

DR. MELISA BLACKHALL (Orcid ID : 0000-0002-2350-6608)

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**Effects of biological legacies and herbivory on fuels and flammability traits: A long-term experimental study of alternative stable states**

Melisa Blackhall<sup>1\*</sup>, Estela Raffaele<sup>1</sup>, Juan Paritsis<sup>1</sup>, Florencia Tiribelli<sup>1</sup>, Juan M. Morales<sup>1</sup>, Thomas Kitzberger<sup>1</sup>, Juan H. Gowda<sup>1</sup> and Thomas T. Veblen<sup>2</sup>

<sup>1</sup>Laboratorio Ecotono, INIBIOMA-Universidad Nacional del Comahue, CONICET, Quintral 1250, 8400 Bariloche, Argentina; <sup>2</sup>Department of Geography, University of Colorado, Boulder, CO 80309-0260, USA

\*Corresponding author: meliblackhall@gmail.com

**Running headline:** Legacies and herbivory effects on flammability

**Summary**

1. Ecological memory, often determined by the extent and type of retained biological legacies present following disturbance, may produce persistent landscape patterns. However, after fire, the persistence or switch to an alternative state may depend on the complex interplay of ecological memory (biological legacies) and potential effects of new external factors

influencing the post-fire environment. The current study assesses both the strength of

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ecological memory resulting from biological legacies of pre-burn vegetation types as well as post-fire effects of livestock.

2. Following a severe fire in 1999, we set up a network of long-term exclosures to examine the effects of legacies and cumulative herbivory by cattle on fuel types, amounts, distribution, flammability and micro-environmental conditions in two post-fire communities representing alternative fire-driven states: pyrophobic *Nothofagus pumilio* subalpine forests and pyrophytic *N. antarctica* tall shrublands in northwestern Patagonia, Argentina.

3. Our results show that the retained post-disturbance legacies of tall shrublands and subalpine forests largely determine fuel and flammability traits of the post-fire plant communities 16 years after fire. The importance of biological legacies retained from the unburned plant communities was reflected by the substantially higher amounts of total fine fuel, greater vertical and horizontal fuel continuity and the higher temperatures reached during experimental tissue combustion at post-fire shrubland compared to post-fire forest sites.

4. We show that herbivores may produce antagonistic effects on flammability by decreasing tissue ignitability, total fine fuel and litter depth, and disrupting the vertical and horizontal fine fuel continuity, therefore reducing the probability of fire propagation. However, cattle can increase ratios of dead to live fine fuels, reduce soil moisture, and inhibit tree height growth to canopy size, consequently impeding the development of a closed pyrophobic forest canopy.

5- *Synthesis*. Our results support the hypothesis that biological legacies, most importantly the dominance by pyrophytic woody plants that resprout vigorously versus the dominance by pyrophobic obligate seeders, favour fuel and flammability characteristics at the community level which reinforce the mechanisms maintaining pyrophytic shrublands versus pyrophobic

forests. Herbivory by introduced cattle can partially blur sharp pyrophobic/pyrophytic state boundaries by promoting the development of novel post-fire transitional states.

**Key-words:** ecological memory; livestock effects; non-resprouting species; *Nothofagus* spp.; plant–herbivore interactions; plant population and community dynamics; pyrophobic forests; pyrophytic shrublands; resprouting.

## Introduction

An early recognition of the importance of biological legacy in determining patterns of secondary succession was encompassed in Egler's (1954) concept of initial floristic composition as applied to propagules (seeds, fruits, resprouting vegetative organs) present at the initiation of successional processes. Nowadays the modern concept of biological legacy has grown to encompass not only the flora characterized by differential survival of propagules present prior to disturbance but also a broad suite of other biotic and abiotic characteristics of the affected plant community. Successful species traits and adaptations (i.e. information legacies) or physical structures arising from past biological activity (i.e. material legacies), all together are also referred to as ecological memory (Peterson 2002; Johnstone *et al.* 2016). The extent and type of retained biological legacies present following a disturbance event often depend on its severity and frequency, and accordingly, these legacies may influence the resilience of the ecosystem (Drever *et al.* 2006). In this context, ecological resilience is defined as the degree of disturbance that a system can absorb without undergoing significant transformational change and shifting into another alternative state (Holling 1973; Pickett *et al.* 1989; Mori 2011).

Alternative stable states occur when assemblages of different species coexist side by side in apparently the same environment, and are often separated by sharp boundaries which in general do not correspond to any underlying environmental condition (Petraitis & Latham 1999; Odion, Moritz & DellaSala 2010). In recent decades, there has been a growing awareness of the co-existence of fire-maintained alternative states in a broad range of biomes (Wilson & Agnew 1992; Bond & van Wilgen 1996; Warman & Moles 2009; Odion, Moritz & DellaSala 2010; Hoffman *et al.* 2012; Pausas 2015). Fire-driven alternative vegetation communities may switch between a pyrophobic ecosystem which rarely burns, commonly forest, and a fire-prone system, commonly savannas, grasslands, sclerophyll woodlands or dense shrublands, which are subjected to frequent fire occurrence. Such fire-maintained alternative stable states are recognized for forest and shrubland communities in the Andean-Patagonian region of Southern South America (e.g. Mermoz, Kitzberger & Veblen 2005; Kitzberger *et al.* 2012; Paritsis, Veblen & Holz 2015; Kitzberger *et al.* 2016). Shrublands and forests of the northern Patagonian-Andean landscape have been the object of a series of studies over the past three decades that have identified key elements and mechanisms of fire-driven alternative states reflected by juxtaposed pyrophytic tall shrubland and pyrophobic forests dominated respectively by resprouting versus obligate seeding tree species (Veblen & Lorenz 1988; Mermoz, Kitzberger & Veblen 2005; Paritsis *et al.* 2013). In this landscape, herbivory by introduced animals may influence post-fire vegetation recovery and therefore the potential to shift from one alternative state to another (Veblen *et al.* 1992; Raffaele *et al.* 2011). The current study assesses both the strength of ecological memory resulting from biological legacies of the pre-burn vegetation types (e.g. pyrophytic woody plants that resprout vigorously versus the dominance by pyrophobic obligate seeders) as well as the post-fire effects of livestock which potentially could exacerbate or attenuate differences associated with biological legacies.

In northwest Patagonia, plant community structure and landscape pattern have been historically determined by natural and anthropogenic fire (Veblen *et al.* 2003). Large areas of Andean Patagonia are occupied by either pyrophobic subalpine deciduous forests dominated by the non-resprouter tree *Nothofagus pumilio* (hereafter subalpine forest), or tall shrublands characterized by the dominance of resprouting pyrophytic shrubs, bamboos and small trees like *N. antarctica* (hereafter tall shrublands). *Nothofagus pumilio*, typically forms dense monospecific stands and constitutes the most extensive forest type in southern Argentina and Chile (Veblen *et al.* 1996). Bordering these forests, 3-5 m tall shrublands of woody species are all capable of vigorously resprouting after cutting, browsing or burning. In general, fires start at low to mid-elevation in shrublands and spread upslope but may stop when they reach mature *N. pumilio* forests (Paritsis, Veblen & Holz 2015). Only during extreme drought years do fires burn large areas and spread into the less flammable *N. pumilio* forests (Veblen & Lorenz 1988; Mermoz, Kitzberger & Veblen 2005). Three main mechanisms may contribute to the lower flammability of *N. pumilio* forests as compared to adjacent shrublands (Paritsis, Veblen & Holz 2015): scarcity of fine fuels near the ground surface (i.e. 0-2 m height class), absence of vertical fuel continuity from the understory to the canopy and a cooler and moister microclimate that reduces the rate of fuel desiccation. In comparison to unburned tall forests, flammability of shrublands is promoted by reduced foliar moisture, greater structural connectivity due to the architecture of resprouting species, and a microclimate characterized by high solar radiation, low humidity and high mean air temperatures (Blackhall, Raffaele & Veblen 2012, 2015; Blackhall, Veblen & Raffaele 2015). Scarcity of remnant trees in severely burned patches, limited seed dispersal, absence of seed banks, unfavourable post-fire microclimatic conditions and herbivory may restrict post-fire regeneration of *N. pumilio* to a narrow belt of only a few tens of meters from fire edges (Kitzberger *et al.* 2005; Tercero-Bucardo *et al.* 2007; Raffaele *et al.* 2011). Species in the adjacent tall shrublands and in the

understories of subalpine forests resprout quickly and vigorously after fire providing within a few years abundant fuel to support a subsequent fire (Raffaele *et al.* 2011; Blackhall, Veblen & Raffaele 2015).

Herbivore impacts have been documented as major determinants of post-fire vegetation trajectories in Patagonia (Veblen *et al.* 1992; Kitzberger *et al.* 2005; Tercero-Bucardo *et al.* 2007) as well as in many other biomes across the globe (e.g. Vandvik *et al.* 2005; Fuhlendorf *et al.* 2009; Perry *et al.* 2015). However, the potential capacity of large herbivores to modify fuel or flammability characteristics of post-fire vegetation has only recently been highlighted in Patagonia (e.g. Raffaele *et al.* 2011; Blackhall, Raffaele & Veblen 2012) and elsewhere (e.g. Kirkpatrick, Marsden-Smedley & Leonard 2011; Trauernicht *et al.* 2013; Johansson & Granström 2014; Evans, Ellsworth & Litton 2015). Continued and prolonged herbivory may alter post-fire flammability and successional trajectories through a broad range of mechanisms, including but not limited to selective browsing of plants with particular chemical or morphological properties which in turn may modify vegetation structures and/or alter competitive hierarchies (Rundel 1981, Bond & van Wilgen 1996). Numerous studies have documented important influences of introduced herbivores (e.g. cattle, boar, European hare and red and fallow deer) on the floristic composition and structure of vegetation of a wide range of community types in Northwest Patagonia (e.g. Martin, Mermoz & Gallopín 1985; Veblen *et al.* 1992, Relva & Veblen 1998; Kitzberger *et al.* 2005; Blackhall, Raffaele & Veblen 2008). However, cattle effects on vegetation properties specifically related to fuel and flammability at a community scale have only been inferred from indirect observations (e.g. reduced quantities of surface fuels; Paritsis, Veblen & Holz 2015) or from studies conducted at an individual plant scale (e.g. increased foliar flammability –reduced leaf size and foliar strength, or shorter time to ignition

of tissues– or reduced vertical fuel continuity of palatable species; Blackhall, Raffaele & Veblen 2012; Blackhall, Veblen & Raffaele 2015).

Worldwide, vegetation flammability and fuel characteristics have been studied at different scales -leaf, whole plants and community. Recent work has shown that flammability of small part plants (e.g. species-level leaf traits) can greatly improve fire behaviour models that otherwise only consider conventional fuel parameters such as surface fuel load or understorey cover (Zylstra *et al.* 2016). Commonly, four main components of flammability are emphasized: ignitability, sustainability, combustibility and consumability (Anderson 1970; White & Zipperer 2010). In our study we measured fuel and flammability characteristics covering the four main flammability components through both field and laboratory characterization (Table 1). Implementing this conceptual framework, we examine the effect of cattle on fuel and flammability properties in a network of long-term animal enclosures installed following a severe fire in the year 1999, in two post-fire communities representing alternative fire-driven states, pyrophobic *N. pumilio* subalpine forests and adjacent pyrophytic *N. antarctica* tall shrublands. We established permanent plots from which livestock were excluded and control plots lacking enclosures. During the following years, the experimental exclusion of introduced herbivores revealed that cattle had significant effects on the cover and mean heights of all plant life forms in both community types and also showed that differences in plant functional types (including sprouting and seeding traits) influence plant population responses to large herbivores (Raffaele *et al.* 2011). The current study experimentally examines the effects of legacies and cumulative herbivory by cattle on fuel types, amounts, distribution, flammability and micro-environmental conditions. We hypothesize that after 16 years (early post-fire stage), post-fire fuel and flammability characteristics will diverge in the burned tall *N. pumilio* forest and *N. antarctica* shrubland, evidencing strong biological legacies which contribute to the maintenance of these

juxtaposed fire-driven alternative states. Furthermore, we expect that cattle herbivory will contribute to the post-fire shift from burned pyrophobic forest and pyrophytic shrubland to a homogenised novel pyrophytic state.

## Materials and methods

### Study area

The study was conducted at Cerro Donat (41°26'19''S, 71°36'18''W; 1150 m) in Nahuel Huapi National Park, northwest Patagonia, Argentina. In this area, a set of experimental exclosures against cattle were installed following a large fire that occurred in January 1999. The fire burned mostly at high severity across ca. 5000 ha of diverse vegetation communities, including large areas of typical *N. pumilio* subalpine forests and tall shrublands dominated by the shrubby tree *N. antarctica* (Salguero *et al.* 1999). The burned subalpine forests, from 1000-1100 m to the upper tree-line were characterized by the dominance of stands of > 20 m tall *N. pumilio*. A few common small trees and shrubby species dominate the understory of the subalpine forests, including *Berberis* spp., *Schinus patagonicus*, *Maytenus chubutensis* and the bamboo *Chusquea culeou* (plant nomenclature follows Correa 1969-1997). These understory species also typically accompany *N. antarctica* in tall shrublands and all of them, including the *N. antarctica*, characteristically resprout vigorously after fire, cutting or browsing, and usually replace forest following burning (Veblen *et al.* 2003). Both *Nothofagus* spp. are palatable species; however, the inhibitory effect of livestock is greater on the growth and survival of *N. pumilio*, since *N. antarctica* is capable of resprouting even under heavy browsing (Raffaele *et al.* 2011).

The intensity and timing of livestock use of the study sites represents the common pattern of livestock use of *N. pumilio* subalpine forests and *N. antarctica* tall shrublands in the National Reserve zone of Nahuel Huapi National Park where limited livestock use is



permitted (Raffaele *et al.* 2011). Cattle have been present in moderate numbers at the sample sites for at least 30 years prior to the 1999 fire, as reported by the owner of the livestock and local officials of the National Park. Since the 1999 fire, cattle forage at the site mainly from spring to autumn (October to April) and a few wild cattle remain at the site all year (approximately 0.03 head of cattle/hectare for the area; Seoane 2015). Similarly, the introduced European hare (*Lepus europaeus*) is abundant at the study sites but its effect on the vegetation is less severe than that of the livestock (Raffaele *et al.* 2011). During the periodic re-measuring of permanent plots at the site, we did not observe evidence of presence of any native mammalian herbivores.

Mean annual temperatures in the area range between 1.9 and 15.6 °C (min. to max. annual means from 2000-2010, at the closest climate station – Bariloche Aerodrome Station data). Mean annual precipitation at the experimental site is approximately 1700 mm and mostly occurs during autumn and winter months, whereas summer precipitation is scarce. At the sample sites, soils are derived from volcanic ash deposits overlying glacial and periglacial topography.

#### Experimental design, data collection and variables

To conduct this analysis, we collected data in long-term livestock exclosures installed in 2001 in a post fire subalpine forest and in a juxtaposed tall shrubland. For each vegetation type, we randomly installed five fenced cattle exclosure plots and five permanent unfenced control plots (each 25 m × 25 m). All the plots were located following a paired plot experimental design (Sokal & Rohlf 1981) and placed in severely and homogeneously burned areas lacking surviving aboveground vegetation (Raffaele *et al.* 2011). In summer 2015, 16 years after fire and 14 years after we installed permanent plots, we measured fuel

characteristics, collected samples for flammability experiments and monitored micro-environmental conditions at both sites.

### *Fuel characterization*

At each fenced and unfenced permanent plot, stand structural fuel data were collected following the point-intercept method (Mueller-Dombois & Ellenberg 1974). In each plot we systematically located a grid of  $5 \times 5$  points separated 3 m from each other (25 points per plot, 125 per fenced or unfenced treatment at each post-fire habitat). At each point we recorded all species of vascular plants that intercepted a 4 m vertical pole, which was divided into 16 intervals (strata) of 0.25 m height. Species intercepts were recorded only for fine fuel material (< 0.6 cm in diameter) and additionally we classified these into dead and live tissues. Proportion of fine fuel material may be the best correlate of overall surface area:volume ratio; the greater the surface area in relation to the fuel volume, the faster the fuel will be heated and burned during a fire (Countryman and Philpot 1970). At each measuring point we also recorded litter depth (cm).

To relate fuel amounts and distribution to vegetation type and cattle pressure we evaluated the following variables through the analysis of vegetation intercepts: percentage of total fine fuel, percentage of dead/total fine fuel, vertical distribution of total and dead fine fuel, litter continuity (%), and mean horizontal fine fuel continuity (%) across the vertical distribution of fuel intervals. For estimating the percentage of total fine fuel, at each measuring point (25 points per fenced or unfenced plot), mean fuel intercepts at each height interval were estimated by pooling all species intercepts recorded within each strata and then computing the percentage of height intervals intercepted by fine fuel per measured point. The same procedure was used for estimating percentage of dead fine fuel. Vertical distribution of fuel was estimated by adding all intercepts per strata per plot and then calculating means per

plot type. Fuel horizontal continuity was estimated by calculating for each measuring point in the 5 × 5 grid, the proportion of next-measuring point (3 m distance) that intercepted the same fuel type; these values were estimated for each height interval, and one value per strata was calculated per plot and then averaged per type of plot. The same procedure was used for estimating the proportion of litter continuity. We estimated litter depth (cm) by averaging values per plot.

#### *Foliar moisture and plant-level flammability measurements*

Five species were selected for foliar moisture and flammability tests based on their importance in previous vegetation measurements at the sites (i.e. from 2001 to 2014; Raffaele *et al.* 2011). All the species selected are native woody or semi-woody species and are abundant in each type of community, comprising together on average more than 63 % of total woody and semi-woody species intercepts per type of habitat (reaching in some plots more than 80% of fuel intercepts for these life-form groups). The species sampled at both sites were the spiny shrub *B. buxifolia* (Berberidaceae), the semi-woody bamboo *C. culeou* (Poaceae) and the shrub or shrubby tree *S. patagonicus* (Anacardiaceae). We also sampled individuals of the shrubby tree *N. antarctica* (Nothofagaceae) at the shrubland site and saplings of the tree *N. pumilio* (Nothofagaceae) at the subalpine forest. Fifteen individuals per type of plot and per species in each community type (i.e. three individuals per plot) were sampled for flammability tests during the same days of field fuel data collections. Samples included leaves and small twigs (< 2.5 mm in diameter). From each sampled plant, we randomly harvested approximately 10 g of fresh well developed, fully expanded non-senescent and healthy leaves attached to the small twigs (i.e. no evidence of pathogens or herbivory), corresponding to the last growing season. All the material was enclosed in air tight plastic bags and stored in coolers until its analysis in the laboratory.

In the laboratory and immediately after field sampling, approximately 1 g of fresh material of six individuals per species and condition (three individuals from two plots per condition) were used to measure leaf moisture percentage using an OHAUS Moisture Analyzer (Model MB25). The device was set for calculating leaf moisture based on dry mass as follows =  $[(\text{fresh mass} - \text{dry mass})/\text{dry mass}] \times 100$ . At the same time, 3.5 g of leaves attached to the small twigs per each sample collected in the field (15 individuals per species and condition) were used to perform the flammability tests using an infrared quartz-silica epiradiator (500 W; Helios Italquartz ®, Milan, Italy), following the protocol in Blackhall, Raffaele & Veblen (2012) and Pausas *et al.* (2012). The epiradiator consists of an electric heating resistance that reaches a standard surface temperature of 420 °C. Samples were placed on a 10-cm diameter silica disk once the electric radiator was well heated. A thermocouple (Type K, range: 50°C - 1000 °C) connected to a data-logger (TES Model 1384; Time resolution: 2 s) was placed 8 cm above the epiradiator disk for recording flame and heat temperature during complete combustion. Flammability experiments were conducted in a closed environment to prevent any drought disturbance (temperature controlled, 20-22°C). For each sample the following parameters were recorded using the digital timer from the thermocouple data-logger: (1) time to ignition, in seconds, measured as the time from placement of the sample on the silica disk to appearance of the first flame, and (2) flame duration, in seconds, determined by flame extinction. In general the ignition frequency (percentage of samples that ignited) was 100 %, except for few samples of *C. culeou* and *S. patagonicus* (6.7 % and 13.3 % failed ignitions, respectively); these failed tests were not considered for computing flammability variables.

Leaf moisture and results from flammability tests for all species were pooled per plot for each cattle treatment and habitat type (pool of four species per condition for both vegetation types, including *N. pumilio* for subalpine forest and *N. antarctica* for tall

shrubland), providing a single community value which allowed a general comparison for the two community types and two cattle treatments. For all the variables derived from flammability tests we calculated the weighted pooled means considering the frequency at each plot (estimated from fuel intercepts) for each species of the pool of the four species. The variables derived from flammability tests were time to ignition (s) and flame duration (s). Shorter times for the former and longer times for the latter indicate higher flammability. Additionally we studied the trend over time of the temperature during three phases of the complete combustion: the temperature needed to achieve flame appearance, maximum temperature reached and temperature during flame extinction, for both cattle treatments and at both types of communities (adapted from Saura-Mas *et al.* 2010).

#### *Micro-environmental conditions*

From December 2014 to March 2015 we monitored air temperature (C°) and relative humidity (%) by placing a Hygrochron iButton data logger (DS 1923, Maxim Integrated) at three plots per type of plot, programmed to record values at 1-h intervals. Data loggers were placed at 1.0 – 1.5 m above the ground and protected from direct sunlight and precipitation using a covering roof. To examine microclimatic characteristics from different vegetation types and cattle treatments and under conditions most likely to be associated with fire, we calculated mean maximum air temperature per day (°C) and mean minimum relative humidity per day (%) for December and March (i.e., early and late fire season). In addition, in December 2014 and in March 2015 we recorded surface and 20 cm depth soil moisture (g H<sub>2</sub>O/g soil) at each fenced and unfenced plot (three to five measuring points per plot and three replicates per point) with a Theta Probe type ML2X (Delta-T devices) and following the protocol in Kitzberger *et al.* (2005). Microclimatic and soil parameters were averaged per plot.

## Data analysis

To relate fuel characteristics to vegetation types and cattle presence, we evaluated the following variables measured in the field: total and dead fine fuel vertical distribution (assessing sustainability), litter and fine fuel horizontal continuity (assessing sustainability), litter depth (assessing ignitability), and percentage of total fine fuel and percentage of dead/total fine fuel (these latter two to assess consumability). For analysing fuel vertical distribution and horizontal continuity we performed Kolmogorov-Smirnov tests to test the null hypothesis that samples are drawn from the same distribution, by comparing the frequencies among the different height classes (Conover 1980). This test is sensitive to differences in the location and general shapes of the distributions in the two samples (e.g. differences in means, average ranks, dispersion, skewness). We developed a general linear mixed model to independently evaluate the influence of two categorical fixed predictors (vegetation type: subalpine forest/tall shrubland, and cattle: fenced/unfenced plots), their interaction and blocks as a random effect, on litter depth, percentage of total fine fuel and percentage of dead/total fine fuel (Di Rienzo, Macchiavelli & Casanoves 2011).

To relate the laboratory measurements of flammability to vegetation types and cattle presence we analysed the following variables: leaf moisture and time to ignition (to assess ignitability), flame duration (to assess sustainability) and the trend over time of the temperature during the three phases of the complete combustion (assessing combustibility). As previously described, the general linear mixed model was independently applied to the data analysis of leaf moisture, time to ignition and flame duration, with vegetation type (subalpine forest/tall shrubland) and cattle (fenced/unfenced) as categorical fixed predictors and blocks as a random effect (except for leaf moisture). The differences between cattle treatments and between each vegetation type with reference to the temperatures at which the

flammability phases arose were analysed by performing a general linear mixed model with repeated measures, considering blocks as a random factor. Between-subject factors were herbivory treatments (fenced/unfenced plots) and vegetation type (subalpine forest/tall shrubland), and we considered the flammability phase as the within-subject factor (with three levels). We determined if differences between factors in trends over time in the response variables were statistically significant.

Finally, the following micro-environmental characteristics were evaluated independently for December and March: mean maximum air temperature per day, mean minimum relative humidity per day, surface and 20 cm depth soil moisture. As previously noted, these variables were analysed by applying the general linear mixed model with vegetation type (subalpine forest/tall shrubland) and cattle (fenced/unfenced) as categorical fixed predictors and blocks as a random effect.

For all variables, when significant interactions of factors were observed, we performed multiple comparisons tests (LSD Fisher; Kuehl 2001) to determine significant differences between group means. Normality of residuals was evaluated using Shapiro-Wilk's test and homogeneity of variances was assessed using Levene's test. InfoStat© software (v 2011; FCA, Universidad Nacional de Córdoba, Argentina) was used for running general linear mixed models and non-parametric tests. R was used for repeated measures linear mixed effect models. Response variable means were reported with standard errors (means  $\pm$  SE).

## Results

### Fuel amounts and distribution

Total fine fuel varied depending on vegetation type and the fencing treatment (Fig. 1a; see Table S1 in Supporting Information for details of statistical analysis; cattle  $\times$  vegetation type:  $P < 0.01$ ). Fine fuel amount was almost 250 % higher in shrubland fenced plots in

comparison to unfenced shrubland plots and fenced and unfenced subalpine forest plots.

Unfenced plots were associated with reduced total amount of fine fuel in both types of vegetation, but unfenced and fenced did not differ significantly in the subalpine forest. On average for both vegetation types unfenced plots showed more than six fold lower litter depth in comparison to fenced plots (Fig. 1c; Table 1S; cattle:  $P < 0.01$ ), and this litter depth reduction was greater at the shrubland site, (cattle  $\times$  vegetation type:  $P = 0.05$ ). Overall and regardless of cattle presence, total fine fuel and litter depth were considerably greater at tall shrubland sites in comparison to subalpine forest (Fig. 1a,c; vegetation type:  $P \leq 0.05$ ). On average, proportion of dead / total fine fuel was almost twofold greater at unfenced plots in comparison to fenced plots for both vegetation types (Fig. 1b; Table 1S; cattle:  $P < 0.01$ ).

Even though in unfenced plots we observed a greater amount of fine fuel in the first 0.25 m height interval at the shrubland site, plots with cattle showed significantly lower amounts of total fine fuel across all other height classes (Fig. 2;  $KS\ 0.56$ ,  $P < 0.02$ ). Cattle had no significant effect over the distribution of dead fuel amounts in fuel height strata in *N. antarctica* shrubland plots ( $KS\ 0.44$ ,  $P < 0.1$ ). At the subalpine forest site distribution of total fine fuel in height classes was similar between fenced and unfenced plots ( $KS\ 0.38$ ,  $P < 0.2$ ), whereas the amount of dead fine fuel in the first 1.5 m height classes was greater in the unfenced plots in comparison to fenced plots ( $KS\ 0.63$ ,  $P < 0.01$ ).

Mean horizontal continuity of fine fuel varied between cattle treatments in the tall shrubland (Fig. 3;  $KS\ 0.63$ ,  $P < 0.01$ ) and in the subalpine forest ( $KS\ 0.5$ ,  $P < 0.05$ ). In the tall shrubland, unfenced plots were characterized by lower horizontal continuity in all height classes, except for the 0.25 m interval which showed almost no differences, in comparison to fenced plots. In the unfenced plots of the subalpine forest, horizontal fuel continuity was zero above a height of 1.25 m (Fig. 3). In the post-fire subalpine forest, taller strata include mostly *N. pumilio* whereas in the shrubland these higher strata include numerous resprouting species,



such as *N. antarctica* and *C. culeou*, which can tolerate heavy cattle browsing. Despite the strong difference between fenced and unfenced plots, vertical distribution and horizontal continuity of fine fuel 16 years after fire are considerably greater at the tall shrubland site in comparison to the subalpine forest (Figs 2 and 3).

#### Fuel flammability

We did not observe differences between sites or by cattle presence for foliar moisture and flame duration for the weighted pool of four characteristic plant species growing at the shrubland plots in comparison with plants growing in the post-fire subalpine forest (Fig. 1d,f and S2;  $P > 0.05$ ). Time to ignition was on average 13% longer at unfenced plots in comparison to fenced plots (Fig. 1e; cattle:  $P < 0.05$ ), and no differences were observed between sites (vegetation type:  $P > 0.05$ ). Repeated measures analysis showed that, despite similar temperatures at the time of flame appearance between sites, plants growing at the shrubland site reached higher temperatures in later phases of the combustion process in comparison with plants from the subalpine forest (Fig. 4; Table S3; vegetation type  $\times$  phase:  $P = 0.05$ ).

#### Micro-environmental conditions

In December mean maximum temperature was 18.2 °C ( $\pm 0.4$ ) and mean minimum relative humidity per day was 45.1 % ( $\pm 0.5$ ) on average for all plots (Fig. 5). Microclimate conditions were warmer and drier in March, at the end of summer season, in comparison to December records, with a mean maximum temperature of 21.9 °C ( $\pm 0.3$ ) and mean minimum relative humidity of 32.1 % ( $\pm 0.5$ ) for all plots in March. Sixteen years after fire occurrence and regardless of cattle presence, no significant differences were observed across summer season for mean maximum air temperature and mean minimum relative humidity per

day between the two post-fire vegetation types (Table S4; vegetation type:  $P > 0.05$ ).

However, in both vegetation types mean maximum temperature per day in March was slightly higher in unfenced plots in comparison to fenced plots (on average 0.7 °C; cattle:  $P < 0.05$ ). This difference was not observed in the December records (cattle:  $P > 0.05$ ).

We did not observe differences in soil moisture between vegetation types in December (vegetation type:  $P > 0.05$ ). In March, at the end of summer, soil surface moisture was similar in all plots (cattle and vegetation type:  $P > 0.05$ ), but soil moisture at 20 cm depth was lower in *N. antarctica* shrubland plots in comparison to *N. pumilio* forest (vegetation type:  $P < 0.01$ ). In December for both vegetation types soil surface moisture and soil moisture at 20 cm depth were on average 55 % and 34 % lower, respectively, at unfenced plots in comparison to fenced plots (Fig. 6; Table S4; cattle:  $P < 0.01$ ).

## Discussion

### *Biological legacies affect fuel and flammability characteristics*

Our results show that the retained post-disturbances legacies of *N. antarctica* shrublands and *N. pumilio* forests largely determine fuel and flammability traits of the post-fire plant communities and consequently their successional trajectories 16 years after fire events. Regardless of cattle presence, the importance of biological legacies retained from the unburned plant communities was reflected by the substantially higher amounts of total fine fuel as well as higher vertical and horizontal continuity of fine fuels at post-fire shrubland versus post-fire forest sites. In addition, despite initial creation of more uniform temperatures and relative humidities at recently burned sites of both vegetation types, the higher temperatures reached during combustion of characteristic woody species of each site type revealed a higher inherent combustibility of plants growing at shrubland sites in comparison to subalpine forest sites.

The four components of flammability analysed in this study showed important differences between the two vegetation types. A higher total fine fuel (i.e. % of total intercepts of live and dead fine fuel; an indicator of potential consumability) and a higher vertical and horizontal continuity of fine fuel (an indicator of sustainability) at shrubland site in comparison to subalpine forest are consistent with previous studies documenting rapid vegetation (and fuel) recovery in *N. antarctica* shrublands following burning (Raffaele *et al.* 2011; Paritsis, Veblen & Holz 2015). Unburned *N. antarctica* tall shrublands are characterized by abundant fine fuel loads and greater continuity of fine fuels due to vigorous resprouting of woody species in comparison to the understorey of unburned *N. pumilio* subalpine forest (Paritsis, Veblen & Holz 2015). Following fire at both vegetation types, buried rhizomes, roots and lignotubers from resprouting species are capable of rapid regeneration. In the shrublands, this pre-disturbance legacy allows quick accumulation of abundant fuels in only a few years. In contrast, regeneration of the dominant species of *N. pumilio* forests is a slow process dependent on seed dispersal from unburned forest edges or in some cases from scarce survivors of the fire in the burned patch. In the subalpine forest woody fuel recovery is limited to rare *N. pumilio* seedlings and resprouts of woody species recorded in both vegetation types, but in low abundances under the closed canopies of unburned *N. pumilio* forests (Raffaele *et al.* 2011; Paritsis, Veblen & Holz 2015).

In our study, regardless of cattle presence we found higher litter depth in the shrubland compared to the subalpine forest sites. Larger leaf size and low fuel bed compactness favour better ventilation (Scarff & Westoby 2006), so that deeper litter of fine and dry flammable fuel may contribute to greater ignitability and also promote more rapid horizontal propagation and greater sustainability of fire once fuel is ignited (Anderson 1982; Curt *et al.* 2011). The two-fold difference in mean litter depth is consistent with the more than two-fold higher amount of standing live fine fuel at shrubland fenced plots in

comparison to fenced subalpine forest plots. Another condition promoting differences in potential fire behaviour between the two post-fire communities included higher soil moisture at 20 cm depth during March (the period of higher hydrological stress) in subalpine forest plots in comparison to tall shrubland. During a fire, the water loss of the upper layers of the soil is strongly influenced by the water content of the underlying soil and is likely to influence temperatures attained during the fire (Campbell *et al.* 1995). In general, the presence of surface organic layers and dry soil conditions retard soil heating, while wet and bare mineral-soil surfaces can be heated rapidly (Neary *et al.* 1999). Post-fire regeneration may be strongly influenced by pre-disturbance litter characteristics and inherent soil properties since temperatures reached in soil layers during a fire can affect belowground resprouting organs and responses of seeds to heat (Keane & Finney 2003).

Fuel combustibility (i.e. the intensity with which plant material burns in experimental assays) was higher for plants growing in the tall shrubland in comparison to plants growing in the burned subalpine forest. Regardless of cattle presence, the temperatures reached during tissue combustion were higher for plants from the shrubland site in comparison to plants from the subalpine forest. This was observed for the pool of species (means weighted according to species frequency) sampled in each vegetation type and also for individual species and non-weighted means. Although *N. antarctica* showed lower foliar moisture in comparison to *N. pumilio* (M. Blackhall, E. Raffaele, J. Paritsis & F. Tiribelli, unpublished data), foliar moisture of the four pooled species was similar between both sites. Higher temperatures during complete combustion indicate higher amounts of heat released and therefore higher probabilities of triggering ignition in neighbour plants by driving moisture out of living and dead tissues (Rundel 1981; Pausas *et al.* 2012). Previous studies in Patagonian post-fire vegetation have shown that more flammable foliar traits (lower foliar moisture, smaller leaf size and reduced specific leaf area) are more frequent at the warm dry micro-climate

associated with recent burns in comparison to unburned sites (Blackhall, Raffaele & Veblen 2012). In the present study, post-fire shrubland and post-fire subalpine forest showed similar values for mean maximum air temperatures, mean minimum relative humidity and soil surface moisture, 16 years after the strong homogenizing effect of fire. Therefore, except for the two *Nothofagus* species which clearly showed differences in foliar moisture, the heat released by the combustion of plants growing in a particular site may be inherently determined by other intra-specific factors than micro-environmental conditions.

Overall, these results support the idea that ecological memory produces persistent landscape patterns by establishing feedback loops between fire spread and vegetation type. However, after fire disturbance, the maintenance of alternative states depends not only on ecological memory and associated biological legacies left from the pre-disturbance community but also may be influenced by new external drivers of vegetation change affecting the post-fire environment, such as herbivory by introduced livestock.

#### *Herbivores as modifiers of fuel community traits and post-fire vegetation trajectories*

Our fencing experiment showed that 14 years after cattle exclusion there were important differences attributable to presence or absence of cattle, yet their implications for flammability were complex and sometimes antagonistic. We observed that introduced livestock can strongly affect the amounts, structural distribution and flammability of fuels, and thus potentially modify fire behaviour at each vegetation type. Although cattle increased the proportion of dead / total fine fuel in the community, livestock presence also drastically decreased total fine fuel and litter depth, and disrupted the vertical and horizontal fine fuel continuity. The latter two changes are consistent with the interpretation that at shrubland sites cattle may reduce the probability of fire propagation. However, in addition to increasing the proportion of dead / total fine fuel, cattle also impede the regeneration of the subalpine forest

to a non-flammable mature *N. pumilio* community by dwarfing tree saplings and preventing the attainment of a tall closed vegetation canopy (Raffaele *et al.* 2011). Through these different mechanisms, cattle not only may alter flammability and the potential for fire but also the resilience of the systems driving them into different alternative states.

Although worldwide livestock herbivory has been regarded as reducing fire frequency and/or intensity through reduction of fine fuel biomass, especially in ecosystems dominated by palatable grasses, (Davies *et al.* 2010; Leonard, Kirkpatrick & Marsden-Smedley 2010; Evans, Ellsworth & Litton 2015), their effects on fire regimes of tall shrublands and forests are less clear (Belsky & Blumenthal 1997; Blackmore & Vitousek 2000; Williams *et al.* 2006; Johansson & Granström 2014; Williamson, Murphy & Bowman 2014). Our results indicate that by reducing biomass at both vegetation types but especially at the shrubland site, cattle decreased fine fuel amount (associated with consumability), litter depth (fine dead fuel associated with ignitability), and the vertical and horizontal distribution and continuity of fine fuel and litter (associated with sustainability). This reduction in fine fuel, reflected at both sites by reduction or even lack of vertical and horizontal continuity, may reduce the probability that surface fire reaches the canopy or propagates horizontally (Anderson 1982; Flannigan *et al.* 2009). Our results are consistent with the interpretation that herbivory can reduce fire propagation and severity, especially in the tall post-fire shrubland. In addition, for the pool of species growing in the presence of cattle, we recorded a longer time to ignition, once tissues are exposed to a heat source, indicating a lower ignitability. This response is the sum of the specific response of each species (each weighted according to its frequency), which may vary depending on tissue chemical and physical characteristics (e.g., secondary compounds, specific leaf area, or leaf toughness; Rundel 1981). These traits are also associated with resistance to herbivory (Crawley 1983; Read *et al.* 2009), indicating that cattle pressure can modify tissue flammability (Blackhall, Raffaele & Veblen 2012). These

results highlight the need for further research on the leaf-scale mechanisms underlying effects of herbivory on tissue flammability.

On the other hand, our results also showed that cattle substantially increase the proportion of dead/total fine fuel in the community (associated with consumability), and in the subalpine forest this dry fuel is present at greater heights above the ground. This increase in the percentage of senescent tissues may be associated with stress produced on browsed individuals, as has been observed at an individual plant scale for the woody resprouting species (Blackhall, Veblen & Raffaele 2015). Under these circumstances, the rapid ignition and combustion of retained dead material can more readily drive out the moisture of living fuels (even in tissues with lower ignitability) and therefore contribute to the energy released in a fire (Countryman & Philpot 1970; Schwilk 2003).

At the surface level in both vegetation types, cattle reduced litter depth and litter horizontal continuity which would be expected to reduce potential surface fire propagation. On the other hand and possibly directly associated with litter effects, plots under cattle pressure showed decreased soil moisture at the surface and at the 20 cm depth at the beginning of summer season. Besides trampling effects, domestic livestock consume the vegetation biomass available to be converted into litter, consequently increasing the proportion of bare soil (Belsky & Blumenthal 1997). By indirectly reducing surface soil moisture cattle may favour more rapid desiccation of the remnant litter biomass and increase the probability of ignition. This effect can be amplified by the air temperatures observed at plots under cattle pressure, where mean maximum air temperatures reached during the warmest and driest month of the summer season for both post-fire vegetation types were on average 0.7°C higher at unfenced plots in comparison to plots without cattle. Under higher desiccation rates, less energy is needed for triggering ignition and the weather ignitability threshold decreases (Rundel 1981).

## *Integrating the effects of biological legacies and herbivores*

In the current study, we experimentally documented that by various mechanisms cattle can have antagonistic effects on post-fire vegetation and sites that in turn may modify the edges between alternative fire-driven states, pyrophytic shrublands and pyrophobic forests. In the tall shrublands cattle increase micro-environmental conditions conducive to increased ignitability but they also reduce fine fuel quantity and connectivity and increase the time needed to start ignition of tissues. Under moderate livestock pressure, post-fire resprouting woody species can tolerate herbivory so that despite a reduction in total fuel there is still sufficient fuel to sustain burning even only a few years following fire (Raffaele *et al.* 2011; Blackhall, Veblen & Raffaele 2015).

On the other hand, post-fire regeneration of *N. pumilio* is dependent on slow seed dispersal from scarce survivors of the fire or from the unburned forest edge (Veblen *et al.* 1996). Thus, following burning of these subalpine forests, cattle pressure impedes the survival and growth of *N. pumilio* in communities whereas the accompanying shrubs are able to quickly recover even in the presence of cattle (Tercero-Bucardo *et al.* 2007; Raffaele *et al.* 2011). Overall, despite the reduction in fine fuels, the longer-term effect of cattle on post-fire vegetation flammability is the inhibition of tree regeneration and therefore the shift from a former closed canopy forest to an open-canopy shrubland vegetation susceptible to more rapid fuel desiccation. By reducing height growth of *N. pumilio* saplings as reflected by lower fuel height of unfenced plots in the current study, cattle retard or even impede post-fire recovery to closed canopy pyrophobic forest.

Unfenced plots, in both burned shrubland and subalpine forest, constitute a different state where fuel characteristics more strongly reflect cattle presence and less strongly reflect biological legacies (Figs 1 to 3). In presence of cattle, contrasting ecological memory does not confer greater resilience; moreover, cattle may blur the boundaries of alternative stable



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fire-driven states, driving a post-fire community into a different pyrophytic novel transitional state. This scenario is widely replicated across northwestern Patagonia where in the late 19<sup>th</sup> to early 20<sup>th</sup> centuries, European settlers sharply increased fire activity by burning to open land for grazing and agriculture and affecting vast areas of forests (Veblen *et al.* 2003). Today, under current climate trends, large and severe fires related to warmer summers and stronger droughts often spread from pyrophytic shrubland into pyrophobic forests both of which are typically subjected to herbivory by livestock (Veblen *et al.* 2011).

A conceptual and simplified model of the subalpine forest and tall shrubland landscapes is shown in Fig. 7, where we synthesize results of the current research and findings from previous studies (e.g. Raffaele *et al.* 2011; Blackhall, Raffaele & Veblen 2012; Blackhall, Raffaele & Veblen 2015; Paritsis, Veblen & Holz 2015, Kitzberger *et al.* 2016). In a scenario without herbivory by introduced cattle, strong ecological memory contributes to the maintenance of the sharp boundaries dividing fire-driven alternative states. In a landscape under moderate cattle pressure, inhibition of the pathway from pyrophytic to pyrophobic vegetation after fire also is expected. Furthermore, herbivory by livestock, depending on timing and intensity of pressure, may contribute to the blurring of the alternative state boundaries, partially decreasing the effect of biological legacies on the system regeneration and homogenizing the post-fire degraded landscape.

## Conclusions

Our results show that biological legacies of burned plant communities characterized by woody plants that resprout vigorously, as opposed to those dominated by obligate seeders, favour fuel and flammability properties at the community level which reinforce mechanisms maintaining pyrophytic shrublands versus pyrophobic forests. Characteristics measured to indicate flammability components—ignitability, sustainability, combustibility and

consumability—indicate in general greater flammability of post-fire vegetation following the burning of tall shrublands in comparison to burning of tall closed canopy forests (i.e. greater values for total fine fuel, litter depth, fuel vertical distribution, horizontal fuel continuity, and maximum temperatures reached during combustion of tissues samples). The experimental removal of cattle from both vegetation types indicates that cattle have significant but in some cases antagonistic influences on flammability. Total fine fuels, vertical and horizontal fuel continuity and tissue ignitability are reduced by cattle. However, increased ratios of dead to live fine fuels, reduced litter depth and therefore reduced soil moisture, and inhibition of tree height growth which impedes the development of a closed forest canopy are important ways by which cattle contribute to a shift from less flammable forest to more fire-prone shrublands. Thus, control of livestock access to recently burned forests or at least individual protection of *N. pumilio* saplings is essential for post-fire pyrophobic forest recovery.

#### **Author's contributions**

ER, TK, TTV, MB and JP conceived the ideas and designed methodology; ER, JP, FT, TK, JHG collected the data; FT, MB, JP and JMM analysed the data; MB, FT and TK prepared the Figures and Tables; MB and TTV led the writing of the manuscript.

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## Data accessibility

Data available at the public archive figshare <https://figshare.com/s/bb5fd2ebdb88d92b792c>

(Blackhall *et al.* 2017).

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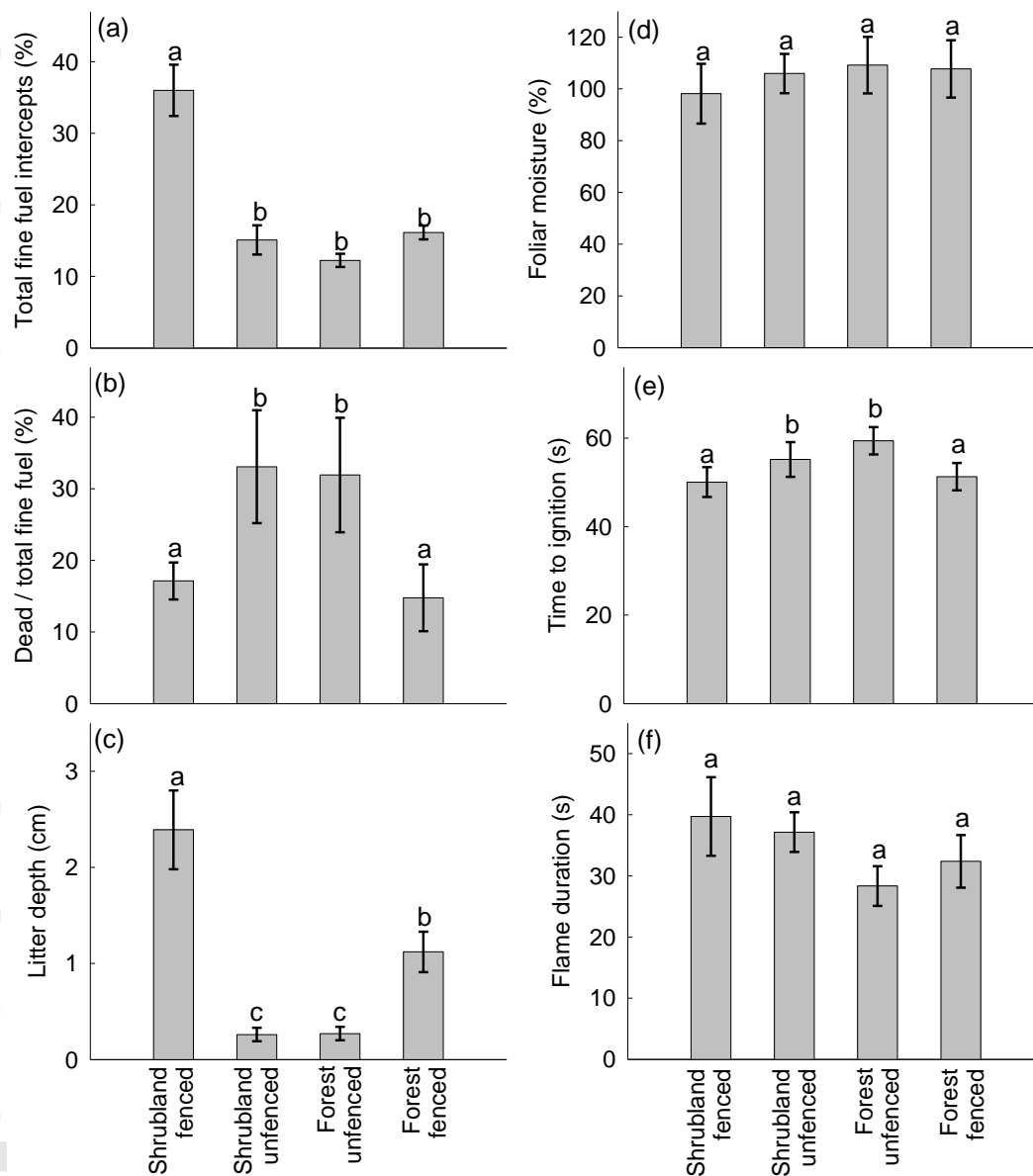
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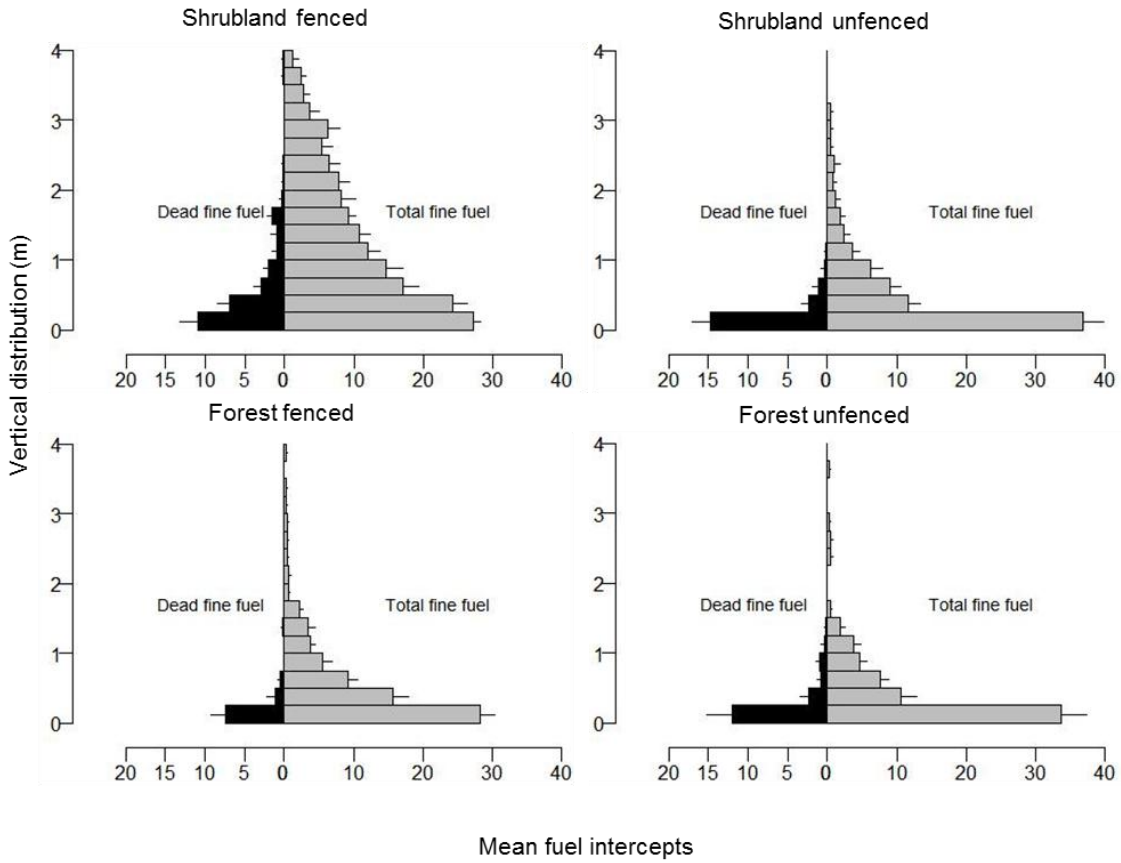
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**Table 1:** Definitions of the four flammability parameters first described by Anderson (1970) and modified by White & Zipperer 2010. For each parameter a few examples of associated characteristics of the vegetation are given, detailing the scale of study: field studies (patch or stand scale) or laboratory assays (typically conducted at the scale of plant parts). The specific variables analyzed in our study for each flammability parameter are highlighted in bold letters. References: Anderson 1970; Anderson 1982; Gill & Zylstra 2005; Behm et al. 2004; White & Zipperer 2010; Blackhall, Raffaele & Veblen 2012; Cobar-Carranza et al. 2014; Bianchi & Defossé 2015; Blackhall, Veblen & Raffaele 2015.

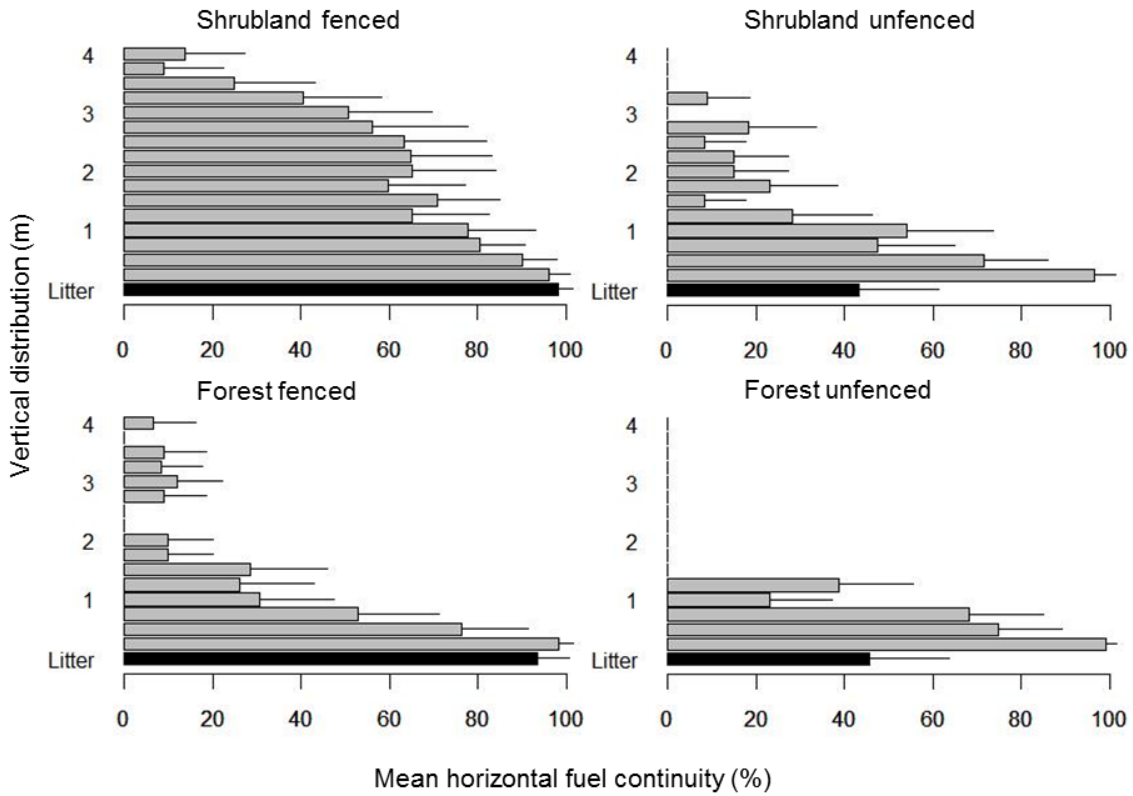
<i>Flammability Parameter</i>	<i>Definition</i>	<i>Examples of associated characteristics of the vegetation</i>	
		<i>Field studies</i>	<i>Laboratory assays</i>
Ignitability	Time until ignition once exposed to a heat source	<b>litter depth</b> ; height to lowest branch	<b>ignition delay time, moisture content</b> , thickness of tissues
Sustainability	The ability to sustain fire once ignited	plant bulk density, <b>vertical and horizontal continuity of fuel</b> , surface area burned	heat of combustion, <b>duration of combustion</b> , total heat released
Combustibility	Measures the rapidity of combustion or how well plant material burns	fire intensity, length of flame	<b>peak temperature</b> , rate of temperature increase, the flame length
Consumability	Considers the proportion of the original mass consumed by the combustion	<b>amount of live and dead fine fuel biomass</b> in an individual or in the community	mass loss rate in combustion tests



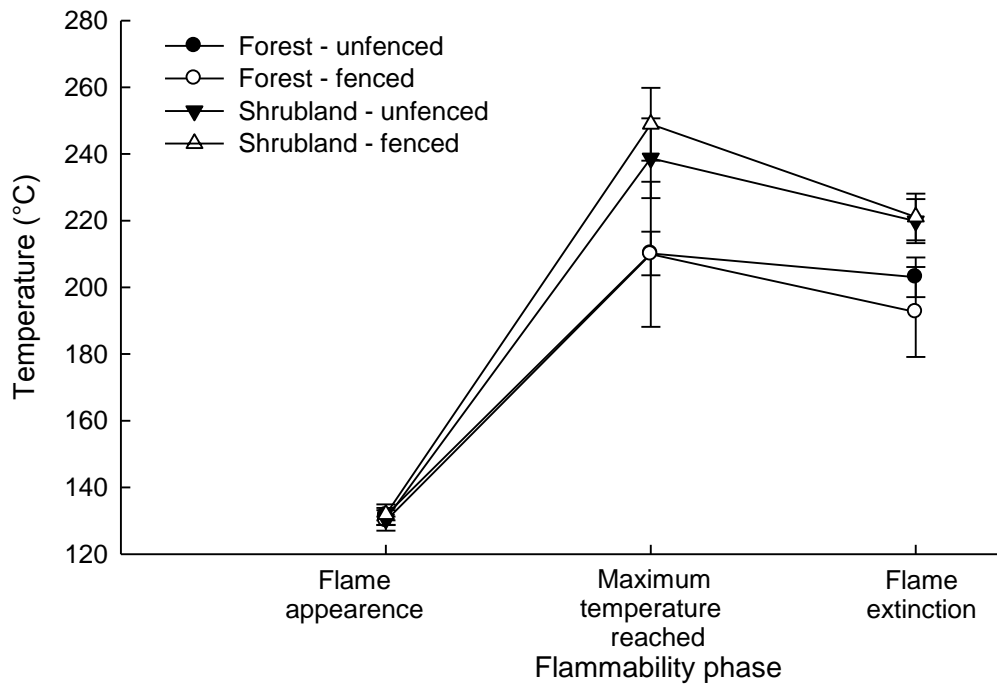
**Fig. 1:** Means ( $\pm$ SE) for fuel and flammability characteristics: (a) percentage of total fine fuel intercepts (%), (b) proportion of dead/total fine fuel (%), (c) litter depth (cm), (d) foliar moisture (%), (e) time to ignition (s) and (f) flame duration (s), at post-fire *Nothofagus pumilio* subalpine forest and post-fire *N. antarctica* shrubland sites, for unfenced and fenced plots. Weighted means are shown for flammability variables for the pooled four most characteristic woody species (see Methodology). Different letters are shown for variables with significant differences between site or cattle effects ( $P < 0.05$ ).



**Fig. 2:** Mean fuel intercepts of fine fuel in 0.25 m height classes used for assessing fuel vertical distribution at post-fire *Nothofagus pumilio* subalpine forest and post-fire *N. antarctica* shrubland sites, for unfenced and fenced plots. Bars show mean dead and live fine fuel intercepts ( $\pm$ SE).

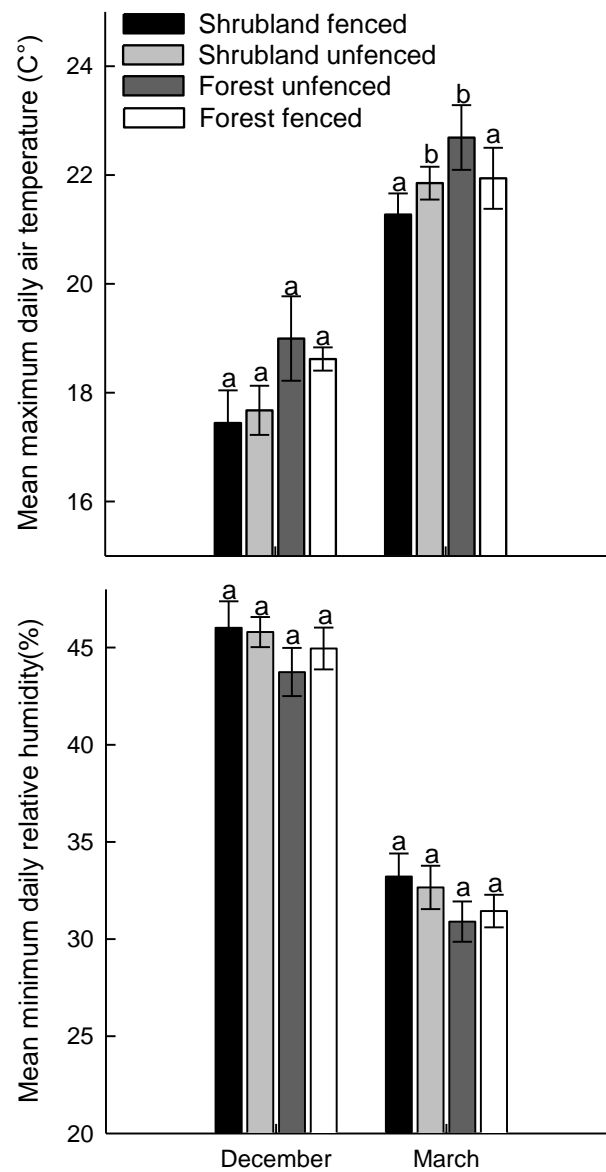


**Fig. 3:** Mean horizontal fuel continuity (expressed as percentages; see Methods for details) for litter (surface level) and for each 0.25 m height class ( $\pm$ SE) at post-fire *Nothofagus pumilio* subalpine forest and post-fire *N. antarctica* shrubland sites, for unfenced and fenced plots.

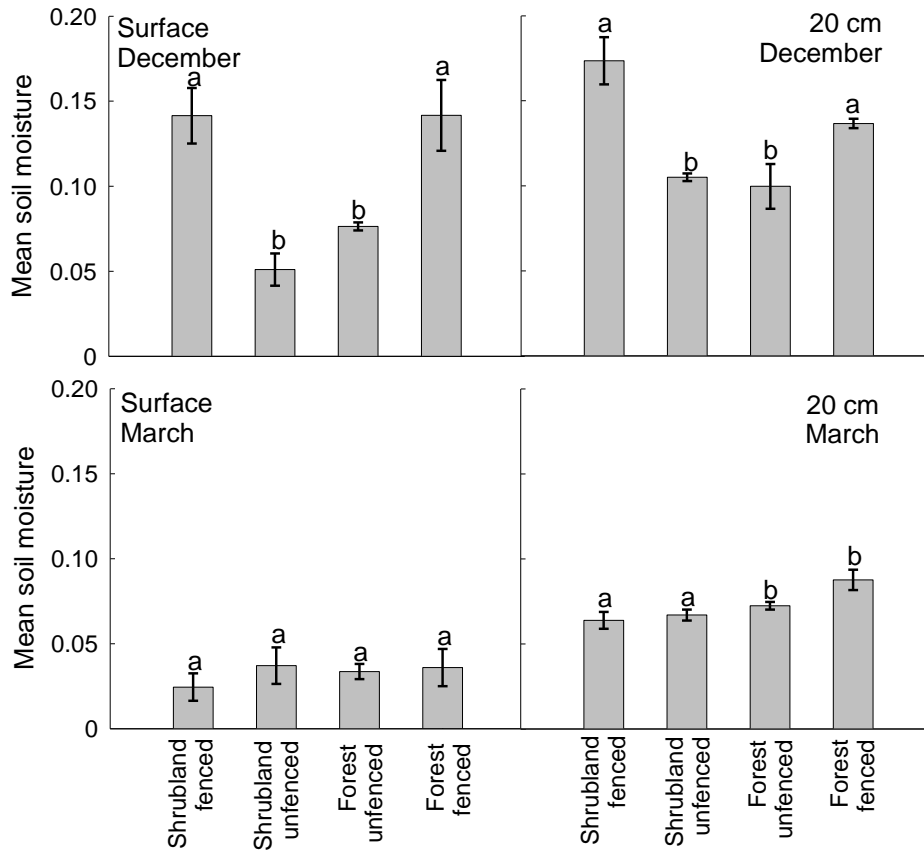


**Fig. 4:** Mean ( $\pm$ SE) of temperature recorded in the following phases of the complete combustion: flame appearance, maximum temperature reached and flame extinction. Curves are shown for post-fire *Nothofagus pumilio* subalpine forest and post-fire *N. antarctica* tall shrubland in fenced and unfenced plots. Means are weighted averages for the pooled four most characteristic woody species (see Methodology). See Table S3 for statistical significances.

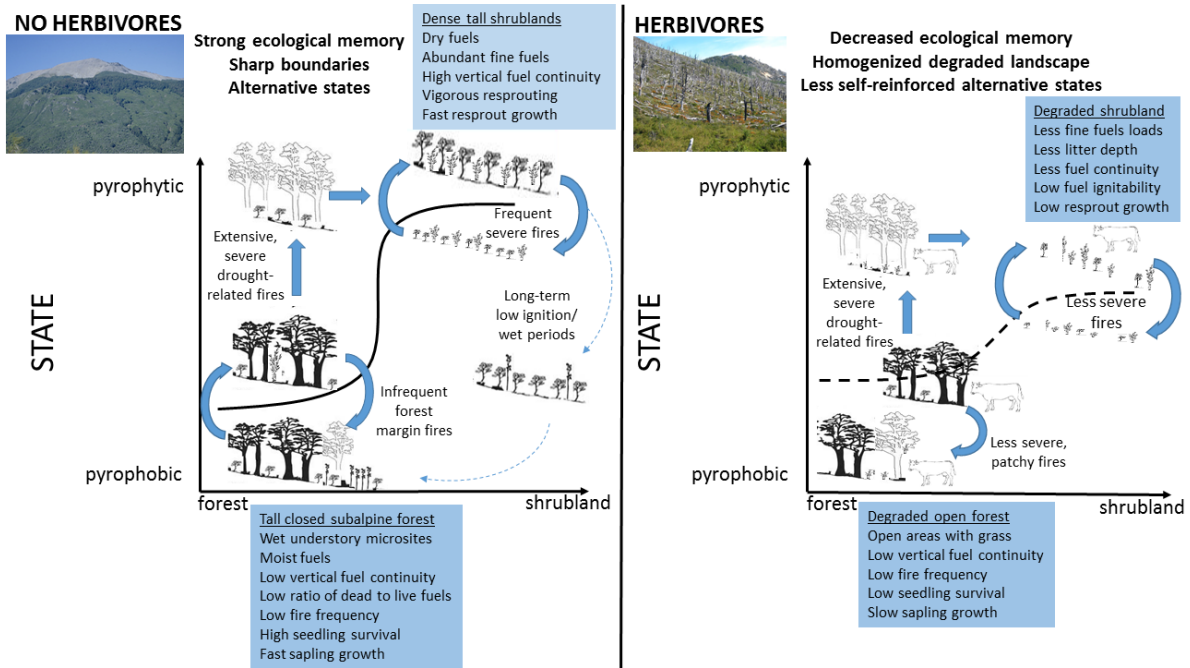




**Fig. 5:** Mean maximum daily air temperature (C°) and mean minimum daily relative humidity (%) ( $\pm$ SE) for December 2014 and March 2015, at post-fire *Nothofagus pumilio* subalpine forest and post-fire *N. antarctica* shrubland sites in unfenced and fenced plots. Different letters are shown for variables with significant differences between site or cattle effects ( $P < 0.05$ ).



**Fig. 6:** Mean ( $\pm$ SE) soil moisture (g H<sub>2</sub>O / g soil) at the soil surface and at 20 cm depth in December 2014 and March 2015 at post-fire *Nothofagus pumilio* subalpine forest and post-fire *N. antarctica* shrubland sites, for unfenced and fenced plots.



**Fig. 7:** Conceptual model of the fire-driven transitions between the alternative states in landscapes of *Nothofagus pumilio* subalpine forests and *N. antarctica* tall shrublands, and the potential effects of different fire regimes and herbivory by introduced cattle in northwestern Patagonia. On the left side of the figure and in absence of cattle, strong ecological memory contributes to the maintenance of sharp boundaries dividing fire-driven alternative states (represented by the solid curved line with a steep slope). On the right side and under moderate cattle pressure, herbivores contribute to the blurring of the alternative states boundaries by reducing the effect of biological legacies on the system regeneration and homogenizing the post-fire degraded landscape (represented by the dashed curved line with a lower slope).