



Original article

Litter and soil properties are not altered by invasive deer browsing in forests of NW Patagonia

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ABSTRACT

It is largely accepted that large mammalian herbivores can indirectly influence ecosystem properties by changing the quantity and quality of litter inputs to soil through selective browsing on plant communities. However, idiosyncratic effects (positive, neutral and negative) have been found for different vegetation types, herbivory and soil properties. In this study we tested whether browsing by exotic deer introduced into Patagonian forests 90 years ago alters physical, chemical and biological soil properties and litter quantity and quality. As in many terrestrial ecosystems, N is the main nutrient that limits plant growth in Patagonia. Consequently, any disturbance that alters the N cycle, such as changes in the type or intensity of herbivory, is expected to affect these forest ecosystems. We compared soil and total litter from inside and outside five 7-yr old exclosures located on Isla Victoria, Parque Nacional Nahuel Huapi, Argentina. Despite introduced deer has significantly affected the composition, abundance and structure of the understory vegetation, we found no differences between browsed and unbrowsed areas in the physical (bulk density, moisture), chemical (pH, base cations, organic C and total N) and biological (potential microbial respiration and net N mineralization) soil properties. This could be attributable to the high capacity of volcanic soils to stabilize organic matter, buffering disturbance-induced changes. However, the quantity and quality (C, N and C/N ratio) of total litter were also not different between browsed and unbrowsed areas. Although non-significant differences were found between treatments in both compartments, litter and soil, most variables showed a slight trend toward higher values in unbrowsed areas. This suggests that 7 years of browsing exclusion would be not enough to detect changes induced by browsing, particularly in highly stable volcanic soils.

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1. Introduction

Ungulate herbivores are considered important regulators of nutrient cycling. By selectively browsing on plant communities they alter plant species composition and, consequently, the quantity and quality of litter (Ritchie et al., 1998; Wardle et al., 2002; Singer and Schoenecker, 2003; Harrison and Bardgett, 2004; Carline and Bardgett, 2005; Pastor et al., 2006). Indirect effects of ungulate herbivores are also commonly associated with changes in the physical properties of soil, especially a reduction in water and oxygen availability caused by compaction, which can affect rates of organic matter decomposition and nutrient cycling independently of litter quantity and quality (Powers et al., 2005; Gass and Binkley, 2011).

Although the effects of large mammals on nutrient cycles, especially nitrogen, are accepted worldwide, idiosyncratic results (positive, neutral and negative) were found for different vegetation types, species composition, soil properties and grazing intensities (Binkley et al., 2003). It is generally accepted that deer overabundance, or its introduction into a new habitat, can have strong effects on the abundance, structure and composition of the forest understory (Bellingham and Lee, 2006; Bailey et al., 2007; Dolman and Wäber, 2008; Martin et al., 2010). For example, the introduction of Sika deer (*Cervus nippon*) in New Zealand has significantly prevented the recruitment of *Nothofagus solandri* seedlings (a species that is highly preferred by deer; Husheer et al., 2006), while the introduction of black-tailed deer (*Odocoileus hemionus*) into Haida Gwaii (Canada) has caused a dramatic reduction in plant cover and species richness (Stockton et al., 2005).

Similar results have been found in Patagonian forests (Veblen et al., 1989; Relva et al., 2010) where exotic deer, mainly red deer (*Cervus elaphus*), introduced at the beginning of the 20th century for sport hunting purposes, became invasive and currently inhabit

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forests, steppe, wet meadows and riparian habitats. Fallow deer (*Dama dama*) were also introduced for hunting purposes but remain low in number (Flueck, 2010). However, belowground effects of introduced deer in this region are unknown.

Monospecific forests of conifers (*Austrocedrus chilensis*, *Fitzroya cupressoides* and *Araucaria araucana*), broad-leaved evergreens (*Nothofagus dombeyi*, *Lomatia hirsuta* and *Maytenus boaria*) and broad-leaved deciduous species (*Nothofagus pumilio*, *Nothofagus antarctica*, *Nothofagus nervosa* and *Nothofagus obliqua*) occupy a narrow strip in western Argentinean Patagonia associated with soils formed from volcanic materials, and located along a west–east decreasing precipitation gradient. These soils are characterized by a low degree of development, due to the frequent deposition of volcanic ash from Chilean volcanoes by the prevalent western winds (Broquen et al., 2005; Gaitán and López, 2007; Satti et al., 2007). Since these soils are very young and nitrogen deposition in South American temperate forests is remarkably low (Holland et al., 1999), vegetation is limited mainly by nitrogen (Perez et al., 1998; Diehl et al., 2008). Therefore, any change in the N cycling induced by disturbance is expected to have profound effects on these forest ecosystems.

In this work, we tested the hypothesis that heavy browsing by introduced deer (red and fallow deer) in northern Patagonian forests alters physical, chemical and biological soil properties as well as plant litter quantity and quality. We predicted that higher compaction and lower litter quantity in browsed areas would result in lower soil organic C, lower N concentrations in soil and litter, and slower rates of potential soil respiration and net N mineralization. To test these predictions we compared soil and total litter samples from five paired browsed and unbrowsed areas (with 7 years of deer exclusion) in a temperate forest in NW Patagonia.

2. Materials and methods

2.1. Study site

The study was conducted in Isla Victoria, an island of 3710 ha in Lago Nahuel Huapi, Parque Nacional Nahuel Huapi, Argentina (40°57'S; 71°33'W). Isla Victoria extends NW to SE and has varied topography including flat, shallow valleys and elevations up to 1025 m a.s.l. Mean annual precipitation is 1700 mm (Barros et al., 1983), mostly occurring in autumn and winter (March to September) in the form of rain and snow. Most soils are deep, well drained Andisols of sandy loam texture, classified mainly as Hapludands according to U.S. Soil Taxonomy (Ayasa et al., 2002; Gaitán and López, 2007). Isla Victoria is covered by pure southern beech *N. dombeyi* forests, pure *Austrocedrus chilensis* forests and mixed *N. dombeyi* – *A. chilensis* forests as dominant tree species, with several subdominant tree species (*Luma apiculata*, *M. boaria*, *L. hirsuta*) and dense understory vegetation composed of shrubs (*Aristotelia chilensis*, *Berberis heterophylla*, *Maytenus chubutensis*, *Ribes magellanicum* and *Schinus patagonicus*) which reach an average height of 0.50 m (Relva, unpublished). The herbaceous layer includes native species such as *Uncinia* sp. and exotics such as *Digitalis purpurea* and *Cynoglossum creticum*. Structurally, the forests on Isla Victoria have a mean basal area ranging from 43 (shrublands) to 90 m²/ha (*N. dombeyi* and *A. chilensis* forests), and a mean adult tree density ranging from 5755 (*N. dombeyi* forest) to 19,000 individuals/ha (*A. chilensis* forest) (Barrios García et al., 2012a).

The main large mammalian herbivores on the island are Red deer (*C. elaphus*) and fallow deer (*D. dama*), which were introduced between 1917 and 1922. Native deer have become very rare (*Pudu puda*, pudu) on the island, or extinct in the case of *Hippocamelus bisulcus* (huemul). At present, the mean density of introduced deer, estimated through the dung clearance plot method, is 32

individuals per km² (Relva, unpublished data). Even though Isla Victoria belongs to the National Park Administration, no culling program is being carried out to reduce the exotic deer population, so their abundance is very high. This density is elevated compared to densities in other forests in the region; for example, in *N. pumilio* and *N. antarctica* forests mean density estimates are 4 and 2–9 individuals per km², respectively (Ferreyra and Sanguinetti, 2010). In addition, wild boar arrived to the island ca. 1999, presumably by swimming, and currently occurs in all plant communities (Barrios García, unpublished data).

2.2. Experimental design

In 2002 five paired exclosures and control areas were established in a 1000 × 1000 m area of *A. chilensis* forest to determine the effects of exotic deer on different plant community traits (further details are given in Relva et al., 2010). Exclosures are 20 × 20 m in size and 2 m high, and are constructed of wire mesh with apertures to allow access for rodents. Control areas, where introduced deer browse freely, were placed adjacent to the exclosures. As introduced deer have been present on the island for ca. 90 years, the response of the vegetation is more a case of recovery as a result of deer exclusion than a return to the pristine situation which existed when deer were absent on the island. Regular monitoring of the exclosure and control areas indicated that exotic deer was the dominant ungulate in the area up to the time of soil sampling. Rooting signs and faeces of wild boar were rarely observed in the area. In addition, recent data (Barrios García et al., 2012b) from forests and shrublands on Isla Victoria indicate no effects of wild boar on physical, chemical and biological soil properties after 4 yr exclusion.

2.3. Soil and litter analyses

Soil and litter were sampled in May 2009 (mid-autumn in the Southern Hemisphere). Each soil sample consisted of composite samples of 10 subsamples taken randomly at 0–15 cm depth along a transect within each control and exclosure ($n = 5$). Soil bulk density was measured in the topsoil (0–10 cm) by the core method and soil moisture was determined gravimetrically by oven drying the samples at 105 °C during 72 h (Dane and Topp, 2002). Air-dried soil ground to pass through 2-mm mesh was used to analyze pH, extractable P and exchangeable base cations (Ca, Mg and K). Organic C and total N were analyzed in samples ground to pass through a 0.5-mm mesh. The following analyses were carried out according to Sparks et al. (1996): pH in water (1:2.5), pH in 1M KCl (1:2.5), P extracted in 0.5 M NaHCO₃ by the molybdate ascorbic acid method, exchangeable cations in 1M NH₄OAc extracts by atomic absorption spectrometry, and total C and N by elemental analysis (Flash EA112 Elemental Analyzer, ThermoFinnigan). To confirm the acidic properties of the soil, pH was also measured in 1:50 1 M NaF solution (Fieldes and Perrot, 1966).

Biological soil properties were evaluated in field-moist soils sieved through a 2 mm mesh and maintained at 36% soil moisture (approximately field capacity). Potential microbial respiration (pResp) and potential net N mineralization (pNmin) were measured as indicators of substrate quality, i.e., the fractions of soil C and N easily available for heterotrophic microorganisms and nitrifiers. pNmin was estimated in 16-week incubations of 100-g samples (in 0.25-L plastic jars) at field capacity and 25 °C without light (Kowaljow and Mazzarino, 2007; Satti et al., 2007). On six sampling dates (0, 10, 28, 56, 84 and 112 days) three replicates were extracted, jars were left open for approximately 1 h and soil moisture was gravimetrically adjusted. At each time, samples were extracted with 2 M KCl (1:5, soil: solution ratio) and NO₃⁻-N and NH₄⁺-N were

Table 1Physical and chemical soil properties in browsed and unbrowsed sites. Values are means of $n = 5$ (\pm SD). Results of a paired sample t -test are given (t , P).

	SOC ^a %	TN ^b %	pH in water	pH in KCl	pH in NaF ^e	Extr. P ^c mg kg ⁻¹	Ca	Mg	K	Moisture %	B.D ^d kg dm ⁻³
							cmol kg ⁻¹				
Browsed	9.03 (1.06)	0.46 (0.04)	6.30 (0.15)	5.70 (0.10)	9.80 (0.24)	2.30 (0.78)	19.50 (2.50)	2.40 (0.50)	0.50 (0.10)	36.20 (4.30)	0.50 (0.03)
Unbrowsed	9.51 (1.96)	0.53 (0.16)	6.40 (0.05)	5.80 (0.06)	9.50 (0.14)	2.80 (1.27)	23.30 (3.00)	2.70 (0.40)	0.50 (0.04)	35.70 (4.90)	0.48 (0.04)
t	0.41	1.02	1.48	1.37		1.02	1.58	0.88	0.53	0.37	0.64
P	0.70	0.37	0.21	0.24		0.37	0.19	0.43	0.62	0.72	0.56

^a SOC: organic C.^b TN: total N.^c Extr. P: extractable P.^d B.D. bulk density.^e pH in NaF is a qualitative indicator, values are not statistically comparable.

determined in the extracts by copperized Cd reduction and the Berthelot reaction, respectively (Keeney and Nelson, 1982). pNmin was calculated as the inorganic N (NO_3^- -N + NH_4^+ -N) for each sampling date minus the initial concentration at t_0 . pResp was evaluated by determining the CO_2 evolved during 16 weeks in 1.5-L glass jars containing 75 g soil samples incubated at 25 °C in the dark (Kowaljow and Mazzarino, 2007). The CO_2 was trapped in 20 mL of 0.5 M NaOH in glass vials placed in each jar. Vials were replaced and analyzed on 6 dates. As for N mineralization, at each date, jars were left open for 1 h, and soil moisture adjusted to field capacity. Potential microbial respiration was estimated as the cumulative CO_2 evolution during the incubation period.

Total litter was collected from the ground in 5 randomly selected quadrats (0.25 m²) within each enclosure and control area, stored in paper bags, and weighed after drying at 60 °C for 72 h (all foliar litter components and woody litter components <1.0 cm wide were considered). Composite samples of the 5 quadrats per sampled area were ground to powder and analyzed for C and N employing the elemental analyzer mentioned above.

A paired-sample t -test was conducted to compare litter and soil properties of browsed and unbrowsed areas. In the case of pNmin and pResp only the last incubation date (day 112) was analyzed (Satti et al., 2007). The null hypothesis was rejected at $P < 0.05$.

3. Results and discussion

Previous results from the same sites indicated that introduced deer significantly affect the abundance and composition of native understory vegetation, favoring the dominance of less browsed species such as *B. heterophylla* and *S. patagonicus*, and reducing highly browsed species such as *Aristotelia chilensis* and *R. magellanicum* (Relva et al., 2010). Exotic deer also have a detrimental effect on the growth in height of saplings of the native dominant tree *Austrocedrus chilensis* (a 77% decrease) after 4 yr exclusion (Relva et al., 2010). However, in the present work no differences in the

physical and chemical properties of the soil were found between browsed and unbrowsed areas (Table 1). Mean values of pH in NaF varied between 9.5 and 9.8, confirming the acidic nature of the soils (in many regions, including ours, values higher than 9.2–9.4 indicate the presence of active Al, one of the main properties of Andisols; see Fieldes and Perrot, 1966; Broquen et al., 2005). This was also confirmed by high concentrations of organic C and total N, bulk density lower than 0.9 kg dm⁻³, and very low values of carbonate-extractable P suggesting high phosphate retention (Shoji et al., 1993). Andisols are characterized by variable charge (i.e., mineral colloids can be negatively or positively charged depending on the soil solution pH). In this work, the actual soil pH (pH in water) was slightly acidic and higher than potential pH (pH in KCl) by 0.6 units, which indicates the prevalence of negative charge and cation exchange capacity. Values of exchangeable Ca were relatively high (around 20 cmol kg⁻¹) as in other Hapludands of the region (Broquen et al., 2005).

Biological properties are usually considered to be more sensitive than chemical ones in the detection of changes induced by ecosystem disturbance (Hart et al., 1994). It has been suggested that rates of N mineralization are particularly sensitive to large mammal browsing, although reported results are contradictory, indicating a slight increase (Carline and Bardgett, 2005), negative effects (Ritchie et al., 1998; Singer and Schoenecker, 2003) or no changes (Harrison and Bardgett, 2004). In our case, there was no difference in indicators of microbial activity between control and enclosure soils (Figs. 1 and 2), neither for potential N mineralization ($t = 2.04$, $P = 0.11$) nor for microbial respiration rates ($t = 0.46$, $P = 0.67$). Besides, rates of potential N mineralization lay within the typical values of other *Austrocedrus chilensis* forests in the region (Buamscha et al., 1998; Satti et al., 2007), which are less affected by deer, or not affected at all. This could be due to the high capacity of volcanic soils to stabilize organic matter, which contributes to the regulation of water dynamics and the buffering of chemical and biological changes, minimizing nutrient losses after disturbance

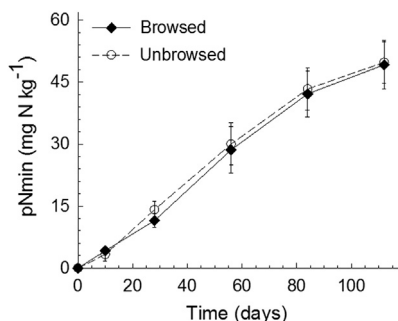


Fig. 1. Potential net N mineralization (pNmin) of browsed and unbrowsed soils in 16-week incubations under controlled conditions of moisture and temperature.

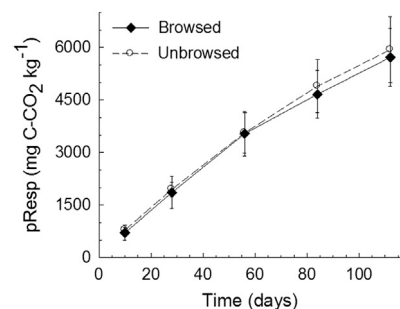


Fig. 2. Potential microbial respiration (pResp) of browsed and unbrowsed soils in 16-week incubations under controlled conditions of moisture and temperature.

Table 2
Comparison of the effects of native and introduced deer on soil properties in several temperate forests.

Source	Location	Herbivore type	Vegetation type	Soil type	Sampling depth (cm)	Soil changes	General trend	Method	Number replicates	Study length (yr)
Stritar et al., 2010	Arizona, USA	Introduced elk	Broad-leaved deciduous forest	Mollisols, Alfisols	0–15	<SOC ^a , TN ^b , N-MB ^c	Mostly negative	Exclosures	6	6–20
Harrison and Bardgett, 2004	Scotland, UK	Native deer	Broad-leaved deciduous forest	Podisols	0–10	<DOC ^d , NO ₃ ⁻ , NH ₄ ⁺ , Nmin ^e , >C/N in MB	Negative	Exclosures	4	14
Binkley et al., 2003	Colorado, USA	Native elk reintrod.	Broad-leaved deciduous forest	Not available	0–15 and 15–30	>Bulk dens., >pH, no changes in SOC and TN	Little	Exclosures	1	35
Ritchie et al., 1998	Minnesota, USA	Native deer	Broad-leaved deciduous woodland	Sandy, N-poor soils	0–20	No changes in C and TN in soil and plant, <N availability	Little	Exclosures	5	7
Mohr et al., 2005	Cologne, Germany	Native deer	Broad-leaved deciduous forest	Shallow, acid soil	0–5	>SOC, TN, microbial activity	Positive	Exclosures	4	2
Mohr and Topp, 2005	Idem	Idem	Idem	Idem	Idem	<SOC, TN, Ca, avail. P in steep slopes, very acid soils	Negative in worse sites	Exclosures	4	~10
Kumbasli et al., 2010	Istanbul, Turkey	Native deer, reintrod.	Broad-leaved deciduous forest	Alfisol	0–5	<Litter quantity, SOC, pH; >compaction	Negative	A deer breeding area vs. a control	1	40
Carline and Bardgett, 2005	Northern Britain	Simulated browsing	Broad-leaved deciduous forests	Acid Alfisol	Not available	No changes in most biological prop. (Enzymes, N and C-MB ^f); Nmin slightly>	Little	Mesocosm	4	2
Gass and Binkley, 2011	Rocky Mtn., USA	Native elk reintrod.	Broad-leaved deciduous and riparian trees	Inceptisol	0–15	> Bulk density, <soil moisture, SOC and TN	Negative	Exclosures	12	15
St. John et al., 2011	New Zealand	Exotic deer	Conifer-hardwood forests	Andic and crystalline soils	0–30	No changes in total ecosystem C, including 30 cm soil	No changes	Exclosures	Nation-wide network	20–60
This study	NW Patagonia, Argentina	Exotic deer	Evergreen conifer forest	Andic	0–15	No changes in physical, chem. and biological soil properties	No changes	Exclosures	5	7

^a SOC: organic carbon.

^b TN: total N.

^c N-MB: N retained in microbial biomass.

^d DOC: dissolved organic C.

^e Nmin: N mineralization rate.

^f C-MB: C retained in microbial biomass.

(Sollins et al., 1984; Ewel et al., 1991; Shoji et al., 1993). In volcanic soils, organic matter content is much higher and decomposition and mineralization rates lower than in crystalline soils due to the high physical and chemical protection of organic matter from microbial attack, as well as sorption of degradation enzymes, P deficiency induced by high P retention, and/or water saturation of very fine aggregates (Martin and Haider, 1986; Ugolini and Dahlgren, 2002; Buurman et al., 2007). Thus, disturbance effects by deer browsing may be expected to be less marked than in other temperate forests on crystalline soils.

A comparison of soil changes induced by ungulate herbivores in different temperate forests is offered in Table 2. Almost all soils in these examples are dominated by crystalline minerals and, in general, a trend toward negative or little effect prevails. Although most negative results were related to longer-term studies, it is worth pointing out that results from a wide network of exclosures in New Zealand established 20–60 yr ago indicate no changes in C storage in soil and vegetation. This was attributed to the fact that deer impact small pools of C, mainly understory vegetation (St. John et al., 2011). Positive deer effects were observed in only one study and this was explained by the deposition of faeces and urine in very shallow soils (Mohr et al., 2005). In our case, the lack of differences between soil properties of browsed and unbrowsed sites may be due to the high stabilization of volcanic soils, as already mentioned, but also to the short time of the study. As introduced deer have been present on the island for ca. 90 yr, the length of the study period (7 yr) was possibly insufficient for the detection of differences between treatments. Soil sampling depth could also be a significant factor, with effects possibly being more evident in shallower samples (see Table 2 for examples of soil sampling depths).

To test whether browsing could be affecting litter quantity and quality, we measured and analyzed total litter. Although we observed a trend toward higher litter quantity and quality (higher N, lower C/N) in unbrowsed areas (Table 3), differences were not significant or they were marginally significant. This could imply no effect on the quantity and quality of litter produced at the site. However, visual observations as well as plant abundance and composition measurements (Relva et al., 2010) suggest that this lack of difference could be due to the rapid decomposition of the foliar litter of several highly palatable species that only occurs within the exclosures. To evaluate this possibility the collection of litter fall throughout the year and the measurement of litter decomposition in the field would be necessary. We cannot discard, however, a possible effect of the low number of replicates, since in the case of N in litter values were close to significance at the 5% level (Table 3).

In conclusion, no effects of introduced deer on soil and litter were evident in this forest ecosystem after 7 years of exclusion. Different explanations are possible, ranging from the length of measurement period to the high capacity of volcanic soils to buffer disturbance-induced changes. It is also possible that alteration of understory vegetation is not enough to induce changes at the belowground level, as suggested recently by St. John et al. (2011) for New Zealand forest ecosystems quite similar to ours.

Table 3

Total litter quantity and quality in browsed and unbrowsed sites. Values are means of $n = 5$ (\pm SD). No significant differences were found between treatments for any of the variables ($P < 0.05$). Results of a paired sample t -test are given (t , P).

	Dry matter g m^{-2}	C %	N %	C/N
Browsed	417.1 (103.3)	45.0 (1.2)	0.99 (0.17)	46.4 (8.8)
Unbrowsed	692.7 (263.9)	46.5 (1.9)	1.20 (0.23)	41.9 (10.2)
t	1.78	1.32	2.52	1.37
P	0.15	0.26	0.06	0.24

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