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Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina

Estela Raffaele, Thomas T. Veblen, Melisa Blackhall & Norlan Tercero-Bucardo

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Raffaele, E. (correspondence author: estelaraffaele@yahoo.com.ar), **Blackhall, M.** (meliblack33@yahoo.com.ar) & **Tercero-Bucardo, N.** (ntbucardo@gmail.com): Laboratorio Ecotono, Universidad Nacional del Comahue, INIBIOMA-CONICET, Quintral 1250, 8400 Bariloche, Argentina
Veblen, T.T. (Thomas.Veblen@colorado.edu): Department of Geography, University of Colorado, Boulder, CO 80309-0260, USA

Abstract

Question: We investigated how cattle and European hares, the two most widespread exotic herbivores in Patagonia, affect species composition, life-form composition and community structure during the first 6 years of vegetation recovery following severe burning of fire-resistant subalpine forests and fire-prone tall shrublands. We asked how the effects of introduced herbivores on post-fire plant community attributes affect flammability of the vegetation.

Location: Nahuel Huapi National Park, northwest Patagonia, Argentina

Methods: We installed fenced plots to exclude livestock and European hares from severely burned subalpine forests of *Nothofagus pumilio* and adjacent tall shrublands of *N. antarctica*. The former is an obligate seed reproducer, whereas the latter and all other woody dominants of the shrubland vigorously resprout after burning.

Results: Repeated measures ANOVA of annual measurements over the 2001-2006 period indicate that cattle and hare exclusion had significant but complex effects on the cover of graminoids, forbs, climber species and woody species in the two burned community types. Significant interactions between the effects of cattle and hares varied by plant life forms between the two communities, which implies that their synergistic effects are community dependent.

Conclusions: Following severe fires, the combined effects of cattle and hares inhibit forest recovery and favour transition to shrublands dominated by resprouting woody species. This herbivore-induced trend in vegetation structure is consistent with the hypothesis that the effects of exotic herbivores at recently burned sites contribute to an increase in the overall flammability of the Patagonian landscape.

Introduction

In the context of global warming, changes in land-use practices and ecological effects of introduced species can potentially create positive feedbacks resulting in non-linear increases in wildfire activity (D'Antonio & Vitousek 1992; Brooks et al. 2004; Peters et al. 2004; Bowman et al. 2009). For example, introduced mammalian herbivores may select plants with particular chemical or morphological properties, alter competitive hierarchies and directly alter vegetation structure in ways that either promote or diminish potential wildfire activity (Mutch 1970; Madany & West 1983; Bond & Midgley 1995; Blackmore & Vitousek 2000; Holmgren 2002). Although the role of native and introduced herbivores, as consumers of fine fuels, in reducing fire potential is well documented (Bond & Keeley 2005; Borman 2005), the potential ability of introduced mammalian herbivores to shift fire-resistant community types to more fire-prone communities has been less studied. The current study investigates changes in plant community composition and structure due to introduced herbivores and evaluates how such changes may shift post-fire successional trajectories towards more flammable community types in northern Patagonia, Argentina. In the context of resilience theory (Holling 1973; Gunderson 2000), fire-resistant tall forests and fire-prone tall shrublands in northern Patagonia constitute alternative stable states for which transitions are governed by interactions between fire and introduced herbivores. The

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working hypothesis underlying this and parallel studies (Veblen et al. 2003, 2008; Kitzberger et al. 2005b; Mermoz et al. 2005; Blackhall et al. 2008) is that many of the same plant traits that allow persistence under pressure from mammalian herbivores also favour species persistence following recurrent fires. Furthermore, the effects of both herbivores and recurrent burning contribute to more flammable vegetation properties, thus resulting in a positive feedback towards increased fires (as explained below).

Major differences in the post-fire regeneration success of potential dominant species under browsing pressure may result in recovery to community types that differ significantly in their flammability due to differences in plant morphology and community structure (Mills 1986; Hobbs & Gimingham 1987). For example, mammalian herbivores tend to severely damage apical meristems of trees and shrubs, often triggering resprouting and the growth of lateral shoots (Haukioja & Koricheva 2000). Browsed woody species that otherwise would have excurrent growth forms (strong apical dominance) tend to develop decurrent growth forms, in which the lateral branches grow as large as the main trunk (Zimmerman & Brown 1971). Furthermore, woody obligate seeders are more likely to be eliminated by browsing than are species that resprout vigorously after damage by herbivores and other disturbances (Bond & van Wilgen 1996; Bellingham 2000). There are many multi-stemmed shrub species, which resprout after damage by fire, that appear to be resilient to chronic browsing (Bond & van Wilgen 1996; Higgins et al. 2000; Espelta et al. 2003; Pausas & Lavorel 2003). Chronic browsing may prevent post-fire regeneration of obligate seeders that are the dominants of tall forests, and promote a shift towards dominance of resprouting shrub species with fire-promoting architectures (Rundel 1981; Papió & Trabaud 1991; Bond & Midgley 1995; Schwilk & Ackerly 2001).

Northern Patagonia is an ideal landscape for examining potential feedbacks of introduced herbivores on vegetation flammability because of the juxtaposition of fire-resistant forests with fire-prone tall shrublands, the dominance of the former by obligate seed-reproducing trees and the latter by resprouting shrubs, and the pervasive influence of introduced mammalian herbivores in the region (Kitzberger et al. 2005b; Mermoz et al. 2005). In the current study, severe fire associated with extreme drought resulted in the replacement of a fire-resistant forest by more pyrogenic shrubland vegetation. In general, shrublands are more fire prone (compared to closed forests) because their internal microclimates are more susceptible to rapid desiccation (Countryman 1956; Torn & Fried 1992) and because shrub architectures promote the spread of surface fires into the canopy (Rundel 1981; Papió & Trabaud 1991). In northern Patagonia, Mermoz et al. (2005) showed that fire extent and fire spread into *Nothofagus pumilio* forests is dramatically less than in neighbouring tall shrublands dominated by *N. antarctica*. Sharp and persistent boundaries between forest and tall shrubland in this landscape, where there are no corresponding changes in the underlying abiotic environment, have long been interpreted to be the result of the self-reinforcing relationship of shrublands with fire (Veblen & Lorenz 1988). Such sharp boundaries are common elsewhere where positive feedback processes promote long-lasting "vegetation switches" (Wilson & Agnew 1992).

Along the steep west-to-east gradient of declining precipitation in the lee of the Andes, tall mesic forests are often bordered by dense 2-5 m tall shrublands dominated by small shrubby trees, tall shrubs and bamboos (Veblen et al. 2003). Fire, both natural and anthropogenic, historically has been the dominant disturbance determining community structure and landscape pattern. In areas bordering dense shrublands, the dominant trees of the mesic forests are long-lived (> 350 years) obligate seed-reproducing species that commonly reach heights > 25 m and include *Nothofagus pumilio*, *N. dombeyi* and the conifer *Austrocedrus chilensis* (Veblen et al. 2003). In contrast, the dominants of dense 3-5 m tall shrublands are all capable of vigorously resprouting after burning, cutting or browsing and include shrubby tree or tall shrub species, such as *Nothofagus antarctica*, *Schinus patagonicus*, *Berberis* spp., *Diostea juncea*, *Lomatia hirsuta* and the bamboo *Chusquea culeou*.

In northern Patagonia, fires often spread upslope through the shrublands and stop when they encounter the adjacent subalpine *N. pumilio* forests due to differences in the flammability of these two community types (Veblen & Lorenz 1988; Mermoz et al. 2005). The closed canopies of the subalpine *N. pumilio* forests create shady, mesic understories that typically do not exceed 2 m in height and consequently do not provide vertical fuel continuity with the tree canopy at heights of ca. 20 m. In contrast, in the *N. antarctica* tall shrublands the decurrent multi-stemmed growth form of the shrubs creates an open upper canopy beneath which temperatures are high, relative humidity is low, and fuels are vertically continuous. Abundant climbing plants (*Mutisia* spp., *Vicia nigricans*) as well as the 3-6 m tall bamboo *Chusquea culeou* provide fine fuels at all heights, further facilitating fire spread vertically from the ground surface to the top of the canopy. All the dominant woody species of this ecosystem type resprout quickly after fire, so that fuel quantity is sufficient to support a subsequent fire in only a few years.

In northern Patagonia, large native herbivores, such as the huemul deer (*Hippocamelus bisulcus*) and the guanaco (*Lama guanicoe*) are extirpated or rare, and have been partially replaced by introduced herbivores, including

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livestock, red deer, fallow deer, boar and European hare (Daciuk 1978; Merino et al. 2009). These introduced herbivores have been shown to have important influences on the floristic composition and structure of a wide range of community types (Martín et al. 1985; Veblen et al. 1992; Raffaele & Veblen 2001; Kitzberger et al. 2005b; Tercero-Bucardo et al. 2007).

In the current study, we examine how cattle and European hares, the two most widespread exotic herbivores in Patagonia, affect species composition, life-form composition and community structure during the first few years of vegetation recovery following severe burning of a subalpine *Nothofagus pumilio* forest and an adjacent *N. antarctica* tall shrubland. We experimentally controlled access of cattle and hares to recently burned sites of each community type to determine the separate and interactive effects of the two herbivores on changes in life-form groups (woody species, graminoids, forbs and climbers), and general vegetation structure (plant cover and height). Our goal is to identify effects of introduced herbivores on post-fire plant community attributes that in turn may affect flammability of the vegetation.

Methods

Study area and species

The area where we installed animal exclosures and control plots is located at Cerro Donat (41°26′19″S, 71°36′18″W; 1150 m) in Nahuel Huapi National Park, northwestern Patagonia, Argentina, where a severe fire in January 1999 burned ca. 5000 ha of subalpine *N. pumilio* forests and tall shrubland (Salguero et al. 1999). The burned sector studied here includes both stands of > 20-m tall subalpine forest of *N. pumilio* and patches of dense 3-m to 5 m tall shrublands dominated by *N. antarctica*. The sites selected for study were chosen because they represent the typical juxtaposition of subalpine forest and tall shrubland communities. Similar *N. pumilio* forests characterize the subalpine zone from 1000 to 1100 m to the upper treeline at ca. 1450 m. The *N. antarctica* stand included in our study is on a dry, northerly exposure adjacent to tall *N. pumilio* forest at higher elevation and closer to a small stream.

The study area is within the National Reserve zone of NHNP, where limited livestock use is permitted (Lauría Sorge & Romero 1999). The owner of the livestock and local officials of NHNP reported that cattle were present in moderate numbers at our sample sites for at least 30 years prior to the 1999 fire. Thus, the sites fit the common pattern of livestock use of *N. pumilio* forests and *N. antarctica* shrublands in the National Reserve zone of NHNP. Following the 1999 fire, cattle were continuously present in moderate numbers at the sample sites from October through April (spring to autumn), and a few wild cattle forage at the site year round. The introduced European hare (*Lepus europaeus*) is common throughout NHNP, and is abundant at the sites studied here. The only native herbivores found in the community types studied are small vole-like mice, which are omnivores (Pearson 1983). However, during 6 years of re-measuring permanent plots we did not observe any burrows, scat or other evidence of presence of native rodents.

Mean annual precipitation at the experimental site is approximately 1700 mm (Barros et al. 1983) and occurs mainly during April through September (mostly as snow). Water deficits are severe in late spring and summer (December to March) when warm temperatures are suitable for plant growth (Paruelo et al. 1998). At the closest climate station (Bariloche Airport at 860 m elevation), mean monthly temperature ranges from ~2°C in winter (July) to ~14°C in summer (January). Soils at the sample sites are derived from volcanic ash deposits overlaying glacial and periglacial topography (Del Valle 1998).

In and surrounding the stands studied, the 1999 fire killed all above-ground vegetation and consumed the forest floor litter (Alauzis et al. 2004). The pre-burn vegetation types were mapped from aerial photographs taken prior to the 1999 fire (Salguero et al. 1999). In the field in summer 2000, the pre-burn community types were confirmed by identifying the burned stems of woody species from their architectural attributes and leaf traits on the resprouts.

Experimental design

In 2001 we installed fences to exclude livestock and European hare in each of the two burned community types (subalpine forest and tall shrubland), and also established non-fenced control plots to address the following questions. (1) How does herbivory by cattle and hares affect post-fire floristic composition, life-form composition, plant cover and height of woody plants? (2) Does herbivory by introduced animals impede regeneration of the obligate seeder *N. pumilio*, and consequently promote conversion of the burned forest to a shrubland composition and structure? (3) Do cattle and hares have different and possibly synergistic influences on post-fire vegetation changes in these two community types?

To test for possible differences in soil properties between the two burned community types, at the beginning of the experiment at each site we collected 0.5 kg of the top 10 cm of soil in five randomly located points. Soils were air-dried, ground to pass a 2-mm mesh, and analysed for extractable P. Organic C and total N were analysed in samples ground to pass a 0.5-mm mesh. Soils were analysed for: P extracted in 0.5 M $NaHCO_3$ using the molybdate–ascorbic acid method,

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total N with semi-micro-Kjeldahl and organic C with the Walkley-Black wet digestion method. Nitrogen retained in microbial biomass was determined by a modification of the chloroform fumigation incubation technique (Vitousek & Matson 1985) employing field-moist soils, sieved to 2 mm and re-wetted to field capacity when necessary.

All exclosures and control plots were installed in severely burned areas lacking any surviving above-ground vegetation. In each of the two community types, we randomly located five fenced cattle exclosure plots and five permanent control plots (each 25 m × 25 m), following a paired plot experimental design (Sokal & Rohlf 1981). Within each 25 m × 25-m m plot, we systematically located five 2 m^2 circular microplots in which we annually made the following measurements from 2001 through 2006: (1) percentage cover for all vascular species; (2) maximum height of woody species (trees, shrubs and bamboos) and semi-woody climber species; and (3) a four–class rating of mammalian browsing for each woody species and the semi-woody climbers (following Veblen et al. 1992). The browse ratings were made independent of type of browser but observation of faeces indicates that the only mammalian herbivores present were cattle and hares. Microplots inside each cattle exclosure (25 microplots in each community type) were placed at least 5 m from the fence to avoid any edge effects.

For the hare exclosure experiments, within each 25 m × 25 m cattle exclosure and control plots, five 2-m^2 microplots were randomly selected and permanently fenced against hare. Each hare exclosure consisted of 2-cm mesh wire 1.4-m high and extending at least 0.3 m below the ground. Five microplots were left unfenced as controls. The same vegetation measurements noted above for cattle exclosures were taken annually in the hare exclosure and control plots. Summarizing, re-measurements of vegetation parameters were taken from 2001 through 2006 in a total of 100 2-m^2 microplots per community type for the following experimental treatments: (1) fenced out cattle but hares present (−C, +H), (2) unfenced to cattle and no hares (+C, −H), (3) fenced out cattle and no hares (−C, −H), and (4) unfenced to cattle and hares present (i.e. controls; +C, +H).

Data analyses

In order to determine the effects of introduced mammalian herbivores on the vegetation attributes of the subalpine forest and tall shrubland, we graphically described trends over time and tested for statistical significance of changes through time using repeated-measures ANOVA (Gurevitch & Chester 1986). The response variables were percentage plant cover (total cover and by four life form groups) and total height (cm) of woody and semi-woody climber species. The four life-form groups were: forbs, graminoids, climbers and woody species (tree and shrub species, including the bamboo *Chusquea culeou*). The treatments were: +C = cattle (i.e. fenced versus unfenced to cattle); +H = hares (fenced versus unfenced to hares); and T = time (years 2001-2006). The general linear model (Nelder & Wedderburn 1972) was used to perform the data analysis, following a two-by-two factorial design with repeated-measures ANOVA (Gurevitch & Chester 1986). Fixed variables were grazed treatments by both herbivores (cattle and hare). We determined if differences between treatments in trends over time in the response variables were statistically significant. Normality of the residuals between observed and predicted values of dependent variables was confirmed using normal plots (Sokal & Rohlf 1981). Response variable means were reported with standard errors (means ± SE). For these analyses, plant covers were grouped into five groups: total cover of all species, woody species, forbs, climbers and graminoids.

To assess the effectiveness of treatments (i.e. presence or absence of herbivores) and browsing effects by plant species, browsing rates estimated in the field were used to compute the following indices (following Rose & Burrows 1985; Veblen et al. 1989). (1) Browse index (BI): estimate of the total amount of browsing on a species in the area sampled, BI = Σbrowse ratings. (2) Percentage total browse (%TB): amount of browsing on a species as a proportion of total browsing on all species in the area sampled, %TB = 100 BI/Σ(BI of all species). (3) Browse pressure index (BPI): measure of the degree of browsing on a species in relation to the abundance of that species, BPI = BI/n, where n is the number of plots in which a species is present. (4) Mean browse index (MBI): summary statistic indicating the intensity of browsing on all species in the area sampled, MBI = Σ(BI for all species)/N, where N is the total number of plots in the area.

Results

Soil properties in the two community types

The soil properties sampled did not differ significantly between the two community types. In the subalpine forest and tall shrubland burns, respectively, mean (± SE) soil properties were 17.0 ± 5.3 and 17.0 ± 3.1 (mg N kg^{-1}) for microbial biomass, 4.1 ± 1.0 and 3.4 ± 0.8 (mg kg^{-1}) for P, 0.32 ± 0.03 and 0.34 ± 0.01 (g kg^{-1}) for N and 5.0 ± 0.6 and 5.3 ± 0.5% for organic carbon.

Plant cover and heights

Repeated-measures ANOVA indicates that when plant covers in the burned subalpine forest are analysed for change over time, the climber life form is the only group

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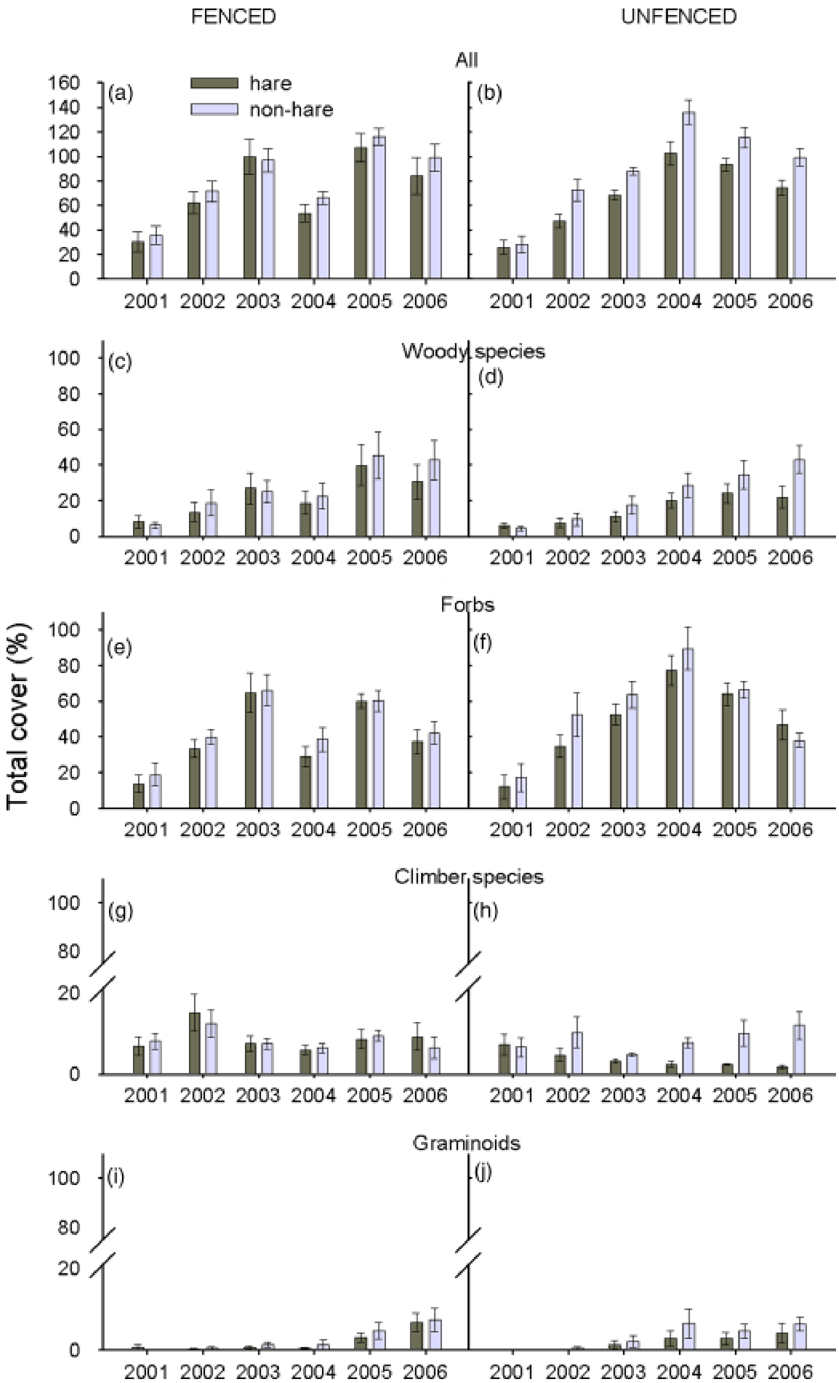

Fig. 1. Mean total cover (%) for all vascular plant species and by life-form groups by year in *Nothofagus pumilio* forest. Results are shown for plots fenced and unfenced to cattle and for hare and non-hare plots.

showing significantly reduced cover in the presence of both herbivores (Fig. 1g and h; +C +H, $P < 0.01$, supporting information Table S1). Cattle presence is associated with higher cover values for forbs and graminoids (Fig. 1e, f, i and j; T x +C, $P < 0.01$ and $P < 0.05$, respectively, Appendix S1). Total cover of all species combined was significantly higher in plots with cattle presence over time (Fig. 1a and b; T x +C, $P < 0.01$, Appendix S1). However, the higher total cover values for unfenced plots (+C) mainly occurred in 2004, and by 2006, cover values for all species were similar between fenced (−C) and unfenced plots (+C). In contrast, hare

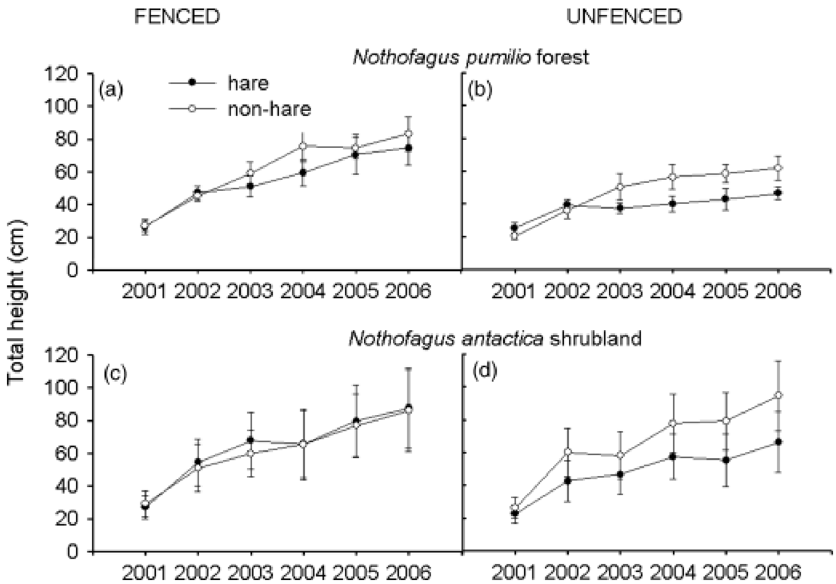

Fig. 2. Mean total height (cm) by year of woody and climber species at the burned subalpine *Nothofagus pumilio* forest and the *N. antarctica* tall shrubland. Results are shown for plots fenced and unfenced to cattle and for hare and non-hare plots.

presence (+H) was associated with reduced cover of all species (Fig. 1a and b; $P < 0.05$, Appendix S1) but the interaction with time was not significant ($P > 0.05$). The cover of woody species decreased significantly, both with cattle (T x +C) and with hares over time (T x +H) (Fig. 1c and d; $P < 0.05$, Appendix S1).

In the burned subalpine forest, mean total height of woody and climber species (Fig. 2a and b) decreased with both cattle (T x +C, $P < 0.05$), and hares (T x +H, $P < 0.01$), over time (Appendix S1). In 2006, mean total heights were 83.2 cm ± 10.3 in plots from which both herbivores were excluded (−C, −H) versus 46.4 cm ± 3.7 in the plots accessible to both herbivores (+C, +H, Fig. 2a and b).

At the tall *N. antarctica* shrubland site, cover values for woody and climber species decreased with cattle presence over time (Figs 3c, d and 1g, h; T x +C, $P < 0.01$; Appendix S1). In contrast, forb cover increased over time in the presence of both hares and cattle (Fig. 3e and f; T x +C, T x +H, $P < 0.01$, Appendix S1). Total cover of all species increased in the presence of cattle over time (Fig. 3a and b; T x +C; $P < 0.01$, Appendix S1). Total cover of all species was reduced in the presence of hares (+H) (Fig. 3a and b; $P < 0.05$) but the interaction with time was not significant ($P > 0.05$, T x+H, Appendix S1). Graminoid cover was higher in the presence of cattle (+C) (Fig. 3i and j; $P < 0.05$), but the interaction with time was not significant ($P > 0.05$, T x +C, Appendix S1). Although mean cover values for woody species in 2006 appear greater in the plots from which hares were excluded (−H) but cattle were present (+C) (80% versus 50% mean cover) (Fig. 3c and d) the difference was not statistically significant ($P > 0.05$). In contrast, forb cover increased over time in the presence of both cattle and hares [Fig. 3f; $P < 0.01$, (+C, +H) in Appendix S1].

In both the tall shrubland and the subalpine forest increases in forb cover associated with the presence of cattle and hares were mainly due to exotic species. At the end of the experiment in 2006, at sites with both cattle and hares (+C, +H) exotic species accounted for 87.1% and 80.9% of the total forb cover in the tall shrubland and subalpine forest sites, respectively.

In the tall shrubland, cattle alone (+C) did not have a significant influence on mean total height of woody and climber species (Fig. 2c and d; $P = 0.11$, Appendix S1). At sites where cattle were excluded, mean total height was essentially the same in plots with (−C, +H) and without hare presence (−C, −H) (Fig. 2c and d). In contrast, at sites with cattle (+C, −H), mean total height of woody and climber species was higher where hares were excluded (Fig. 2c and d; $P < 0.05$, Appendix S1). The trend towards greater plant height under hare exclusion and cattle presence intensified over time (+C, −H, Fig. 2c and d). By the end of the experiment (2006), in the presence of cattle, mean total height was on average ca. 42% taller in plots from which hares had been excluded, 66.3 cm ± 18.6 (+C, +H) versus 94.6 cm ±21.4 (+C, −H).

Preferred browse species

In the subalpine forest, the greatest percentages of the diets of browsing animals are provided by the bamboo *Chusquea*

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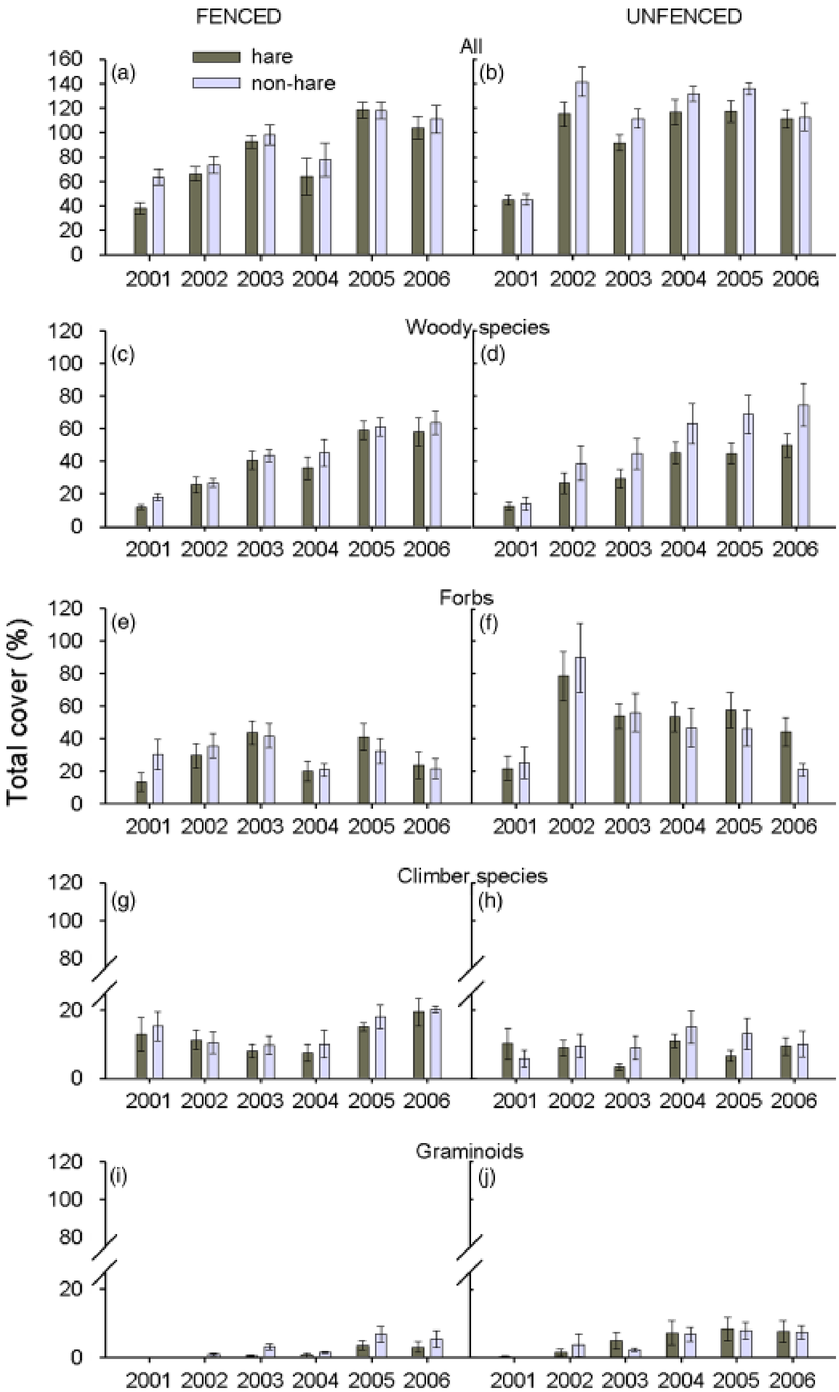

Fig. 3. Mean total cover (%) for all vascular plant species and by life-form group by year in *N. antarctica* shrubland. Results are shown for plots fenced and unfenced to cattle and for hare and non-hare plots.

culeou, the shrubs *Ribes magellanicum*, *Gaultheria mucronata* and *Schinus patagonicus*, and the climber *Vicia nigricans* (Table 1). All of these preferred browse species lack spines. The species with the highest browsing pressure relative to their abundance (i.e. high Browse Pressure Indices ≥ 1.0) were *R. magellanicum*, *C. culeou* and *N. pumilio* (Table 1). The species with the lowest browse pressure index (BPI < 0.20), but that are also frequent in the subalpine forest, are three *Berberis* species of spiny shrub (Table 1)

Plants in the burned tall shrubland were more heavily browsed than the burned subalpine forest, as indicated by the two-fold difference in mean browse indices (MBI;

Table 1. Species frequencies and measures of browsing on woody and climber species at the burned *Nothofagus pumilio* forest and the *N. antarctica* tall shrubland in 2006. Browse indices (explained in the text) are: total browsing percentage (% TB), browse pressure index (BPI), and mean browse index (MBI).

	Frequency	% TB	BPI
Nothofagus pumilio forest			
Ribes magellanicum	31	32.81	1.35
Chusquea culeou	24	24.22	1.29
Gaultheria mucronata	26	14.84	0.73
Vicia nigricans	39	12.5	0.41
Schinus patagonicus	15	9.37	0.8
Berberis serrato-dentata	16	2.34	0.19
Nothofagus pumilio	3	2.34	1
Berberis buxifolia	26	0	0
Berberis darwinii	12	0	0
MBI	1.28		
Nothofagus antarctica shrubland			
Chusquea culeou	53	36.21	2.06
Vicia nigricans	67	18.94	0.85
Nothofagus antarctica	26	16.28	1.88
Schinus patagonicus	48	12.29	0.77
Ribes cucullatum	24	10.63	1.33
Ribes magellanicum	4	2.32	1.75
Berberis buxifolia	77	1.66	0.06
Gaultheria mucronata	17	0.66	0.12
Lathyrus magellanicus	8	0.66	0.25
Berberis darwinii	3	0.33	0.33
Maytenus chubutensis	11	0	0
MBI	3.01		

Table 1). The highest percentages of the herbivore diets again were provided by the bamboo *C. culeou*, the shrubs *Schinus patagonicus* and *Ribes cucullatum*, and the climber, *Vicia nigricans*. In addition to these preferred browse species, the former dominant of the tall shrubland, *N. antarctica*, provides the third highest percentage of the herbivore diet and experiences the second highest browsing pressure relative to its abundance (BPI = 1.88; Table 1). Among the species with the lowest BPIs, again were the spiny and prickly shrubs *Berberis buxifolia*, *B. darwinii* and *Gaultheria mucronata*. *Maytenus chubutensis* had a BPI of zero, despite being more abundant than several species that were browsed (Table 1).

Discussion

Changes in plant cover and heights

The experimental exclusion of two introduced herbivores (cattle and hares) from the recently burned subalpine *N. pumilio* forest and *N. antarctica* shrubland revealed significant effects of herbivores, acting individually and synergistically, on cover and height of woody plants during the 6-year period of observation. The current study showed that early succession in both systems is affected differently by presence of cattle and hares. In general, livestock effects are stronger than the effects of hares in both community types. The exclusion of cattle had significant effects on the cover of all life forms in both community types. Hare exclusion significantly increased the cover of woody plants and climbers in the subalpine forest sites and decreased the cover of forbs in the tall shrubland. In both community types, exclusion of hares is associated with higher cover of woody plants regardless of the presence of cattle. In contrast, hare exclusion tended to be associated with either a decrease or no change in forb cover. Hare exclusion is associated with greater climber cover, especially in the presence of cattle in the subalpine forest sites. The relatively large reductions in cover of woody species and climbers in the presence of both herbivores imply a synergistic and negative influence on these life forms.

In the tall shrubland, towards the end of the experiment, forbs had higher cover values in the presence of cattle and hares. Potentially, the reduction of woody plant cover by the combination of cattle and hare browsing resulted in a release of forbs from competitive suppression by woody species in the shrubland. This trend towards increasing forb cover in the presence of both herbivores is more evident at the end of the experiment in both habitats, perhaps due to competitive release, but also reflects the increase over time in the presence of exotic forbs.

The synergistic effects of cattle and hares on mean heights of woody plants are clearly evident in both community types. In areas fenced from cattle, there is essentially no difference in mean heights between plots with and without hares in both community types. In contrast, in areas unfenced to cattle, mean heights are 33% and 42% lower in plots with hares in the subalpine forest and tall shrubland, respectively. Cattle alone also result in reduced plant heights in the subalpine forest, but in the absence of cattle in the tall shrubland sites, hares have little effect on plant height.

Preferred browse species

Both of the former dominants of the burned communities, the obligate seeder *N. pumilio* as well as the resprouter *N. antarctica*, are browsed (Table 1). In the subalpine forest, the high BPI on the relatively scarce seedlings of *N. pumilio* forest implies that even when seeds are dispersed to the site, browsing and trampling of seedlings are likely to impede successful regeneration. Low BPIs on the spiny *Berberis* shrubs indicate that these species thrive under browsing effects. Although the bamboo *Chusquea culeou* provides a high percentage of the total browse, 7 years after the fire it was one of the most frequent and dominant (by

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height and cover) species in plots accessible to both cattle and hares. This pattern of browse preference is consistent with the interpretation that under continued heavy browsing, the burned subalpine forest is being converted to a tall shrubland dominated by C. *culeou, Schinus patagonicus, Berberis* spp. and other shrubs.

In contrast, browsing patterns in the tall shrubland imply that under continued browsing, the burned shrubland will return to a composition and structure similar to its pre-burn condition. Again, the spiny *Berberis* spp. and *Gaultheria mucronata*, which has a sclerophyllous leaf with a prickly point, have low BPIs, indicating that they are less preferred than undefended species. The lack of browsing on *Maytenus chubutensis* is consistent with its high content of sesquiterpenes (González et al. 1994). Despite the high BPI of *N. antarctica*, it is relatively abundant and had a high cover value 7 years after the burning of the tall shrubland that it formerly dominated. Thus, despite the heavy browsing of this species, its capacity for vigorous resprouting following both fire and browsing assures its continued abundance at the burned site. Likewise, despite significant browsing on *C. culeou*, *S. patagonicus* and the small shrub species that formerly dominated the site, these species were abundant in the tall shrubland in 2006.

Potential feedbacks promoting vegetation flammability

The trends in community structure and floristic composition in the current study support the hypothesis that herbivory at recently burned sites contributes to an increase in the overall flammability of the northern Patagonia landscape. The fire-resistant subalpine forest dominated by *N. pumilio* that burned in 1999, has converted to a relatively long-lasting shrub and bamboo-dominated community. Cattle and hare presence, independently and together, are associated with reduced height of woody species in the post-fire *N. pumilio* site. Thus, the reduced stature of tall shrubs and arboreal species under herbivore pressure contributes to a more shrubland-like community structure, which in turn is more flammable than the original forest cover, and results in a positive feedback favouring post-fire resprouting woody species at the expense of the obligate seed-reproducing *N. pumilio*. Presence of cattle, and in particular the combined presence of cattle and hares, further reduce the likelihood that seedlings originating from new dispersals of *N. pumilio* will survive and attain dominance. The seed of *N. pumilio* is a small winged nut, and nearly all seeds fall within the radius of the crown of the seed tree (Rusch 1987). Despite the killing of all local seed trees (i.e. within 200 m) by the fire in 1999, some relatively long-distance dispersal of seed of *N. pumilio* allows a slow rate of seed dispersal to the burned sites. The relatively rare seedlings of *N. pumilio* recorded the third highest BPI among woody species at this site. The ability of exotic herbivores to impede the survival and height growth of naturally dispersing *N. pumilio* is demonstrated in our experimental exclusion study. Similarly, 2 years of monitoring survivorship of planted *N. pumilio* seedlings at our subalpine forest experimental site revealed that exposure to herbivory by livestock and hares reduces seedling survival (Tercero-Bucardo et al. 2007). The current study complements the above study by showing that natural dispersal of *N. pumilio* occurred within a few years of the fire, that seedlings are able to establish under the relatively harsh (high temperatures and low soil moisture) post-fire environment, but that their growth and development are negatively influenced by herbivores.

Even as seed availability of *N. pumilio* at the site of the 1999 burn slowly increases over the next few decades, the vigorously resprouting shrub and bamboo species are likely to continue to dominate the burned forest site for many decades and are highly resilient to herbivory by cattle and hares. At both the subalpine forest and tall shrubland burned sites, the current dominants (*Chusquea culeou, Schinus patagonicus, N. antarctica*, and *Berberis* spp.) are able to withstand high levels of herbivory, as indicated by their abundance, while also providing high percentages of total browsing. These are all species that have morphologies contributing to a higher flammability compared to that of *N. pumilio*. For example, *C. culeou* provides abundant fine fuel in its thin foliage and over time accumulates standing dead vertical culms, *S. patagonicus* provides abundant fine twig fuel from resprouts at its base, as does *N. antarctica*, particularly in the presence of cattle, and all the *Berberis* spp. have high canopy porosities favourable to combustion (unpublished data). *Vicia nigricans* is a climbing species that connects the lower and higher fuel strata, and has foliage that dies back in late summer, providing abundant dry fine fuel.

An additional feedback that favours a shift towards more fire-prone vegetation is the higher level of herbivory by hares and cattle in more open non-forest vegetation (Kitzberger et al. 2005a). In the current study, the higher mean browse indices in the burned tall shrubland compared to the burned forest implies that herbivore pressure will reduce any chances of former shrubland sites converting to tall forest. This is consistent with negative influences of introduced herbivores on height growth of the other two potentially dominant tree species (*Austrocedrus chilensis, N. dombeyi*) of nearby habitats (Veblen et al. 1989; Relva & Veblen 1998; Blackhall et al. 2008). The cover values and heights of resprouting woody species attained in just a few years after the 1999 fire at our experimental site show that fuels recover quickly

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after burning despite the presence of cattle and hares. Thus, introduced animals prevent regeneration of the potential dominants of fire-resistant forests while simultaneously allowing rapid recovery of woody fuels.

Introduced annual and biennial forbs were abundant in both habitat types soon after burning, especially in the presence of cattle. The overall tendency for the forb life form to increase in abundance in the presence of cattle and hares primarily reflects an increase in these exotic species and is a further contribution to enhanced flammability of these post-fire communities. The exotic forbs increasing in abundance in the presence of herbivores include species such as *Cirsium vulgare*, *Cardus thoermeri* and *Rumex acetosella*, all of which die back at the end of the growing season, thus providing abundant dry fine fuel in the form of dry leaves at the end of the growing season.

Conclusions

Numerous studies support the idea that ecological communities can be found in one of several possible stable states (Beisner et al. 2003), and that transitions among stability domains are often associated with human activities (Gunderson 2000). Empirical documentation of how changes in underlying parameters lead to shifts to an alternative stable state is particularly strong for aquatic ecosystems (Dent et al. 2002) but is less thoroughly understood for most terrestrial ecosystems, other than perhaps semi-arid rangelands. For example, in savanna landscapes, transitions between alternative stable states of open woodlands with mostly grassy cover versus dense woody thickets may be mediated by grazing pressure and resultant changes in fire regime (Dublin et al. 1990; Walker et al. 1997). Less common are studies that document alternative stable states of closed-canopy forests versus tall shrublands, where transitions are mediated by interactions between fire and herbivores.

The self-reinforcing relationships of sclerophyll shrublands to fire in northern Patagonia are similar to the positive feedbacks that favour retention of pyrogenic vegetation in juxtaposition with more fire-resistant forests in other ecosystems (e.g. Jackson 1968; Odion et al. 2009). However, our study also establishes an important influence of introduced animals in further contributing to retention of the pyrogenic shrublands. The independent and synergistic effects of two common exotic herbivores on recently burned subalpine forests and tall shrublands in northern Patagonia are important in promoting changes in post-fire plant community attributes that enhance flammability. Most significantly, the combined influence of cattle and hares shifts post-fire successional trends away from recovery to a fire-resistant forest and towards fire-prone shrublands. Under effects of introduced herbivores, there has been a shift in dominance from a non-serotinous obligate seeder to a multitude of woody species that resprout from fire-resistant organs (lignotubers, root crowns and rhizomes).

The shift in dominance of a forest dominated by an obligate seeder to a shrubland dominated by resprouting woody species is a logical expectation of the differences in plant functional types that would be expected to govern the response of plant populations to fire. Furthermore, our study shows that this shift in dominance is also a consequence of differences in plant functional types (including sprouting and seeding traits) that influence plant population responses to large herbivores. In our study area, the vital attributes that govern the responses of the dominant plant populations to fire are highly correlated with those that determine responses to herbivory by large animals. In northern Patagonia, wildfire activity is likely to continue to be promoted through regional warming and drying trends (Carril et al. 1997; Vera et al. 2006), and the effects of introduced herbivores on vegetation attributes will probably contribute a further positive feedback to increased flammability of the landscape.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Results of repeated-measures ANOVA for effects of cattle (C) and hares (H) on total cover (aggregated by life form) and plant height of woody and climber species in the burned subalpine *Nothofagus pumilio*

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forest and in the *N. antarctica* tall shrubland during 6 years (T, 2001–2006). Only the main factors (C, H, T and B = Block) and significant interactions are included. Bold values indicate significant results. Error (a) refers to principal effects error, and Error (b) refers to repeated-measures error.

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