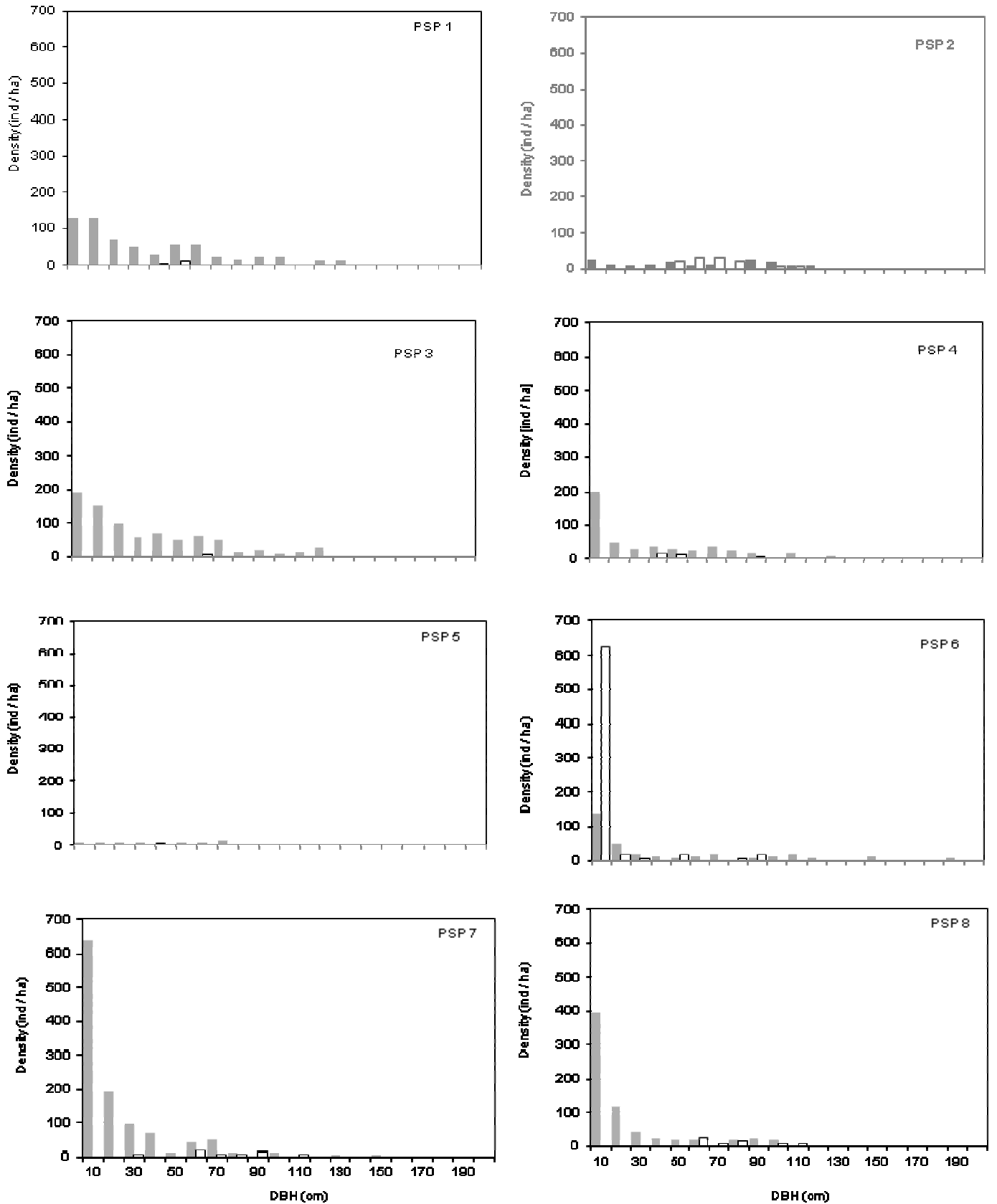


Figure 2: Diameter-class frequency distribution of *A. araucana* (grey bar) and *N. pumilio* (white bar) within the eight permanent sampling plots (PSP) in Chiuquilihuín Mapuche community.

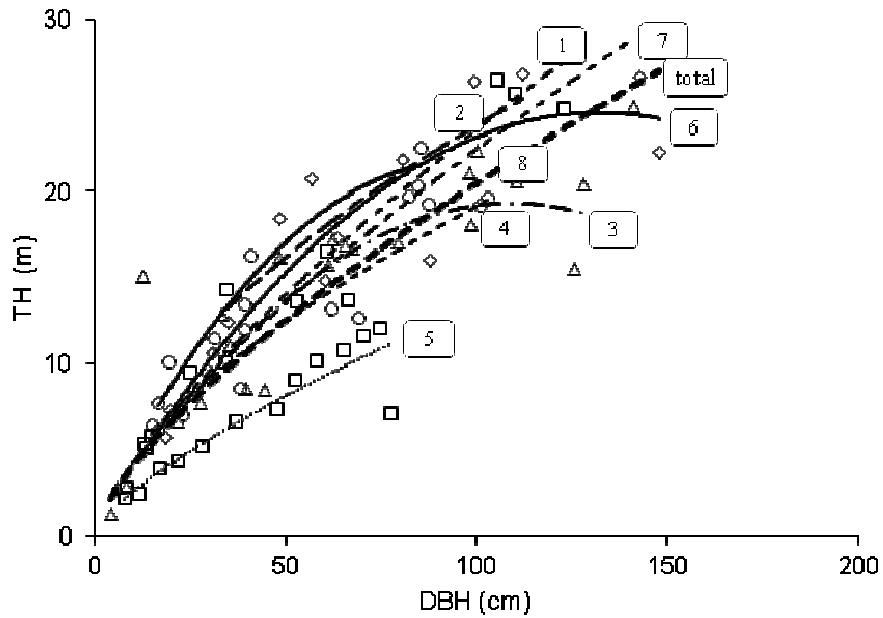


Figure 3: Relationship between diameter at breast height (DBH) and total height (TH) of *A. araucana* adult trees within the eight permanent sampling plots in Chiuquilihuín Mapuche community.

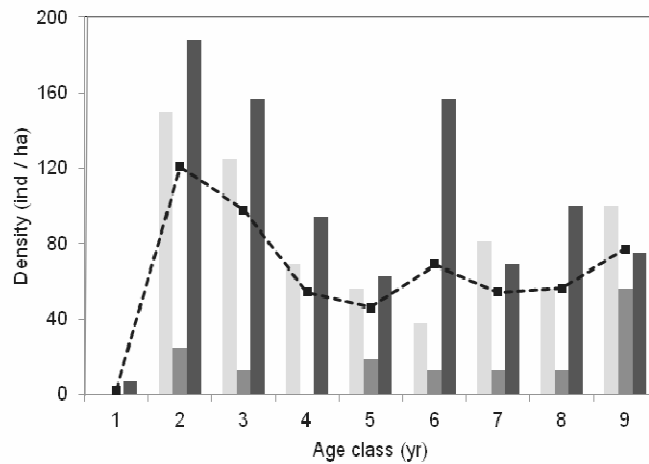


Figure 4: Age-class frequency distribution of adult trees of *A. araucana* in PSP 1 (light grey bar), PSP 2 (dark grey bar), PSP 3 (black bar) and average (squares, dotted line) in Chiuquilihuín Mapuche community. Class 1: 0 - 49.9 years, 2: 50 - 99.9, ..., 9: 400 - 450 years.

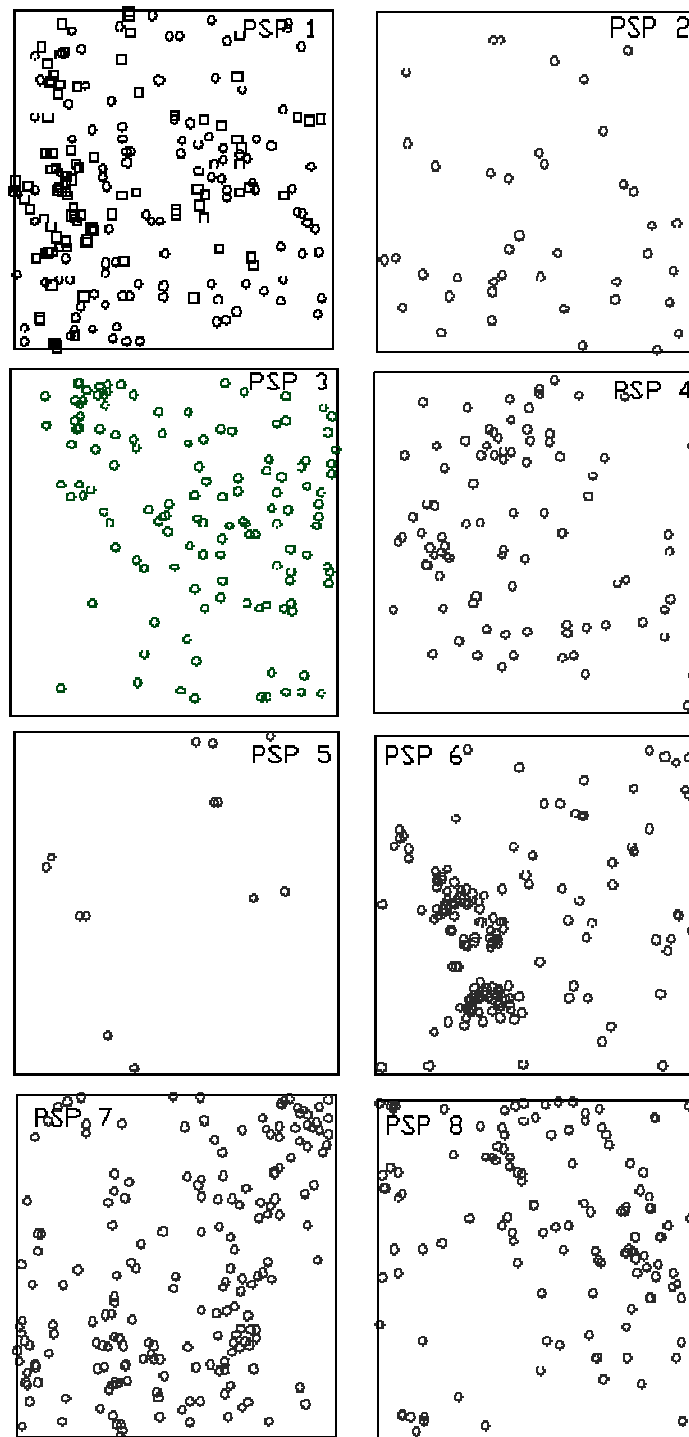


Figure 5: Maps of the 80 x 80 m permanent sampling plots (PSP 1 - 8) that indicate the relative position of adults (circles) and saplings (PSP 1, squares) of *A. araucana* in Chiuquilihuín Mapuche community.

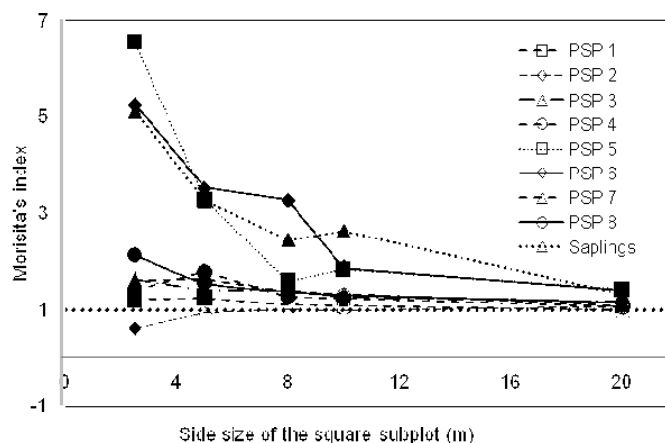


Figure 6: Values of Morisita's index of dispersion (I_M) of *A. araucana* adults (PSP 1 - 8) and saplings (PSP 1) for different subplot sizes within the eight permanent sampling plots (PSP). Grey marks indicate an I_M significantly greater than 1.0 (horizontal dotted line), otherwise I_M does not differ significantly from 1 (X^2 -test, $P < 0.05$).

DISCUSSION

Natural forests accounted for more than half the Chiuquihúin community, and though *N. pumilio* was the most widespread tree species, the pure and mixed *A. araucana* forest covered a large portion of the study area. Conservation status of forest ecosystems tended to be satisfactory as they exhibited negligible or moderate logging, absent or slight erosion and lack of removal of *A. araucana* living trees, and only 12.9 % of the area presented an unsatisfactory condition. However, grazing by domestic livestock covered 93.3 % of the territory, and whose direct and indirect negative impacts were recorded on vegetation (injured or dead young trees) and soil (low plant cover and present erosion). The grazing effect on tree regrowth was uneven. The entire area of monospecific *A. araucana* forests exhibited adequate regeneration, and seedlings and saplings did not show signs of browsing. In the mixed forest affected by grazing, *N. pumilio* young plants showed signs of intense herbivory while those of *A. araucana* experienced no damage. Adequate regeneration was only observed in 19.4 % of the *N. pumilio* forest. Within the sampling plots, that represented undisturbed sites, over 80 % of seedlings and saplings of both species were healthy. Regeneration of *A. araucana* would exhibit physical and chemical defence mechanisms against browsing, based on a thick integument and leaves mucrons, more effective than that of *N. pumilio*.

In *A. araucana*, the current clustered spatial pattern, persistent in adults and juveniles, would be related to biological (associated to vegetative reproduction, masting, large seed weight, slow growth, extended longevity and shade tolerance), environmental (associated to regeneration niche), and ecological factors (associated to interactions with understory vegetation, seed dispersers and predators). Their heavy seeds are dispersed by gravity to short distances, although this distance can be increased by birds and rodents (Darrieu, 1982; Muñoz, 1984; Burns, 1991). Seed predators, which can severely limit plant recruitment, are native mice (e.g., "ratón de pelo largo"

Abrothrix longipilis (Waterhouse), "lauchón orejado" *Phyllotis darwini* (Waterhouse) and "rata de los pinares" *Aconaemys sagei* (Pearson)), and birds (e.g., "choroy" *Ericognathus leptorhynchus* (King) and "cachaña" *E. ferruginea* (Müller)) (Darrieu, 1982; Muñoz, 1984; Burns, 1991). The non-native "wild boar" (*Sus scrofa*, Linnaeus) is an important seed consumer (Sanguinetti & Kitzberger, 2010).

Sanguinetti & Kitzberger (2009) found that distance of seedling to parent trees followed an unimodal frequency distribution, with density reaching a maximum value slightly away from the seed source (3 to 5 m) and then decreasing exponentially up to a maximum distance of about 13 m. This spatial pattern would be caused by the balance between a limited capacity of seed dispersal, which decreases with distance from the source, and survival from granivores, which increases with distance. During masting, regeneration pulses are promoted through an increase in the proportions of seed survivorship and juvenile recruitment. The regeneration pulse, synchronized among trees of a given population, would be limited more by seed production and granivory than by abiotic factors and understory vegetation. This process, associated with large longevity and slow growth, promotes the accumulation of different cohorts under the parent trees. Those plants located on the edge of the seed shadow tend to attain maturity because light condition is more suitable.

In *A. araucana* populations, density and basal area was contrasting, size structures were irregular, age structures were uneven with individuals older than 400 years, proportion of live and healthy trees were very high and mathematical relations between age and diameter showed moderate statistical adjustments, and between height and diameter showed contrasting trajectories. All these features were consistent with a development strategy based on large longevity, slow growth, shade tolerance, continuous regeneration under canopy, large ecological amplitude and large resistance to physical (e.g., freezing, wind, fire, volcanic activity), and ecological mortality factors (e.g., competition) (Schilling & Donoso, 1976; Veblen et al., 1995; Armesto et al., 1996). The size distribution of *N. pumilio* was regular, compatible with an early successional, light-

demanding species that regenerates in gaps of varying sizes, forming even-aged stands or even-aged patches

within mosaic forests (Veblen, 1989; Armesto et al., 1997

Table 3: Area of natural forest and shrubland in Chiuquilihuín. Percentages related to area of (1) woody vegetation and (2) Mapuche community are indicated.

VEGETATION TYPE		AREA (ha)	% ⁽¹⁾	% ⁽²⁾
Forest	<i>Araucaria araucana</i>	270	10.4	5.2
	<i>Nothofagus pumilio</i>	842	32.6	16.4
	<i>Araucaria araucana</i> and <i>Nothofagus pumilio</i>	221	8.5	4.3
	<i>Austrocedrus chilensis</i>	60	2.3	1.2
Subtotal		1,393	53.9	27.1
Shrubland	<i>Nothofagus pumilio</i>	629	24.3	12.2
	<i>Nothofagus antarctica</i>	563	21.8	10.9
	Subtotal	1,192	46.1	23.2
TOTAL		2,585	100	50.3

Table 4: Structure, use and conservation status of natural forest types in Chiuquilihuín Mapuche community (excluded *A. chilensis* forest).

PARAMETER	INTENSITY	<i>Araucaria araucana</i>		<i>Araucaria araucana</i> and <i>Nothofagus pumilio</i>		<i>Nothofagus pumilio</i>		TOTAL	
		ha	%	ha	%	ha	%	ha	%
Canopy cover	Low	23	8.5	26	11.9	101	12.0	150	11.3
	Medium	39	14.4	120	54.5	588	69.8	747	56.0
	High	208	77.1	74	33.6	153	18.2	436	32.7
Erosion	Present	179	66.3	147	66.5	553	65.7	880	66.0
Grazing	Present	250	92.5	221	100	772	91.7	1,243	93.3
Regeneration	Inadequate	0	0	0	0	362	43.0	362	27.1
	Medium	0	0	81	36.7	317	37.7	398	29.9
	Adequate	270	100	140	63.3	163	19.4	573	43.0
Timber extraction	Negligible	119	44.0	155	70.0	639	76.0	914	69.0
	Moderate	75	27.8	25	11.4	184	21.9	284	21.3
	Intense	76	28.0	41	18.6	19	2.2	135	10.1
Conservation status	Unsatisfactory	80	29.5	0	0	92	10.9	172	12.9
	Intermediate	97	35.9	148	66.9	265	31.5	510	38.3
	Satisfactory	93	34.6	73	33.1	485	57.7	651	48.8
TOTAL		270	100	221	100	842	100	1,333	100

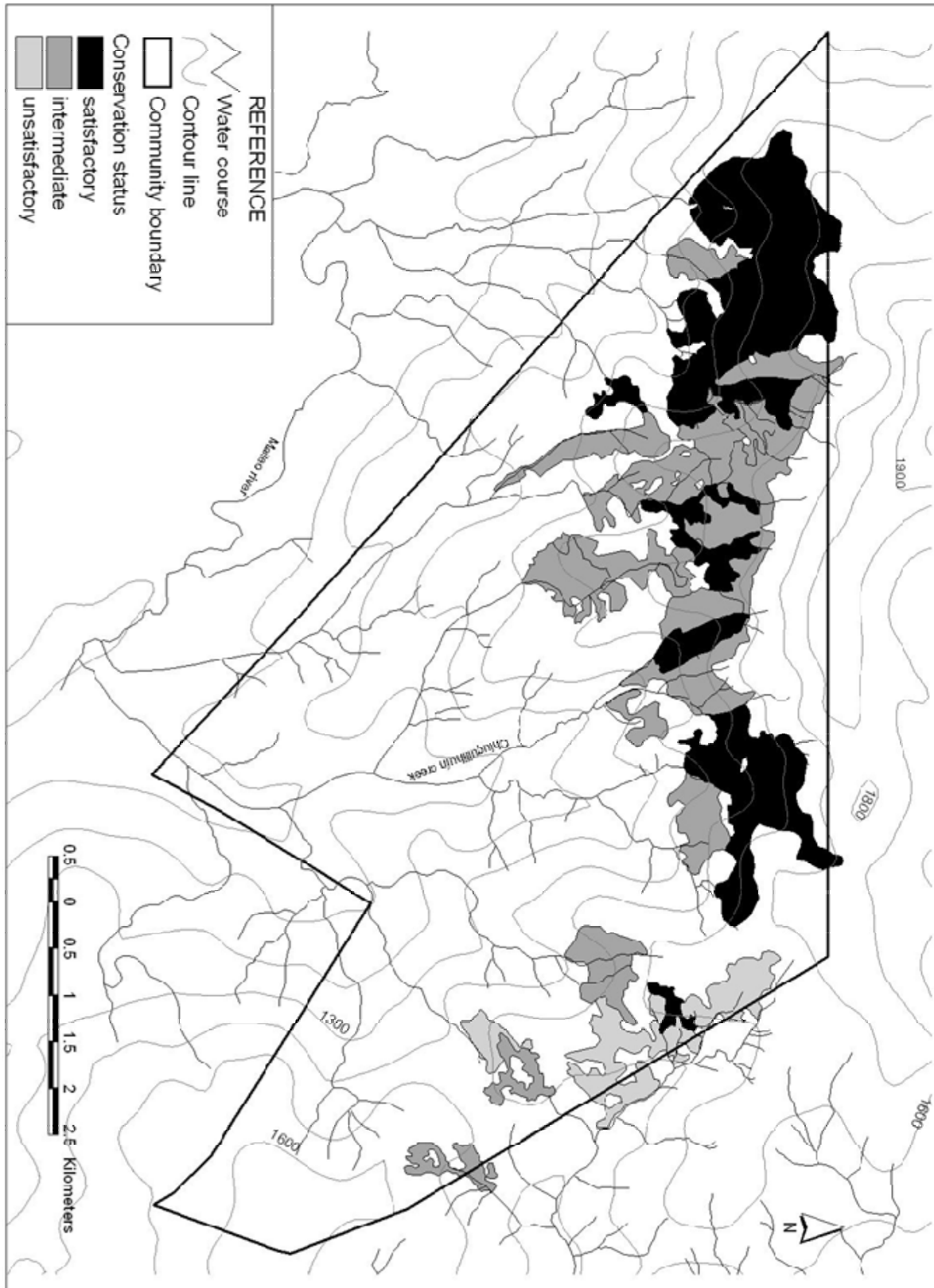


Figure 7: Map of Chiuquihuín Mapuche community indicating the conservation status of natural forests.

CONCLUSIONS

Long-term preservation of values, goods and services associated with *A. araucana*, and to which the Chiuquilihuín Mapuche community is historically linked for cultural and economic motivations, depends on maintenance of components and processes of forest ecosystem in general and those involving *N. pumilio* in particular. The poor condition of *N. pumilio* regeneration and attributable to anthropogenic causes, is a key indicator of unsustainable practises. Although seedlings and saplings are the most fragile phases of life cycle of every tree species, they sustain forest continuity in time and space and therefore represent an indicator of conservative management. Conservation actions, as land-use planning, productive diversification, environmental training, grazing restrictions and stocking reduction, enclosure and tree planting and agroforestry, should be implemented promptly in Chiuquilihuín. During this conservation planning process, a respectful interaction between traditional and western knowledge is required and a major role to local people must be assigned. The information presented in this study can contribute to this purpose.

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