Differential forage use between large native and domestic herbivores in Southern Patagonian *Nothofagus* forests

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Abstract Plant—animal interactions at the land-scape level become particularly relevant when land use is diversified. *Nothofagus* forests in southern Patagonia have been used for timber and cattle grazing purposes during the last century, causing livestock to increase (*Bos taurus* and *Ovis aries*) and large native herbivores, such as guanaco (*Lama guanicoe*), either maintained or decreased their populations. Within this scenario, feeding interactions between guanaco and domestic herbivores were analysed in a mosaic of open habitats and different *Nothofagus* forest types and management histories, whereby a total of six habitat types were identified through satellite image analysis. A total of 205 floristic surveys were conducted to characterize the plant species composition at the landscape level. Diet composition of herbivores was assessed once each season during a year, using microhistological analysis of feces. Results showed higher plant richness in open lands and lower in closed, unmanaged forests. Overall, 43 plant taxa were detected in herbivore feces, which represent 56% of plant richness detected in the field. Both guanacos and domestic herbivores included mainly grasses in their diet, which were found predominantly in open lands. Tree seedlings and saplings were consumed by all herbivores, as well, except during winter. Differential forage use between guanaco and domestic herbivores in southern Patagonian *Nothofagus* forests did exist. However, competition for available resources among theses herbivores resulted in an alternation of feeding sites, which varied throughout the year. Management plans in southern Southern Patagonia (livestock, silvopastoral plans and timber harvesting) do not consider the direct or indirect consequences on guanaco populations. The challenge, therefore, is to generate management decisions to avoid either guanacos or domestic herbivores from becoming detrimental to the sustainability of managed forested ecosystems.

Keywords Browsing · Fecal micro-histological analysis · Forest management · Landscape analysis · Plant life forms

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Abbreviations
NAF	*Nothofagus antarctica* forests
NPF	*N. pumilio* forests
OHF	Old harvested *N. pumilio* forests
PUF	Primary unmanaged *N. pumilio* forests
RHF	Recently harvested *N. pumilio* forests

Introduction

In southern Patagonia, forested landscapes are mosaics of different vegetation types. *Nothofagus* forests are rarely large continuous patches, and usually they are mixed with open lands (grasslands and peatlands) (Lencinas et al. 2008). These landscapes are largely impacted by invasive species (e.g., *Castor canadensis*, Anderson et al. 2009) and by human economic activities, mainly by harvesting and livestock grazing (Martínez Pastur et al. 2002). Timber harvesting impacts on forest structure include decreasing canopy cover and modifying microclimate conditions such as temperature, solar radiation and soil moisture at the understory level (Frangi and Richter 1994; Promis et al. 2010). Consequently, large changes occur in native biodiversity (Spagarino et al. 2001; Deferrari et al. 2001; Ducid et al. 2005; Lencinas et al. 2008, 2009, 2011), including plant understory communities, whose richness and biomass greatly increase (Martínez Pastur et al. 2002; Lencinas et al. 2008, 2011). For their part, local ranching activities base their economy on raising domestic herbivores, mainly cattle (*Bos taurus*) and sheep (*Ovis aries*). Animals usually are free-ranging and feeding in open habitat types such as grass and shrublands, as well as *Nothofagus* forests. On the other hand, native populations of guanacos (*Lama guanicoe*), a large herbivore camelid, are a natural component of austral Patagonian forests (Bonino and Fernandez 1994; Pulido et al. 2000), inhabiting Tierra del Fuego for more than 8000 years (Raedeke 1978).

It is known that herbivores play a central role in ecosystem function, whereby large herbivores can produce important floristic and structural changes at the landscape level, and influence plant productivity and species diversity (Skarpe and Hester 2007). Additionally, herbivory also affects a forest's natural regeneration, which is a necessary component for successful forest management in *Nothofagus* forests. Yet, management of herbivory has not traditionally been considered in southern Patagonia, where large wild populations of guanacos have recovered since hunting was banned in the 1990s. Furthermore, the movement and impacts of livestock traditionally do not depend on ranching management decisions (time and space), since the animals usually are free-ranging in large landscape patches in southern Patagonia.

Within this scenario, competition is expected to result in a change of the use patterns of available resources in the presence of the domestic species (Schoener 1974; Belovsky 1984) and natural populations of guanacos (Raedeke 1978; Montes et al. 2000; Baldi et al. 2001). To predict impacts generated by sympatric ungulates on vegetation in multiple use lands requires the knowledge of how species exploit available resources (McInnis and Vavra 1987). The objective of this work was to determine if differential foraging exists between native and domestic large herbivores in a Southern Patagonian *Nothofagus* forested landscape, analyzing both diet composition along seasons and plant species composition at the landscape level. Tested hypotheses were: (i) plant species diversity (richness and cover) changes in different vegetation types, where open lands offer more food availability for large herbivores, and harvested forests more than unmanaged primary ones (ii) herbivore foraging patterns vary along seasons, and forage selectivity exists among different plant life forms, and (iii) diet overlap between guanacos and domestic herbivores exists, and a differential use of feeding sites along seasons was expected.

Methods

Study site

The study was conducted in a 100 km^2 area within the Argentina portion of central Tierra del Fuego Island (54°20′ SL, 67°52′ WL). Climate is characterized by short, cool summers and long, snowy and frozen winters. Only three months per year were free of mean daily air temperatures under 0°C, and the growing season was approximately five months. Rainfall, including snowfall, reached up to 600 mm year. Annual average wind speed outside forests was 8 km h^{-1}, reaching up to 100 km h^{-1} during storms (Martínez Pastur et al. 2009). The study area lay within 3,500 ha of private land, previously classified with high definition satellite images (Quickbird, March 2008) and verified in the field during a vegetation census. Open lands occupied 28.5% of the area (grasslands 24.9% and peatlands 3.6%) and *Nothofagus* forests occupied 71.3%, where *N. antarctica* forests have 19.4% and *N. pumilio* forests have 51.9%. These forests were classified as

primary unmanaged (29.5%), recently harvested (1–5 years since cuttings) (9.4%) and old harvested (>5 years since cuttings) (13.0%). Finally, lakes and natural ponds occupied a small portion (0.2%) of the area. Recent harvested forests had been logged using a variable retention method (Martínez Pastur et al. 2009, 2011), which included non-harvested aggregated retention areas (30% of the stand area) and harvested areas with 10–15 m^2 ha^{-1} basal area as dispersed retention (70% of the stand area). Old harvestings had been accomplished through selective cuts (40–60% of canopy cover removal). Livestock density in the study area was approximately 14 individuals km^{-2} (8 ind km^{-2} for cattle and 6 ind km^{-2} for sheep). These domestic animals usually range freely, mainly in grasslands from summer to autumn, but they also use *Nothofagus* forests during winter to spring. On the other hand, Montes et al. (2000) estimated a density of 2 ind km^{-2} of guanacos in the study area. During the pre-breeding season (October–November) these native camelids prefer open areas (e.g., forest-steppe area), but during winter they also seek shelter in areas associated with forests (Montes et al. 2000).

Vegetation characterization

Floristic surveys were conducted in the study area during two summer seasons (December—February 2007 and 2008). Six habitat types were defined based on the classification described above and taking into account management schemes applied in the study area: (i) open lands (OL), defined as grasslands and peatlands; (ii) *Nothofagus antarctica* forests (NAF), mainly mature stands of medium–high site quality with 75 ± 12% canopy cover, and used for silvopastoral purposes; and (iii) *N. pumilio* forests (NPF), mainly mature stands with variable canopy cover depending on management history. These last forests were also classified as: (iv) primary unmanaged forests (PUF), mainly stands of medium–high site quality with 88 ± 11% canopy cover, and used for conservation and future timber purposes, (v) recently harvested forests (RHF) with 52 ± 10% remnant canopy cover, and (vi) old harvested forests (OHF) with 43 ± 12% remnant canopy cover.

A total of 206 vegetation surveys were conducted in these habitat types according to their spatial heterogeneity and relative abundance in the study area, which resulted in unequal number of replicates (OL = 30, NAF = 70, PUF = 26, RHF = 48, OHF = 32). Surveys were randomly distributed along habitats using circular plots of 50 m radius (0.78 ha). The Braun Blanquet (1979) sampling method was applied and following Pauchard et al. (2000) for estimations of vegetation cover. Vascular plants (dicots, monocots and ferns) were taxonomically classified by species and origin (native or exotic), based on Moore (1983) and Correa (1969–1998). Understory plant species were also grouped according to their life form as: tree seedlings and saplings (trees less than 1 m height), shrubs, erect herbs, prostrate herbs, caespitose grasses and rhizomatous grasses. Beside this, each species was classified, according its relative abundance, as common (more than 0.02% cover in average for the entire survey) or rare (less than 0.02% cover).

Analysis of feces

Feces of guanaco and domestic herbivores (cattle and sheep) were collected during four seasons (spring, summer, autumn and winter). Four areas in the study site, considered as currently used latrines, were selected for sampling within each different vegetation type. A sampling unit was a mixed group of fresh feces from five dung piles (Hansen and Lucich 1978) (n = 4 per season per herbivore species). Pooled samples were oven dried at 60°C for 48 h, grounded to < 1 mm in a Cole-Parmer analytical mill (USA), depigmented with alcohol 70°, colored with safranina, and mounted on five microscope slides of 24 × 40 mm in glycerine jelly (Williams 1969; Latour and Pelliza Sbriller 1981). Botanical composition found in feces was determined by identifying plant epidermal (Sparks and Malechek 1968) and non-epidermal fragments (Sepúlveda et al. 2004), according to a micro-histological analysis method. Twenty random field observations per slide were performed: thus, a total of 100 fields per pool sample were obtained. Quantification of species components of the diets was achieved through frequencies of each species, following Holechek and Gross (1982). Plant epidermal fragments were identified using 100x magnification at genus or species level, and grouped into different life form categories. In this analysis, two new categories were was also included: mosses and hemiparasitic shrubs (*Misodendrum* sp.). When only genus level

was determined in the feces, we considered for data analysis that all the species of each specific genus found in the vegetation census can potentially be consumed by herbivores. *Nothofagus pumilio* and *N. antarctica* samples were separated through stoma distribution patterns in the epidermis, swelling of cuticle and trichomes (Ragonese 1981). However on many slides, some tree samples could be determined only at the genus level. In this case, these samples were re-assigned between both species (*N. pumilio* and *N. antarctica*), according to the proportion found in each slide for each tree species.

Statistical analysis

Differences in vegetation cover, as classified by life forms, were analyzed with one-way ANOVA with habitat type as factor, while two-way ANOVAs were performed to evaluate differences in plant life form frequencies in diet composition along seasons. Variables that did not fit a normal distribution were square root-transformed prior to statistical analyses. Means were separated with a post-hoc Tukey test ($P < 0.05$). Corrections were not made to consider the differential digestibility of plant species (Bonino and Pelliza Sbriller 1991).

Two sets of detrended correspondence analysis (DCA) were also done to analyze: (i) plant species assemblages in different habitats, using data from floristic surveys, and (ii) plant species relation with the three herbivores' diets using data from seasonal fecal composition.

Diet was characterized through three indexes. (i) Diet overlap based on plant species proportion found in feces was compared between herbivore pairs (guanaco vs. cattle, guanaco versus sheep, cattle versus sheep) using the Pianka (1973) Index, which varies from 0 (no overlap) to 1 (complete overlap of diets). (ii) Feeding selectivity on different life forms was determined using the Ivlev Index (Krebs 1989), which uses vegetation cover to estimate food availability. This index varies between −1 (strong avoidance) and 1 (strong selection). And (iii) habitat selection was defined as a weighted average between plant species proportion in diets and plant species cover in each habitat type, expressed as a percentage of the addition of all habitat type values. This index reflected the use of each environment according to the cover of plant species in the field.

Results

Vegetation cover

A total of 113 species of vascular plants were recorded during the floristic surveys, including 71 dicots, 39 monocots and 3 ferns. Plant richness (Table 3 in Appendix) greatly changed among studied vegetation types, where OL > NPF > NAF (83, 63 and 58 species, respectively). Only 3.5% of the species were shared among all the environment types, and most of the species occurred in only one habitat (44 in OL, 10 in NPF and 6 in NAF). Exotic species were found throughout the landscape (Fig. 1a). In the *Nothofagus pumilio* forests, plant richness also greatly changed in relation to the management history, where PUF < RHF < OHF (26, 44 and 60 species, respectively). A total of 9.5% of the species were shared among all the *N. pumilio* forests; however many species only occurred in harvested units (3 in RHF and 17 in OHF). Exotic species were exclusively found in harvested stands, being entirely absent from primary forests (Fig. 1b).

Significant differences were found when plant life form groups in each habitat type were analysed (Fig. 2a). Cover of shrubs ($F = 52.6$, $P < 0.001$), caespitose ($F = 27.8$, $P < 0.001$) and rhizomatous grasses ($F = 25.8$, $P < 0.001$) were higher in OL, while trees ($F = 38.7$, $P < 0.001$) were higher in NPF. Cover of erect ($F = 25.9$, $P < 0.001$) and prostrate herbs ($F = 90.5$, $P < 0.001$) were similar in both NAF and NPF, and significantly higher than in OL. However, when *N. pumilio* forests were independently analyzed, considering the management history (Fig. 2b), PUF showed higher cover of trees ($F = 27.5$, $P < 0.001$) than harvested stands (RHF and OHF). OHF showed significant increases of shrubs cover ($F = 5.3$, $P = 0.006$), caespitose ($F = 4.1$, $P = 0.019$) and rhizomatous grasses ($F = 17.2$, $P < 0.001$). Finally, erect ($F = 12.1$, $P < 0.001$) and prostrate herbs ($F = 47.4$, $P < 0.001$) were higher in both managed stands.

Seasonal diet composition

A total of 43 plant taxa were detected through feces analysis. Of these, 58% were identified at the species and 42% at the genus levels (Table 4 in Appendix). These plants included 56% of the total taxonomic
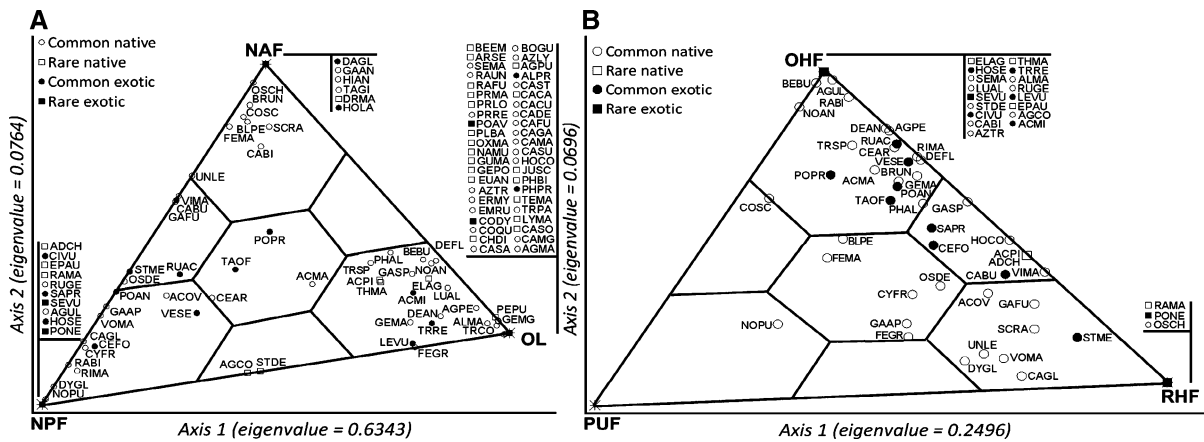
Fig. 1 DCA for the analysis of plant species distribution among (**a**) open lands (*OL*), *Nothofagus antarctica* (*NAF*), and *N. pumilio* (*NPF*) forests; and (**b**) primary unmanaged (*PUF*), recently harvested (*RHF*) and old harvested (*OHF*) *Nothofagus pumilio* forests. Codes for plant species are showed in Table 3 in Appendix
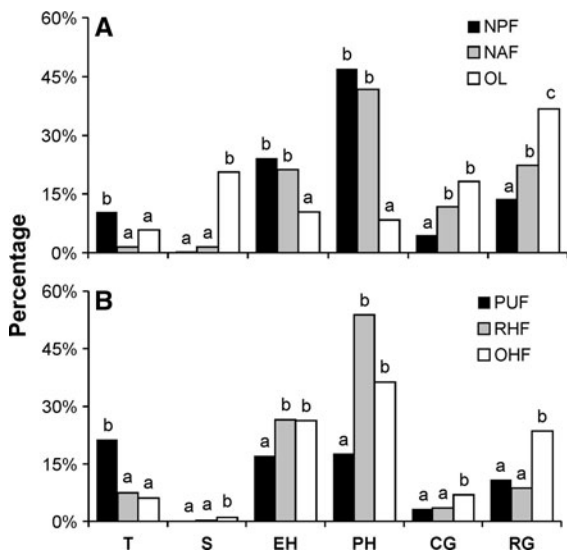

Fig. 2 Cover of understory plant species classified by life forms in (**a**) *Nothofagus pumilio* forests (*NPF*), *N. antarctica* forests (*NAF*) and open-lands (*OL*); (**b**) primary unmanaged (*PUF*), recently harvested (*RHF*) and old harvested (*OHF*) *N. pumilio* forests. *T* tree seedlings and saplings, *S* shrubs, *EH* erect herbs, *PH* prostrate herbs, *CG* caespitose grasses, *RG* rhizomatous grasses. Different letters indicate significant differences among treatments for each life form, using post-hoc Tukey test ($P < 0.05$)

It was possible to identify 38 plant taxa in guanaco feces (34% of the total landscape richness). *Nothofagus pumilio* (19.1%), *Carex* sp. (16.8%) and *Misodendrum* sp. (10.7%) were the most frequent plants found in feces all around the year. Meanwhile, 31 plant taxa (27% of landscape richness) were identified in cattle feces, where *Carex* sp. (29.3%), *N. pumilio* (10.1%) and *Festuca magellanica* (9.6%) were the most frequent plants found all year round. Finally, 43 plants were identified in sheep feces (38% of landscape richness), with *Carex* sp. (20.5%) and *Agrostis* sp. (10.0%) the most frequent plants all around the year.

ANOVAs showed that trees, shrubs, erect herbs and hemiparasitic shrubs were significantly more foraged by guanacos, than the other herbivores. Caespitose and rhizomatous grasses, and mosses were most grazed by cattle. Prostrate herbs did not present significant differences in all the herbivore diets. Sheep diet assumed intermediate values between guanacos and cattle (Table 1). However, the proportion of life form groups in the diets showed significant differences throughout the year (Table 1). Tree seedling and sapling consumption decreased during winter. Erect herbs and mosses were highly consumed during summer, while shrubs were highly browsed during spring and winter, and hemiparasitic shrubs were consumed twice as much during winter than in the other seasons. Only the prostrate herbs and grasses (caespitose and rhizomatous) were equally consumed during all seasons. Significant interactions were detected for frequency of trees, prostrate herbs

richness identified during the field vegetation surveys (species and genera). In contrast, three new taxa were found in feces in a low frequency (<0.6%), but were not found during field vegetation surveys (*Arjona* sp., *Senecio alloeophyllus* and *Erodium cicutarium*).

Table 1 Two-way ANOVA for plant life form cover (% square root-transformed) found in the diet composition of guanaco (*G*), cattle (*C*) and sheep (*S*), along spring (*Sp*), summer (*Su*), autumn (*A*) and winter (*W*)

Factor		Life form cover							
		T	S	EH	PH	CG	RG	HS	M
A Herbivore	G	24.0 b	7.3 b	8.7 b	6.7	12.5 a	28.3 a	10.5 b	2.0 a
	C	11.7 a	2.4 a	3.8 a	7.3	23.7 b	40.2 b	3.5 a	7.5 b
	S	11.2 a	5.0 ab	7.0 ab	10.0	23.5 b	33.2 ab	5.7 a	4.0 ab
	F	*10.12*	*7.84*	*4.47*	*1.42*	*10.69*	*5.77*	*8.40*	*6.62*
	(P)	*(< 0.001)*	*(0.001)*	*(0.017)*	*(0.253)*	*(< 0.001)*	*(0.006)*	*(< 0.001)*	*(0.003)*
B Season	Sp	16.0 ab	7.4 b	4.0 a	6.0	20.3	37.0	5.0 a	4.0 ab
	Su	18.4 b	1.8 a	9.7 b	7.7	19.3	32.0	4.3 a	6.7 b
	A	20.6 b	2.7 a	8.0 ab	12.7	18.0	30.3	5.0 a	3.1 a
	W	7.7 a	7.7 b	4.3 a	5.7	22.0	36.3	12.0 b	4.3 ab
	F	*6.78*	*14.91*	*3.01*	*2.75*	*1.00*	*1.18*	*2.98*	*3.34*
	(P)	*(< 0.001)*	*(< 0.001)*	*(0.040)*	*(0.054)*	*(0.401)*	*(0.330)*	*(0.042)*	*(0.028)*
A × B		5.2	0.59	1.57	3.06	0.66	1.03	1.57	5.87
		(< 0.001)	*(0.736)*	*(0.185)*	*(0.016)*	*(0.682)*	*(0.420)*	*(0.185)*	*(< 0.001)*

Means values are presented without transformation

Plant life forms *T* tree seedlings and saplings, *S* shrubs, *EH* erect herbs, *PH* prostrate herbs, *CG* caespitose grassesl, *RG* rhizomatous grasses, *HS* hemiparasitic shrubs, *M* mosses, *F* fisher test, *P* probability. Letters in each column indicate differences by Tukey test (*P* < 0.05). Text in italics is used to differentiate between the value of statistical parameters (*F* and *P*) and other values

and mosses (Table 1) and can be explained due to changes in the use patterns of these resources among herbivore species. Overall, guanacos were found to browse in trees mostly during the growing season, while domestic herbivores increase their consumption of this life form during winter. Additionally, prostrate herbs were more consumed by sheep and mosses by cattle, except in autumn (data not shown).

For DCA analysis of plant species consumption by each herbivores among seasons, only two ordination axes (1 and 2) were retained for interpretation (Fig. 3). Most of the plant species were consumed by all the herbivores, and a few plants were exclusively associated with only one of the herbivores. The proportion of shared species in diets was higher during summer and winter (24 and 20% of the total species found in feces) than in spring and autumn (6 and 4%).

Carex sp. was equally consumed by all the species throughout the year, and this species grows exclusively in OL (Fig. 1a, 3). In spring, guanacos included more species from the NPF habitat (e.g., *Misodendrum* sp. and *N. pumilio* trees), while domestic herbivores included more OL taxa (e.g., cattle included mosses and *Luzula alopecurus*, and

sheep more *N. antarctica*) and NAF plants (e.g., cattle included more *Blechnum penna-marina* and *Festuca magellanica*, and sheep more *Bromus unioloides* and *Uncinia lechleriana*) (Fig. 1, 3a). In summer, *N. pumilio* trees were foraged in similar proportions by all three herbivores (Fig. 3b), as well as several species from NAF. Cattle also consumed plants from OL (e.g., *Plantago barbata* and mosses), while sheep included other species from OL (e.g., *Achillea millefolium* and *Juncus* sp.) and NAF (e.g., *Bromus unioloides* and *Cotula scariosa*). Guanaco diet presented a wide use of plants from different habitats including the OL and NAF ecotone (e.g., *Berberis* sp., *Geum magellanicum* and *N. antarctica*), as well as OHF species (e.g., *Epilobium australe*). In autumn (Fig. 3c), cattle consumed plants from NAF (e.g., *B. penna-marina* and *C. scariosa*), while sheep diet was asssociated with plants from OL (e.g., *Alopecurus* sp., *N. antarctica, Trifolium repens* and mosses). Guanaco diet was associated with a wide range of habitats, including plants from OL (e.g., *P. barbata*), NAF (e.g., *B. unioloides*) and harvested forests (e.g., *E. australe*). Finally, during winter (Fig. 3d), the proportion of eaten species from OL by the three herbivores increased (e.g., *Agrostis* sp.,
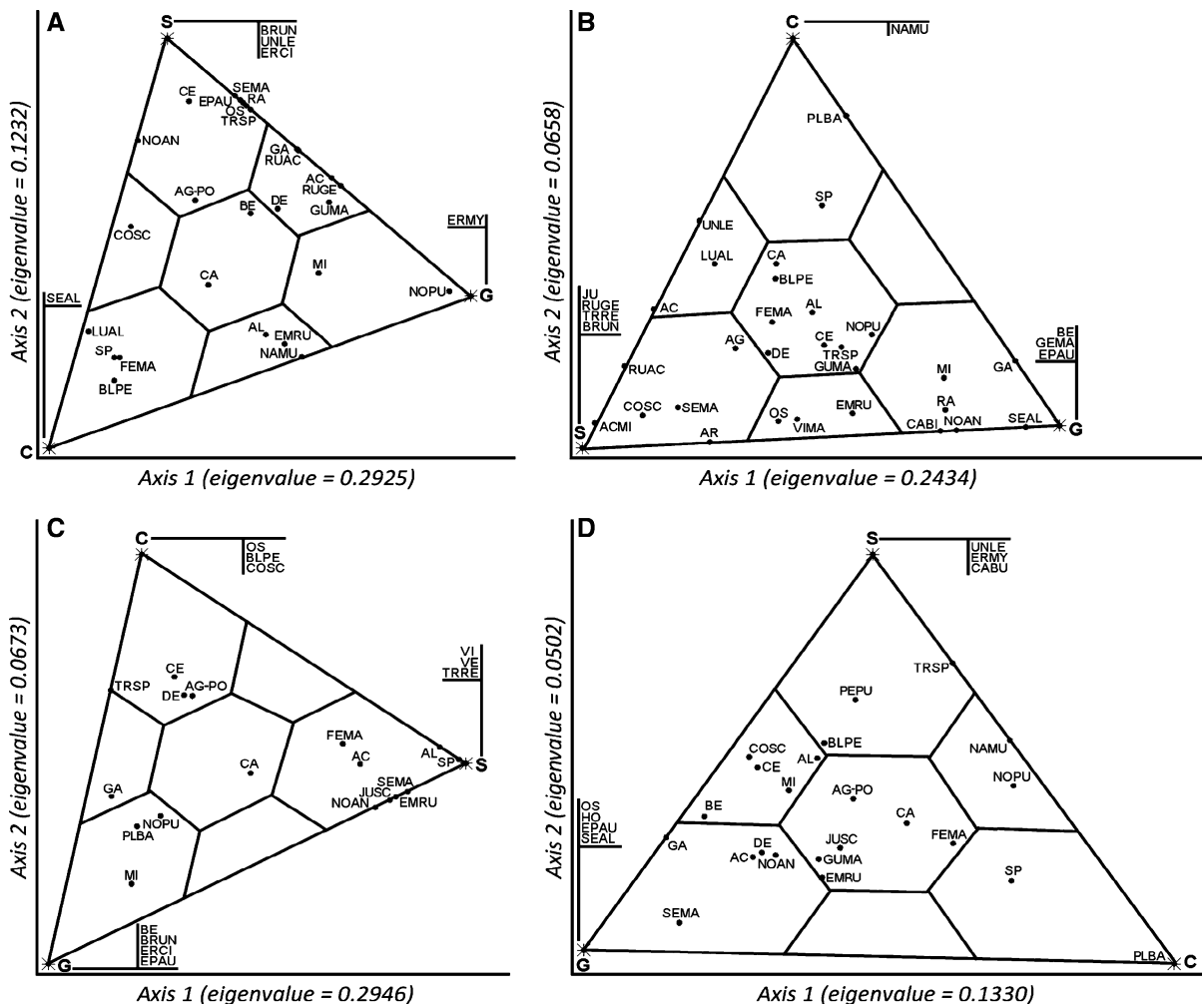
Fig. 3 DCA for the analysis of diet composition of guanaco (*G*), cattle (*C*) and sheep (*S*) according the seasonal sampling in spring (*A*), summer (*B*), autumn (*C*) and winter (*D*). Codes for plant species are showed in Table 4 in Appendix

Gunnera magellanica and *Juncus* sp.). However, other plant species from this habitat were preferred by cattle (e.g., *P. barbata* and mosses) and sheep (e.g., *Erigeron myosotis* and *U. lechleriana*). Yet, domestic herbivores also used NPF as evidenced by the higher percentage of *N. pumilio* plants found in the feces. Guanaco consumed plants from OL (e.g., *Hordeum* sp.), but also species from NAF and NPF (e.g., *E. australe* and *Osmorhiza* sp.).

Diet overlap, feeding selectivity and habitat selection

Diet overlap values varied between 0.52 and 0.80 among the herbivore species and seasons (Table 2).

Table 2 Diet overlap using Pianka Index (mean ± SE) of plant species proportion found in feces of guanaco *(G)*, cattle *(C)* and sheep *(S)*

Season	G versus C	G versus S	C versus S
Spring	0.58 ± 0.01	0.52 ± 0.13	0.71 ± 0.31
Summer	0.68 ± 0.17	0.57 ± 0.13	0.80 ± 0.13
Autumn	0.67 ± 0.07	0.55 ± 0.25	0.57 ± 0.22
Winter	0.59 ± 0.13	0.72 ± 0.15	0.70 ± 0.20
Annual	0.63 ± 0.10	0.59 ± 0.16	0.70 ± 0.20

Values represent average for the four seasons

Overlap between cattle versus sheep showed a greater value (0.70) than guanaco versus cattle (0.63), and guanaco versus sheep (0.59). Major overlap between

cattle versus sheep diets and guanaco versus cattle diets occurred during summer, but guanaco versus sheep overlapped their diets mostly in winter.

Feeding selectivity, analysed using the Ivlev Index, and preferences and avoidances in the different plant life form groups were found for the three herbivores (Fig. 4). Trees and grasses (caespitose and rhizomatous) were selected, while shrubs and herbs were avoided. As was presented in Table 1, regenerating trees were heavily preferred by guanacos (0.60) over the domestic herbivores (0.3–0.33), while grasses were more preferred by domestic herbivores (0.16–0.35) than guanacos (0.04–0.08). Guanacos showed indifferences for shrubs (−0.01), which were heavily avoided by cattle (−0.51). Herbs meanwhile were more rejected by cattle (−0.63 to −0.66) than sheep (−0.45 to −0.53), and guanacos showed greater rejection of prostrate herbs (−0.66) than erect herbs (−0.36).

This feeding selectivity was correlated to habitat selection analyses (Fig. 5) and seasonal diet composition analyses (Fig. 1, 3). All the herbivores mostly selected OL as a feeding site, and this relationship was similar among cattle (43%), sheep (41%), and guanaco (39%). Beside this, guanaco showed a higher preference for PUF (11%) compared to domestic herbivores (5%), with the use of harvested forests (OHF-RHF) and NAF being similar for the three herbivores (5–7 and 4–7%, respectively).
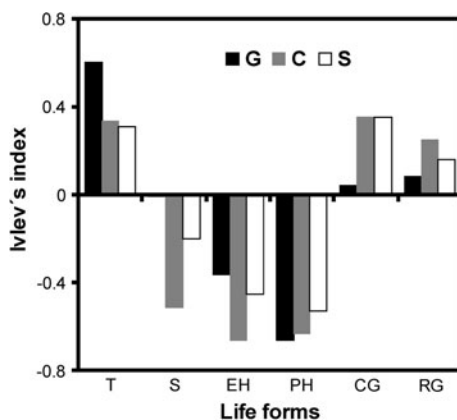

Fig. 4 Feeding selectivity using the Ivlev Index for guanaco (*G*), cattle (*C*) and sheep (*S*) classified by plant life forms: tree seedlings and saplings (*T*), shrubs (*S*), erect herbs (*EH*), prostrate herbs (*PH*), caespitose grasses (*CG*) and rhizomatous grasses (*RG*)
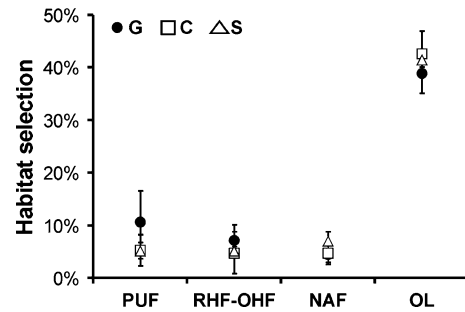

Fig. 5 Habitat selection of guanaco (*G*), cattle (*C*) and sheep (*S*) based on plant species proportion in diets and habitat types: primary unmanaged (*PUF*), and recently and old harvested (*RHF-OHF*) *Nothofagus pumilio* forests, *Nothofagus antarctica* forests (*NAF*) and open lands (*OL*)

Discussion

Vegetation patterns across the landscape and harvesting history

Plant species richness measured in this work corresponded to 21% of the total richness of the Tierra del Fuego Archipelago, according to Moore (1983). Plant richness is usually directly related to environmental variables (e.g., soil properties) (Huston 1994), where different species composition is expected throughout the landscape. Yet, few studies have included vegetation analysis at the landscape level in our study area, and most of them have focused on the understory plants of *Nothofagus* forests. Open lands, however, are know to present higher richness, as well as the northern steppe grasslands of Tierra del Fuego (Collantes et al. 1999; Posse et al. 2000). Understory *Nothofagus* forests richness of our study was comparable with previous studies (51 species) in primary (Lencinas et al. 2008) and managed (Lencinas et al. 2011) forests of Tierra del Fuego, but higher (35 species) than those described by Martínez Pastur et al. (2002) for shelterwood cuts. In our study, forest harvesting history influenced the understory richness, where OHF was higher compared to RHF, NAF and PUF. We agree with Martínez Pastur et al. (2002) and Lencinas et al. (2011), who described the increase of diversity and cover of understory plant species increase (e.g., grasses and herbs) after harvesting, resulting in a change of the original forest understory communities. Harvesting significantly affects forest

structure of productive forest stands by decreasing stand density and overstory canopy cover (Martínez Pastur et al. 2000, 2011; Gea et al. 2004), and by modifying the environmental conditions and allowing the establishment of exotic species (Martínez Pastur et al. 2002; Lencinas et al. 2008, 2011). Many of the exotic plant species have adapted to environmental conditions of Southern Patagonia, extending their distribution into different habitat types of Tierra del Fuego (Moore 1983). These species include several palatable grasses (e.g., *Hordeum comosum* or *Poa pratensis*) for herbivore species.

Herbivore foraging patterns

The guanaco is a generalist species, which can adapt to a wide spectrum of environments for feeding (Raedeke 1980; Puig et al. 1997), ranging from closed forests where guanaco consume leaves and sprouts of *Nothofagus* saplings (Martínez Pastur et al. 1999; Pulido et al. 2000) to high Andean grasslands where grasses and sedges are the main available food (Rebertus et al. 1997). Due to this adaptability, guanaco can modify its behavior according to the changes in density of domestic livestock, trying to avoid them (Raedeke 1980; Montes et al. 2000; Baldi et al. 2001, 2004). For this reason, seasonal switches in the extent of grasses and browse consumption described in our study appear to be a result of pressure from local ranching practices with cattle and sheep, and seasonal differences in forage availability. These habitat shifts have been reported for other guanaco populations (Bonino and Pelliza Sbriller 1991; Bonino and Fernández 1994; Puig et al. 1997; Baldi et al. 2001, 2004; Cavieres and Fajardo 2005) and other native camelids in Argentina (Borgina et al. 2008, 2010). However, this work provides further evidence that guanaco feed relatively more on harvested forests (RHF and OHF) during those seasons when OL are the main feeding sites for livestock. To find out if that is the result of competition for food or just a result of specific habitat selection it will be necessary to include areas with and without livestock to compare the diet in both situations. Beside this, in our study, herbivore foraging patterns varied along seasons, and forage selectivity existed among different plant life forms. It is also necessary to consider the vegetation assemblage at the landscape level, e.g., the three herbivores preferred trees and grasses (caespitose and rhizomatous), while shrubs and herbs were avoided.

Habitat selection for feeding

According to Baldi et al. (2004) and Mishra et al. (2004), potential ungulate competitors have similar preferences for food resources and when they overlap their habitat use, food availability may become limited. In our study, all the herbivores overlaped their diets, due to the fact that they consumed grasses throughout the year (e.g., *Carex* sp. was found exclusively in open lands). Major overlap between guanaco and cattle occurred only in summer, because they used the same environment type as feeding sites (e.g., *Carex* sp., *Deschampsia* sp., *Festuca magellanica* and *Nothofagus antarctica*). Additionally, when forage is scarce during spring and winter, guanaco and sheep shared a common diet, particularly species mainly observed in OL and NAF.

There are more similarities in diet selection between guanaco and sheep, than with cattle and the other grazers. Guanaco and sheep are mixed feeders, foraging on a wide spectrum of plant life forms (Raedeke 1980; Bonino and Pelliza Sbriller 1991; Baldi et al. 2004). In Northern Patagonia, guanaco and sheep show considerable overlap in their diets (Baldi et al. 2001, 2004), where guanaco is displaced to marginal lands where their preferred plant species are less abundant. Yet in Tierra del Fuego, the increase of modified harvested forests may provide alternative sites favorable for guanaco (in shelter and food offerings) (Martínez Pastur et al. 1999; Pulido et al. 2000).

There is a widespread belief that grazing ungulates start using lower quality forage when high quality forage decreases (Puig et al. 1997; Mysterud 2000; Edenius et al. 2002). For this, many herbivores are forced to include more woody plants in their diets when grass biomass decreases (Mishra et al. 2004; Skarpe and Hester 2007). In our study, the domestic herbivores seem to use mostly grasses in their diet, but expand browsing on saplings of *N. pumilio* during the winter to provide additional food to satisfy their requirements. In addition, forest environments could be preferred among other habitat types in winter because they provide shelter against frost, snow and wind. This seasonal impact has direct consequences in the success of silvicultural practices in stands

under forest management, because winter browsing on snow-bare shoots and buds can lead to serious damage for natural regeneration growth and survival (Edenius et al. 2002).

Historically, guanaco and *Nothofagus* forests have coexisted for centuries, and apparently problems in regeneration can be related to the increase of forestry in the region (e.g., browsing of saplings delay growth of natural regeneration in harvested stands) (Pulido et al. 2000; Cavieres and Fajardo 2005). Even now, new proposals for silvopastoral systems applied on *N. antarctica* forests (Peri 2005) are being planned in Tierra del Fuego, but with traditional free ranching

activities carried out on these landscapes. These management plans (livestock, silvopastoral systems and harvesting) have not considered the direct or indirect consequences on guanaco populations. The challenge, therefore, is to generate management planning decisions to avoid that neither guanacos nor the domestic herbivores become detrimental to the sustainability of managed forested ecosystems.

Appendices

See Tables 3 and 4.

Table 3 Plant species determined during vegetation surveys and codes

Name[a]	Code	Name	Code	Name	Code
Acaena magellanica	ACMA	*Colobanthus quitensis*	COQU	*Pernettya pumila*	PEPU
A. ovalifolia	ACOV	*Coronopus dydimus*	CODY	*Phaiophleps biflora*	PHBI
A. pinnatifida	ACPI	*Cotula scariosa*	COSC	*Phleum alpinum*	PHAL
Achillea millefolium	ACMI	*Cystopteris fragilis*	CYFR	*P. pratense*	PHPR
Adenocaulon chilense	ADCH	*Dactylis glomerata*	DAGL	*Plantago barbata*	PLBA
Agoseris coronopifolium	AGCO	*Deschampsia antarctica*	DEAN	*Poa annua*	POAN
Agropyron pubiflorum	AGPU	*D. flexuosa*	DEFL	*P. nemoraris*	PONE
Agrostis magellanica	AGMA	*Draba magellanica*	DRMA	*P. pratensis*	POPR
A. perennans	AGPE	*Dysopsis glechomoides*	DYGL	*Polygonum aviculare*	POAV
A. uliginosa	AGUL	*Elymus agropyroides*	ELAG	*Pratia longiflora*	PRLO
Alopecurus magellanicus	ALMA	*Empetrum rubrum*	EMRU	*P. repens*	PRRE
A. pratensis	ALPR	*Epilobium australe*	EPAU	*Primula magellanica*	PRMA
Arenaria serpens	ARSE	*Erigeron myosotis*	ERMY	*Ranunculus biternatus*	RABI
Azorella lycopodioides	AZLY	*Euphrasia antarctica*	EUAN	*R. fuegianum*	RAFU
A. trifurcata	AZTR	*Festuca gracillima*	FEGR	*R. maclovianus*	RAMA
Berberis buxifolia	BEBU	*F. magellanica*	FEMA	*R. uniflorus*	RAUN
B. empetrifolia	BEEM	*Galium antarcticum*	GAAN	*Ribes magellanicum*	RIMA
Blechnum penna-marina	BLPE	*G. aparine*	GAAP	*Rubus geoides*	RUGE
Bolax gummifera	BOGU	*G. fuegianum*	GAFU	*Rumex acetosella*	RUAC
Bromus unioloides	BRUN	*Gamochaeta spiciformis*	GASP	*Sagina procumbens*	SAPR
Calamagrostis stricta	CAST	*Gentiana postrata*	GEPO	*Schizeilema ranunculus*	SCRA
Calceolaria biflora	CABI	*Gentianella magellanica*	GEMG	*Senecio magellanicus*	SEMA
Caltha sagitata	CASA	*Geum magellanicum*	GEMA	*S. vulgaris*	SEVU
Capsella bursa-pastoris	CABU	*Gunnera magellanica*	GUMA	*Stellaria debilis*	STDE
Cardamine glacialis	CAGL	*Hieracium antarcticum*	HIAN	*S. media*	STME
Carex capitata	CACA	*Holcus lanatus*	HOLA	*Taraxacum gillesii*	TAGI
C. curta	CACU	*Hordeum comosum*	HOCO	*T. officinale*	TAOF
C. decidua	CADE	*H. secalinum*	HOSE	*Tetroncium magellanicum*	TEMA
C. fuscula	CAFU	*Juncus scheuzerioides*	JUSC	*Thlaspi magellanicum*	THMA
C. gayana	CAGA	*Leucanthemum vulgare*	LEVU	*Trifolium repens*	TRRE

Table 3 continued

Name[a]	Code	Name	Code	Name	Code
C. macloviana	CAMA	*Luzula alopecurus*	LUAL	*Triglochin concinna*	TRCO
C. magellanica	CAMG	*Lycopodium magellanicum*	LYMA	*T. palustris*	TRPA
C. sorianoi	CASO	*Nanodea muscosa*	NAMU	*Trisetum spicatum*	TRSP
C. subantarctica	CASU	*Nothofagus antarctica*	NOAN	*Uncinia lechleriana*	UNLE
Cerastium arvense	CEAR	*N. pumilio*	NOPU	*Veronica serpyllifolia*	VESE
C. fontanum	CEFO	*Osmorhiza chilensis*	OSCH	*Vicia magellanica*	VIMA
Chiliotrichum diffusum	CHDI	*O. depauperata*	OSDE	*Viola magellanica*	VOMA
Cirsium vulgare	CIVU	*Oxalis magellanica*	OXMA		

[a] Following Moore (1983) and Correa (1969–1998)

Table 4 Year-long diet composition of guanaco (*G*), cattle (*C*) and sheep (*S*) classified at the level of plant genus or species (mean ± SE) and codes

Names[a]	Code	G	C	S
Acaena sp.	AC	1.6 ± 0.6	1.2 ± 0.3	2.9 ± .8
Achillea millefolium	ACMI		0.1 ± <0.1	1.2 ± 0.5
Agrostis sp.	AG	5.7 ± 0.9	8.7 ± 0.6	10.0 ± 1.2
Alopecurus magellanicus	ALMA	3.1 ± 0.8	2.9 ± 0.5	3.7 ± 0.7
Arjona sp.	AR	0.1 ± <0.1		0.2 ± 0.1
Berberis sp.	BE	3.1 ± 1.01	0.5 ± 0.2	1.1 ± 0.3
Blechnum penna-marina	BLPE	0.9 ± 0.4	1.6 ± 0.3	1.5 ± 0.5
Bromus unioloides	BRUN	<0.1 ± <0.1		0.4 ± 0.2
Calceolaria biflora	CABI	<0.1 ± <0.1		<0.1 ± <0.1
Capsella bursa-pastoris	CABU			<0.1 ± <0.1
Carex sp.	CA	16.8 ± 1.2	29.3 ± 2.0	20.5 ± 1.7
Cerastium sp.	CE	2.3 ± 0.5	4.2 ± 1.1	3.3 ± 0.6
Cotula scariosa	COSC	0.7 ± 0.4	0.5 ± 0.1	2.3 ± 0.7
Deschampsia sp.	DE	9.0 ± 1.1	8.1 ± 1.0	7.4 ± 0.9
Empetrum rubrum	EMRU	2.8 ± 0.6	1.7 ± 0.5	1.3 ± 0.4
Epilobium australe	EPAU	0.5 ± 0.3		0.3 ± 0.1
Erigeron myosotis	ERMY	0.2 ± 0.1		0.1 ± <0.1
Erodium cicutarium	ERCI	0.1 ± <0.1		0.2 ± 0.1
Festuca magellanica	FEMA	3.6 ± 0.7	9.6 ± 1.4	7.2 ± 1.6
Galium sp.	GA	1.2 ± 0.3	0.4 ± 0.2	0.5 ± 0.3
Geum magellanicum	GEMA	2.9 ± 1.2		
Gunnera magellanica	GUMA	0.7 ± 0.2	0.3 ± <0.1	0.5 ± 0.1
Hordeum sp.	HO	0.5 ± 0.4		
Juncus scheuzerioides	JU	2.6 ± 0.9	2.0 ± 0.8	4.4 ± 1.3
Luzula alopecurus	LUAL	0.2 ± <0.1	2.1 ± 0.5	1.2 ± 0.6
Misodendrum sp.	MI	10.7 ± 1.6	3.6 ± 0.7	5.7 ± 1.7
Nanodea muscosa	NAMU	<0.1 ± <0.1	0.2 ± <0.1	0.1 ± <0.1
Nothofagus antarctica	NOAN	2.7 ± 0.8	1.6 ± 0.5	3.8 ± 1.2
N. pumilio	NOPU	19.1 ± 2.3	10.1 ± 1.2	7.3 ± 1.2

Table 4 continued

Names[a]	Code	G	C	S
Osmorhiza sp.	OS	0.3 ± 0.1	$<0.1 \pm <0.1$	0.6 ± 0.2
Pernettya sp.	PE	0.6 ± 0.3	0.5 ± 0.2	1.8 ± 1.0
Plantago sp.	PL	2.1 ± 1.2	1.4 ± 0.4	0.5 ± 0.4
Ranunculus sp.	RA	0.3 ± 0.2	$<0.1 \pm <0.1$	$0.1 \pm <0.1$
Rubus geoides	RUGE	1.3 ± 0.6		1.1 ± 0.5
Rumex sp.	RU	$<0.1 \pm <0.1$	$<0.1 \pm <0.1$	0.1 ± 0.1
Senecio alloeophyllus	SEAL	0.6 ± 0.3	$0.1 \pm <0.1$	$<0.1 \pm <0.1$
S. magellanicus	SEMA	1.1 ± 0.3	0.3 ± 0.1	2.4 ± 0.7
Sphagnum sp.	SP	1.9 ± 0.5	7.8 ± 1.1	3.6 ± 0.7
Trifolium repens	TRRE			0.4 ± 0.3
Trisetum spicatum	TRSP	0.4 ± 0.2	0.9 ± 0.3	1.1 ± 0.6
Uncinia lechleriana	UNLE		0.2 ± 0.1	0.2 ± 0.1
Veronica sp.	VE			$<0.1 \pm <0.1$
Vicia sp.	VI	0.2 ± 0.1	$<0.1 \pm <0.1$	0.5 ± 0.2

[a] Following Moore (1983) and Correa (1969–1998)

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