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Recent fire and cattle herbivory enhance plant-level fuel flammability in shrublands

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Cattle herbivory; Fire ecology; Patagonian shrublands; Plant–herbivore interactions; Resprouting species; Species palatability

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Abstract

Question: Could disturbance by fire and ungulate herbivory alter fire regimes by increasing flammability in shrublands and early-successional forests?

Location: Nahuel Huapi National Park, northwest Patagonia, Argentina.

Methods: We compared four characteristics that influence fuel flammability – fine fuel load, plant bulk density, percentage fine fuel, and percentage dead fine fuel – and the vertical distribution of live and dead fine fuel at recently burned (<15 yr) and unburned (>50 yr) sites, both in the presence and absence of cattle, for six resprouting species: non-palatable *Lomatia hirsuta* and *Diostea juncea*, moderately palatable *Nothofagus antarctica* and *Schinus patagonicus*, and highly palatable *Maytenus boaria* and *Ribes magellanicum*.

Results: Changes in flammability in response to recent fire, and to a lesser extent cattle browsing, were strongly dependent on species identity. Non-palatable *L. hirsuta* tended to increase in flammability following fire, whereas cattle did not affect its fuel properties. *Nothofagus antarctica* showed ambiguous responses: plants had reduced plant bulk density at recently burned sites, implying reduced flammability, but changes in percentage fine and dead fine fuel point to increasing flammability at burned sites with cattle. *Diostea juncea* and *S. patagonicus* showed increased plant bulk density at sites with cattle and increased percentage fine fuel in response to fire. Cattle browsing was the main driver of variability in flammability for highly palatable species, showing increased plant bulk density and percentage fine fuel in response to cattle. Fire had a strong effect on the vertical distribution of live and dead fine fuel, showing an increase of burnable biomass in response to recent fire. The reduction of vertical fuel continuity was extreme on highly palatable species. In contrast, moderately and non-palatable species, which are abundant under herbivore pressure, were characterized by vertically well-distributed fine fuel biomass in the presence of cattle.

Conclusions: Responses of flammability traits to fire and cattle depended on species identity, but the majority of the species studied showed higher fuel flammability at recently burned sites affected by cattle. Domestic livestock, by increasing the flammability of post-fire vegetation, may be key agents in altering fire regimes in forest–shrubland mosaics.

Introduction

Humans have long modified vegetation patterns intentionally or accidentally by altering fire ignition rates and introducing domestic livestock to wildland landscapes (Bachelet et al. 2000; McWethy et al. 2013). However, there is relatively little research on how the combined influences of increased human-set fires and livestock herbivory may increase the vulnerability of landscapes to subsequent fires by enhancing vegetation flammability. In particular, little is known about the potential mechanisms by which an interaction of herbivory and anthropogenic fire may influence plant community flammability and result in positive feedbacks that enhance vegetation flammability at a

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landscape scale. In the current study we examine how effects of introduced herbivores (cattle) in areas recently burned affect plant characteristics, which in turn may alter flammability at the plant and community level.

Plant flammability is related to numerous morphological and chemical traits of plants that can be altered by local abiotic factors (most importantly by microclimate) and by direct and indirect effects of herbivory (Cornelissen et al. 2003). Variability in these plant traits, potentially due to microclimatic conditions or cumulative effects of herbivory, may affect plant flammability, which in turn affects ignition probability, rate of fire spread and fire intensity (Rundel 1981). Common metrics of flammability are: (1) ignitability, i.e. time until ignition once exposed to some heat source; (2) sustainability, i.e. the ability to sustain fire once ignited; (3) combustibility, i.e. the intensity with which plant material burns; and (4) consumability, i.e. the proportion of the original mass consumed by the combustion (Anderson 1970; White & Zipperer 2010).

There are several plant structural traits that have been related to fuel flammability, in terms of structural flammability, and are related to the arrangement, structure and physical characteristics of plant materials (Papió & Trabaud 1991; Behm et al. 2004). The two key properties affecting the total plant contribution of fuel to a community are fuel loading and plant bulk density. Fuel loading (i.e. dry weight of fuel per unit of canopy area) provides a measure of the amount of fuel that is available to burn in a community, and the potential amount of heat released by a fire (Rundel 1981; Papió & Trabaud 1991). Plant bulk density (i.e. weight per unit volume of fuel) can influence fire behaviour both directly, by providing continuity of fuels in living plants, and indirectly, through influences on fuel bed density, time of residence and temperatures in the soil during a fire (Behm et al. 2004; Pausas & Moreira 2012). Plant bulk density (inversely related to fuel porosity) has been associated with the sustainability of burning (Behm et al. 2004). Cruz et al. (2005) related a proportional increase in rate of spread of fire with increasing canopy bulk density, contrary to what is observed for surface fuel bed. Their observations agree with Rothermel's (1972) laboratory experiments, showing that an increase in packing ratio results in an increase in the propagating heat flux until an optimum packing ratio is reached. Low values of fire intensity and rate of spread occur at the two extremes of porosity. Behm et al. (2004) associated higher flammability of a community and high continuity of fuel to plants with high fuel bed bulk density, which may increase the sustainability of fire once the plant is ignited.

Retained dead material is one of the most important types of fuel that may affect plant structural flammability (Papió & Trabaud 1991; Bond & Van Wilgen 1996; Schwilk 2003; Baeza et al. 2011). The rapid ignition and combustion of dry dead material can drive the moisture out of living fuels, and hence contribute to the release of energy in a fire (Countryman & Philpot 1970; Bond & Van Wilgen 1996; Schwilk 2003). Plant fuels can also be classified according to their surface area:volume ratio and therefore into different size classes (foliage, fine woody fuel, coarse woody fuel). The greater the surface area in relation to the fuel volume, the faster the fuel will be heated and burned (Countryman & Philpot 1970). The summed proportion of live and dead fine material in a plant may be the best correlate of overall surface area:volume ratio (Cornelissen et al. 2003), and this metric has been associated with the consumability of fuel (Behm et al. 2004; White & Zipperer 2010). Vertical fuel distribution is another key issue when characterizing fuel and plant flammability in a community. The vertical distribution of dead and live fine fuels in a plant is important for evaluating fire spread, heat transfer to the soil and the probability of surface fire entering the canopy (ladder effect; Papió & Trabaud 1991; Schwilk 2003; Flannigan et al. 2009).

In northwest Patagonia (Argentina), the two most pervasive disturbances are fire and herbivory by large introduced mammals, particularly livestock and introduced red deer (Veblen et al. 1989, 2011). Tall mesic *Nothofagus* forests, composed of tree species that are obligate seeders that lack the capacity to resprout after fire, burn only under the most extreme drought conditions (Mermoz et al. 2005). Following forest burning, tree regeneration often fails due to herbivory or unfavourable post-fire abiotic conditions, so that fire-resistant forests are replaced by fire-prone tall shrublands. commonly dominated by the shrubby *N. antarctica*. In comparison to the tall mesic forests, the drier post-fire microclimatic conditions reduce leaf moisture content and leaf size, thus enhancing foliar flammability (Blackhall 2012; Blackhall et al. 2012).

Furthermore, following forest burning, browsing by large herbivores inhibits the post-fire regeneration of tall tree species, but is less limiting for the vigorously resprouting shrubs and small trees (Tercero-Bucardo et al. 2007; Raffaele et al. 2011). Thus, herbivory by large mammals in this landscape tends to inhibit post-fire forest recovery and favours the perpetuation of fire-prone shrublands. The most important large mammalian herbivores in the region are cattle and in some areas introduced cervids (Merino et al. 2009). Native large herbivores, such as the huemul deer (*Hippocamelus bisulcus*) and the guanaco (*Lama guanicoe*), are absent or extremely rare, particularly in the areas included in this study (Raffaele et al. 2011).

The main objective of the current study is to examine how plant structural properties related to fuel flammability of resprouting shrub and small tree species in northwest Patagonia are affected by presence of cattle, and if these

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characteristics vary in recently burned vs unburned communities. To identify the effect of large herbivores under different histories of fire on resprouter shrub and small tree species, we considered four characteristics believed to affect fuel properties related to structural flammability: fine fuel load, plant bulk density, percentage fine fuel and percentage dead fine fuel. In addition, we analysed the vertical distribution of dead and live fine fuel. We compared these characteristics in the presence or absence of livestock at sites burned within the past 15 yrs and sites not burned for at least 50 yrs.

Methods

Study area, species and sample sites

The study was conducted in Nahuel Huapi National Park, Argentina. Mean annual temperatures range between 1.9 and 15.6 °C (min. to max. annual means 2000–2010; Bariloche Aerodrome Station data). At the study sites, mean annual precipitation declines from west to east, from over ca. 1700 to 1000 mm; it occurs mainly during autumn and winter months, whereas summer precipitation is scarce. Study site elevations range from 766 to 1103 m. In northwest Patagonia, forests are dominated by tall tree species that are obligate seeders and generally do not resprout following fire. At high elevations (ca. 1000–1500 m), the deciduous sub-alpine forests are monospecific stands of *Nothofagus pumilio*. At low to mid elevations (ca. 800–1100 m), the tall evergreen forests are dominated by *Austrocedrus chilensis* and/or *N. dombeyi* (Mermoz & Martín 2005). This landscape of patches of mesic forests and xeric woodland is juxtaposed with patches of dense tall (2–5 m) shrublands; they consist of shrub and small tree species all of which are capable of vigorously resprouting after fire, cutting or browsing, and usually replace forest following burning (Mermoz et al. 2005; Raffaele et al. 2011). These tall shrublands are typically dominated by the shrubby tree *N. antarctica*, the bamboo *Chusquea culeou* and numerous tall shrub and small tree species such as *Lomatia hirsuta*, *Schinus patagonicus*, *Maytenus boaria*, *Diostea juncea*, *Ribes magellanicum*, *Berberis* spp. and abundant climbing plants (e.g. *Mutisia* sp., *Vicia nigricans*; Mermoz & Martín 2005; Raffaele et al. 2011).

The six species chosen for this study met the following criteria: (1) native tall shrub or small tree; (2) abundant in the understorey of young to moderately old post-fire forests (i.e. >50 yr old) or in tall post-fire shrublands that develop following the burning of these forests; and (3) vigorously resprout after fire. The palatability of each species was determined from previous multi-year studies of paired cattle exclosures and controls (Blackhall et al. 2008; Raffaele et al. 2011), and then classified into three classes: not palatable, moderately palatable and highly palatable. The species studied and their palatability classes are: (1) not palatable, *Lomatia hirsuta* (Proteaceae) and *Diostea juncea* (Verbenaceae); (2) moderately palatable, *Nothofagus antarctica* (Fagaceae) and *Schinus patagonicus* (Anacardiaceae); and (3) highly palatable, *Maytenus boaria* (Celastraceae) and *Ribes magellanicum* (Saxifragaceae).

As in Blackhall et al. (2012), the studied species were sampled at 17 sites, each one classified as: (1) recently burned (i.e. within 10–15 yr after fire: early post-fire shrubland vegetation) or alternatively as not burned (i.e. not having burned >50 yr: young to moderately old post-fire forests); and (2) free of livestock or alternatively as having a long history of intense and continuous cattle pressure (i.e. >25 yr). Accordingly, four types of sites were selected: four unburned and without cattle (−B−C), four unburned with cattle (−B+C), four recently burned without cattle (+B−C) and five recently burned with cattle (+B+C). Sites classified as recently burned had burned during extreme droughts in either January 1996 (two +B−C sites) or February 1999 (two +B−C sites and five +B+C sites), which were years of peak area burned in the ca. 60-yr fire history record of Nahuel Huapi National Park (Raffaele et al. 2011). Recently burned sites were typical post-fire successional stages dominated by tall shrubs and small trees (<6-m tall). The microclimates of recently burned sites at browsing heights of one to a few meters was characterized by significantly higher solar radiation, lower relative air humidity, higher diurnal temperatures and lower night temperatures (i.e. higher thermal amplitude) in comparison with unburned sites (Blackhall 2012). Cattle history (>25 yr of intense and continuous cattle pressure, or alternatively cattle absence for at least 10 yr) and current presence or absence were assessed from previous monitoring by National Park authorities (Lauría Sorge & Romero 1999) and verified by our own field observations (Blackhall 2012). Cattle effects across browsed sites were similar for all studied sites (no significant differences for Mean browse index – Mann–Whitney: $U = 8$, $P > 0.05$; Blackhall 2012). None of the sites were affected by any other large herbivore, such as introduced deer, or the native guanaco or huemul deer.

Plants and fuel sampling

Plant samples for fuel measurements were collected during four summer (December–March) seasons, corresponding with the season of maximum fire probability (years 2008–2011). Healthy, non-senescent and well-developed individuals were randomly selected for fuel sampling. At each of the 17 sites, two to five individuals of each species were collected, reaching a total average of nine plants of each

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species for each type of site (−B−C, −B+C, +B−C and +B+C). All sampled plants were tall enough to be potentially available for cattle; and all moderately and highly palatable sampled plants at sites with cattle showed intense cattle browsing signs (browsing index = 2 or 3 where 3 is the most intensive browsing in a three-class ranking system; Blackhall et al. 2008). At sites without cattle, moderately and highly palatable plants did not show evidence of browsing by any herbivores. To avoid sampling plants or stems of highly different ages, only plants of similar heights were sampled. Mean height for all plants and species was 2.03 ± 0.55 m. At sites with heavy cattle pressure individuals of more palatable species were shorter (<1 m) due to the dwarfing effects of cattle browsing.

Fuel measurements

For establishing plant dimensions, the following measurements were recorded in the field for each individual: maximum height; and depending on the shape of the plant, three or four crown widths at the widest point, measured in perpendicular directions (following Papió & Trabaud 1991). These data were used to compute: (1) canopy cover projected on ground (m^2) = $[(A_1 + A_2)/2] \times [(a_1 + a_2)/2] \times \pi$; and (2) canopy plant volume (m^3) = $[(A_1 + A_2)/2] \times [(a_1 + a_2)/2] \times \text{maxH}$). Where A_1 and A_2 are the largest widths, a_1 and a_2 are the smallest widths, and maxH the maximum height of the individual; computations are based on assumption of a circular-elliptic base (Countryman & Philpot 1970; Papió & Trabaud 1991).

Subsequently, all plants were harvested at 0.5-m height intervals (strata) for biomass measurements. In the laboratory, each 0.5-m height section of each individual was classified into dead and live fuel fractions; in turn, each fraction was subdivided into fine fuels (standing foliage and material <5 mm in diameter) and coarse fuels (>5 mm in diameter; Papió & Trabaud 1991; Cornelissen et al. 2003). Dead fine fuel fraction included dead reproductive parts and debris attached to plants. All fuel material was oven-dried at 60 °C during 72 h and weighed. Fine fuel load ($kg \cdot m^{-2}$) was calculated by dividing the total dry fine biomass of each individual by the canopy cover projected on ground; plant bulk density ($kg \cdot m^{-3}$) was calculated by dividing the total dry biomass by the canopy plant volume (Countryman & Philpot 1970; Papió & Trabaud 1991; Behm et al. 2004; Pausas et al. 2012). The percentage fine fuel and the percentage dead fine fuel relative to the total above-ground dry biomass of each individual were also estimated (Saura-Mas et al. 2010). Finally, the vertical distribution of live fine fuel and dead fine fuel was estimated from the surface of the ground to a maximum of 2-m height for each individual (i.e. four strata of 0.5-m height intervals).

Data analysis

To relate structural fuel flammability to time since last fire and herbivory by cattle, and statistical interactions of both factors and species, we evaluated four measured variables: fine fuel load, plant bulk density, percentage fine fuel and percentage dead fine fuel. In addition, we compared percentage live and dead fine fuel for each species in four height classes in order to assess vertical distribution of fine fuel. Means of these variables were evaluated independently using 2 × 2 × 6 factorial ANOVAs (fire = recently burned/unburned; cattle = presence/absence; species = the six studied species; Quinn & Keough 2002). All models included a compound symmetric covariance structure for the residuals grouped by species and site to account for the correlation between plants of each species sampled at the same site (Kuehl 2001). Thus, we avoided treating these observations as being totally independent. InfoStat© software (v 2011; FCA, Universidad Nacional de Córdoba, Argentina) was used for running factorial ANOVAS and for modelling the error. 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 (Quinn & Keough 2002). Logarithmic transformations were applied to improve normality and homogeneity of variances.

Results

Fuel characterization

The main effect for fire was only significant for one of the four fuel properties studied (proportion of fine fuel, fire: $P < 0.05$; Table 1). The same tendency, although not significant, was observed for fine fuel load (fire: $P = 0.05$). By contrast, cattle and species main effects were both significant for three of the four fuel properties (cattle, species: $P < 0.05$). There were significant fire × species interactions for all four fuel properties, indicating that responses to fire were strongly dependent on species identity (fire × species: $P < 0.01$). The cattle × species interaction was significant for proportion of fine fuel and proportion of fine dead fuel ($P < 0.01$), but the fire × cattle interaction was not significant for any of the fuel properties ($P > 0.05$). The three-way interaction (fire × cattle × species) was significant for two of the four fuel properties ($P < 0.05$). These results indicate that changes in flammability in response to recent fire, and to a lesser extent cattle browsing, are strongly dependent on species identity (Figs 1 and 2).

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Table 1. Results of 2 × 2 × 6 factorial ANOVAs [fire (F) = recently burned/unburned; cattle (C) = presence/absence; species (Spp) = six studied species] for four variables: fine fuel load, plant bulk density, percentage fine fuel, percentage dead fine fuel.

Effect	*df*	Fine fuel load		Plant bulk density		Proportion of fine fuel		Proportion of dead fine fuel	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
F	1	3.64	0.05	0.68	0.41	6.41	0.01*	0.01	0.93
C	1	1.43	0.23	16.29	<0.01**	6.31	0.01*	5.04	0.03*
Spp	5	5.40	<0.01**	1.83	0.11	4.28	<0.01**	17.12	<0.01**
F × C	1	0.01	0.99	0.03	0.95	0.87	0.35	0.76	0.38
F × Spp	5	4.05	<0.01**	6.05	<0.01**	6.10	<0.01**	3.74	<0.01**
C × Spp	5	0.74	0.59	1.74	0.13	7.93	<0.01**	3.26	0.01*
F × C × Spp	5	0.56	0.73	2.57	0.03*	2.36	0.04*	2.22	0.05

$*P < 0.05$, $**P < 0.01$.

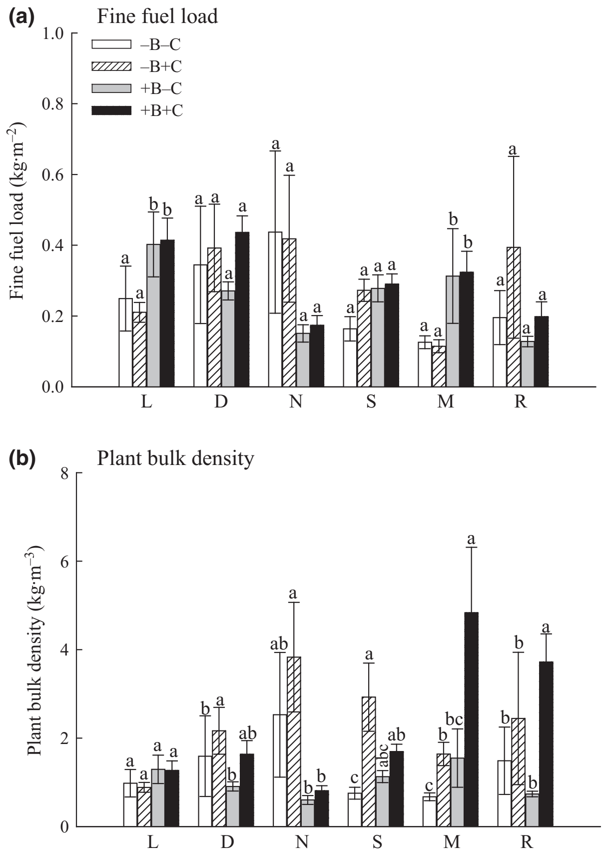

Fig. 1. Means and SE for (**a**) fine fuel loads ($kg \cdot m^{-2}$) and (**b**) plant bulk density ($kg \cdot m^{-3}$) for the six studied species. Species are *Lomatia hirsuta* (L), *Diostea juncea* (D), *Nothofagus antarctica* (N), *Schinus patagonicus* (S), *Maytenus boaria* (M) and *Ribes magellanicum* (R). Treatments are indicated as follows: −B−C (unburned and without cattle); −B+C (unburned with cattle); +B−C (recently burned without cattle) and +B+C (recently burned with cattle). Species are arranged from left to right from not palatable to highly palatable. Different letters above the bars indicate significant differences (*post-hoc* LSD Fisher test: $P < 0.05$) between sites within species, only for significant interactions (2 × 2 × 6 factorial ANOVAs: fine fuel load = F × Spp; plant bulk density = F × C × Spp).

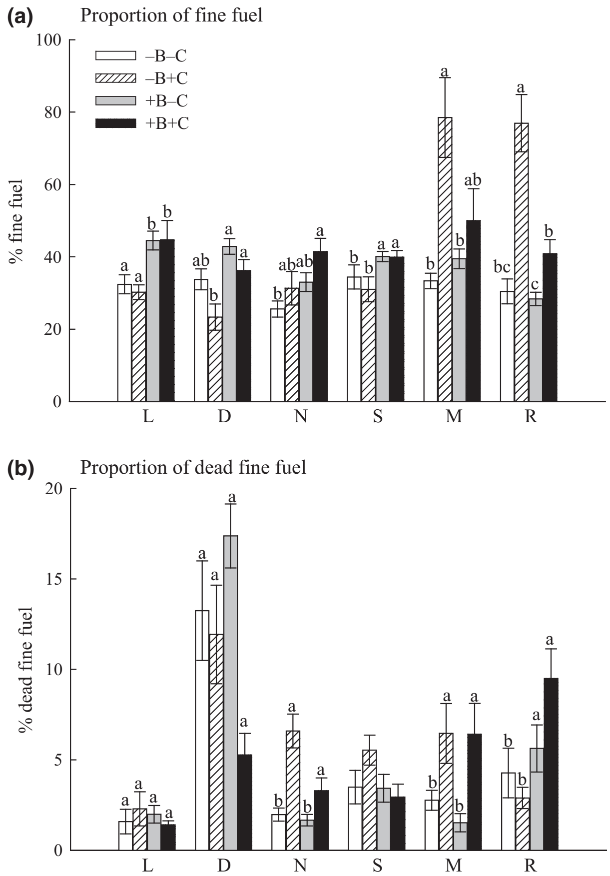

Fig. 2. Means and SE for (**a**) percentage fine fuel and (**b**) percentage dead fine fuel for the six studied species. Species are *Lomatia hirsuta* (L), *Diostea juncea* (D), *Nothofagus antarctica* (N), *Schinus patagonicus* (S), *Maytenus boaria* (M) and *Ribes magellanicum* (R). Treatments are indicated as follows: −B−C (unburned and without cattle); −B+C (unburned with cattle); +B−C (recently burned without cattle) and +B+C (recently burned with cattle). Species are arranged from left to right from not palatable to highly palatable. Different letters above the bars indicate significant differences (*post-hoc* LSD Fisher test: $P < 0.05$) between sites within species, only for significant interactions (2 × 2 × 6 factorial ANOVAs: percentage fine fuel = F × C × Spp; percentage dead fine fuel = F × Spp and C × Spp).

Lomatia hirsuta tended to increase fine fuel load and the proportion of fine fuel with fire (fire × species: $P < 0.001$; *post-hoc* LSD Fisher test: $P < 0.05$; Figs 1 and 2), while no significant differences where observed for bulk density and dead fine fuel (fire × species: $P < 0.001$; *post-hoc* LSD Fisher test: $P > 0.05$). Consequently, when *L. hirsuta* fuel properties did change in response to fire, it was in the direction of increased flammability. Cattle did not affect fuel properties of non-palatable *L. hirsuta*, neither considering cattle × species nor fire × cattle × species significant interactions (*post-hoc* LSD Fisher test: $P > 0.05$).

Nothofagus antarctica showed reduced plant bulk density at recently burned sites, (fire × cattle × species: $P < 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 1b), suggesting reduced flammability. However, *N. antarctica* plants growing at recently burned sites with cattle had significantly higher percentage fine fuel in comparison to plants growing at unburned and without cattle sites (fire × cattle × species: $P < 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2a). In addition, percentage dead fine fuel of this moderately palatable species increased almost twofold in response to cattle pressure (cattle × species: $P < 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2b). Hence, in contrast to the ambiguous plant bulk responses, changes in percentage fine fuel and percentage dead fine fuel of *N. antarctica* suggest increasing flammability at recently burned sites with cattle.

Diostea juncea and *S. patagonicus* had similar responses to fire and cattle pressure: both showed increased plant bulk density at sites with cattle in comparison to sites not affected by fire and herbivory (fire × cattle × species: $P < 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 1b). In addition, both species showed increased percentage fine fuel in response to fire (fire × species: $P < 0.01$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2a), suggesting higher flammability.

Cattle browsing was the main driver of variability in flammability for highly palatable species. This was particularly true for *M. boaria*, with responses in three of the four fuel properties consistent with increased flammability in the presence of cattle (i.e. plant bulk density, percentage fine fuel and percentage dead fine fuel). Both species, *M. boaria* and *R. magellanicum*, tended to increase plant bulk density at recently burned sites with cattle (fire × cattle × species: $P < 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 1b). In addition, both species showed higher percentage fine fuel in response to cattle herbivory, (fire × cattle × species: $P < 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2a), and *M. boaria*, likewise, showed higher percentage dead fine fuel in plants growing under cattle pressure in comparison to plants growing at sites without cattle (cattle × species: $P < 0.01$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2b). *Maytenus boaria* showed increased fine fuel load in response to fire (fire × species: $P < 0.01$; *post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2a). *Ribes magellanicum* showed decreased percentage fine fuel and increased percentage dead fine fuel at recently burned sites (fire × species: $P < 0.01$; *post-hoc* LSD Fisher test: $P < 0.05$). Thus highly palatable species showed less clear change in direction of flammability in response to recent fire.

The combination of recent fire and cattle browsing did not consistently increase or decrease flammability, since fuel properties were not consistently higher or lower than the other treatment combinations (fire × cattle: $P > 0.05$; Table 1). For the species main effect, which was significant for three of the four fuel properties (species: $P < 0.01$; Table 1), *post-hoc* tests showed two groups for fine fuel load: *D. juncea*, *L. hirsuta* and *S. patagonicus* with higher values of fine fuel loading, and *N. antarctica*, *M. boaria* and *R. magellanicum* with lower values (*post-hoc* LSD Fisher test: $P < 0.05$; Fig. 1a). The percentage fine fuel across species evidenced a decreasing gradient from highly palatable species, *M. boaria* and *R. magellanicum*, to *N. antarctica* and *D. juncea* with the lowest values (*post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2a). Finally, *D. juncea* was the species that by far showed the highest percentage dead fine fuel, whereas *L. hirsuta* showed the lowest values (*post-hoc* LSD Fisher test: $P < 0.05$; Fig. 2b).

Vertical distribution of fuel

The main effect for fire was significant across all height intervals of live and dead fine fuel classes, showing an increase of burnable biomass in response to recent fire (fire: $P < 0.01$; Appendix S1, Fig. 3; note the different scales between –B and +B sites). Live fine fuel biomass at 50–100-cm and 100–150-cm height intervals was higher for the six species at recently burned sites compared to unburned sites, and particularly at burned sites without cattle for palatable species: *S. patagonicus*, *R. magellanicum* and *M. boaria* (fire × cattle × species: $P \leq 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$; Appendix S1). The species most affected in their fine fuel vertical distribution by time since fire were *L. hirsuta* and *S. patagonicus*, which showed a higher fine fuel biomass from the ground and across all height intervals in response to recent fire.

The effect of cattle on the vertical distribution of fine fuel (i.e. main effect of cattle, and the combination of cattle × species, and fire × cattle × species) varied with species palatability (Appendix S1, Fig. 3). In the presence of cattle, *S. patagonicus* showed lower live and dead fine fuel biomass at taller intervals (100–150-cm and 150–200-cm height) at sites with cattle in comparison to sites without cattle (cattle × species: $P < 0.01$; *post-hoc* LSD Fisher test: $P < 0.05$). A stronger effect was observed for highly palatable species, since plants of *M. boaria* and *R. magellanicum*

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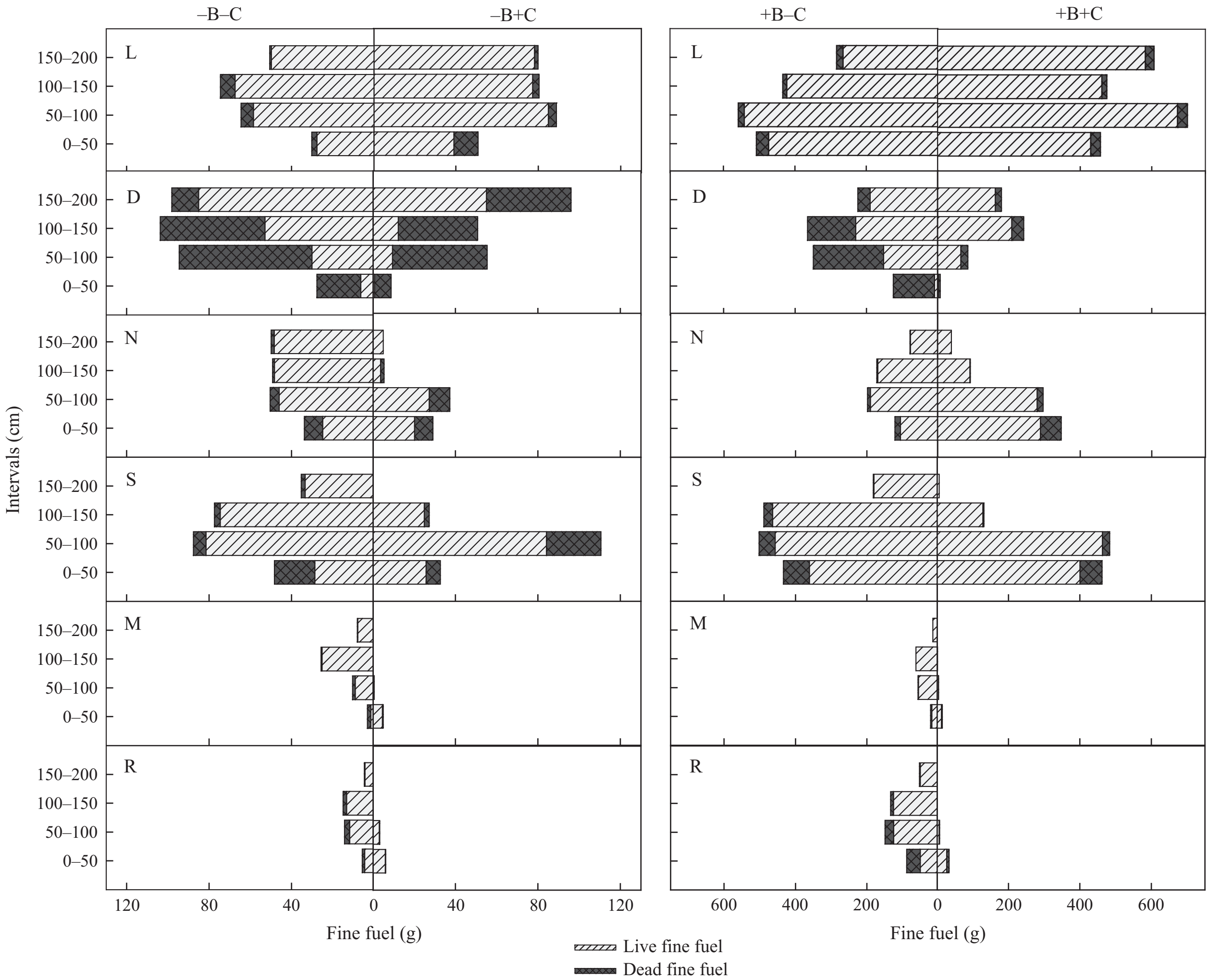

Fig. 3. Means for live and dead fine fuel (g) per individual in four 50-cm height intervals (0–50, 50–100, 100–150 and 150–200 cm) for the six studied species. Species are *Lomatia hirsuta* (L), *Diostea juncea* (D), *Nothofagus antarctica* (N), *Schinus patagonicus* (S), *Maytenus boaria* (M) and *Ribes magellanicum* (R). Treatments are indicated as follows: −B−C (unburned and without cattle); −B+C (unburned with cattle); +B−C (recently burned without cattle) and +B+C (recently burned with cattle). Species are arranged from not palatable (top) to highly palatable (bottom).

showed no continuity of fine fuel vertical distribution (almost absent fuel at 100–150-cm and 150–200-cm height classes), due to the dwarfing effect of cattle herbivory. Both species showed higher biomass of live fine fuel particularly at 50–100-cm and 100–150-cm height intervals at recently burned sites without cattle (cattle × species: $P < 0.01$, and fire × cattle × species: $P \leq 0.05$; *post-hoc* LSD Fisher test: $P < 0.05$). The same pattern was observed for the non-palatable *D. juncea*.

The combination of recent fire and cattle browsing did not consistently modify fine fuel vertical distribution, since live or dead fine fuel biomass for each height interval were not consistently higher or lower than the other treatment combinations (fire × cattle: $P > 0.05$). Finally, the main effect of species on the factorial analysis was significant across all height strata, and *post-hoc* tests showed some general patterns of differences between species. *Lomatia hirsuta* and *S. patagonicus* showed the highest values for live fine fuel for all height strata, while highly palatable species *R. magellanicum* and *M. boaria* showed the lowest values. Dead fine fuel biomass was considerable higher for *D. juncea* in comparison to all the studied species, and across all height strata, whereas *M. boaria* showed the lowest values.

Discussion

In northwest Patagonia, plant structural flammability related to fuel properties of common resprouting shrub and small tree species is strongly affected by time since fire and herbivory history. Moreover, changes in flammability in response to recent fire, and to a lesser extent cattle pressure, are strongly dependent on species identity. Fire tended to enhance flammability traits of most species, whereas cattle affected species differentially depending on their palatability.

Species-specific results show that at recently burned sites plants of the studied species may increase fine fuel load (*L. hirsuta* and *M. boaria*), plant bulk density (*M. boaria*), or the percentage fine fuel (*L. hirsuta*, *D. juncea*, *N. antarctica* and *S. patagonicus*), particularly of dead fine fuel (*R. magellanicum*). Thus, at recently burned sites these changes in fuel characteristics imply a higher structural flammability. On the other hand, it is important to highlight that despite these changes in plant traits that would enhance plant flammability, some results showed the opposite outcome, such as reduced plant bulk density for *N. antarctica* and reduced percentage fine fuel for *R. magellanicum* at recently burned sites. For these two species, the effect of fire on flammability was not as clear as for the other species, since results for some fuel properties indicated increased flammability while others indicated decreased flammability.

The higher fine fuel loads of *L. hirsuta* and *M. boaria*, and the higher plant bulk density of *M. boaria* at recently burned sites probably reflect post-fire site conditions favourable to new plant growth. When scaled up to the community level, these higher fine fuel loads on individual plants imply a higher amount of highly flammable fuel available to burn in a community (Rundel 1981). Similarly, at recently burned sites the percentage fine fuel (i.e. the proportion of fine fuel in relation to the total biomass of each individual) was higher for four of the six species: proportions were higher for *L. hirsuta* by 42%, *D. juncea* by 37%, *N. antarctica* by 30% and *S. patagonicus* by 22%. These four species are included among the most abundant species in shrublands and in the understorey of forests (Mermoz & Martín 2005; Blackhall 2012). Analogous to our findings, in Central Chile in recently burned sites, a higher proportion of vegetative shoots was recorded after fire in sprouting shrubs in comparison to unburned plants, and this consumption of the aerial biomass was interpreted as a ‘rejuvenation’ of the shrubs (Ginocchio et al. 1994). In northwest Patagonia, after a fire event in shrublands and forests, post-fire stands in general are characterized by an increase of soil nutrient availability (if the soil is not severely affected) and higher solar insolation (Albanesi & Anriquez 2003; Paritsis et al. 2006; Blackhall 2012). Plants that can rapidly resprout after fire may take advantage of these post-fire conditions, and benefits may be reflected in the higher growth rates of new tissues in comparison to plants growing under a dense canopy in tall forests. On the other hand, the proportion of fine fuel and of dead fine fuel of *R. magellanicum* were apparently negatively affected by time since fire: plants growing at recently burned sites showed a lower percentage fine fuel and higher percentage dead fine tissues in comparison to plants of unburned sites. *Ribes magellanicum* had 104% higher proportion of dead fine fuel in response to recent fire. Post-fire soil and light micro-conditions that enhance tissue production for other species, as well as the extreme micro-climatic conditions at burned sites (i.e. low relative air humidity and high thermal amplitude; Blackhall 2012), may not be favourable for *R. magellanicum*.

Similarly to the effects of time since fire, higher values of plant bulk density (*D. juncea*, *N. antarctica*, *S. patagonicus*, *M. boaria*, and *R. magellanicum*), percentage fine fuel (*M. boaria* and *R. magellanicum*), or percentage dead fine fuel (*N. antarctica* and *M. boaria*) were recorded at sites with cattle in comparison to sites without cattle. Interestingly, this applies to *D. juncea* despite its lack of palatability, suggesting an indirect influence of cattle on its plant bulk density that merits further research. The reduction of the competition from more palatable species may have benefited the development of abundant new tissues in this unpalatable species. Conversely, the direct effect of cattle on plant bulk density of the moderately and highly palatable species was clearly identified as an increase in the degree of ramification and production of new shoots. In Italy in sclerophyll type vegetation, similar observations have been made for *Phyllyrea angustifolia* after heavy deer and livestock browsing (Massei et al. 2000).

A higher percentage fine fuel in relation to the total biomass of each plant was observed for highly palatable species, *M. boaria* and *R. magellanicum*, in response to cattle herbivory (percentages of fine fuel were 77% and 98%, respectively, significantly higher in the presence of cattle). In addition, for *M. boaria* and also for *N. antarctica* an increase of almost twofold was observed in the percentage dead fine fuel retained in plants growing under heavy cattle pressure. When the effect of cattle is strong, in addition to an increase in the percentage fine fuel or the degree of ramification, there is also an increase in the percentage senescent tissues, probably as a result of the stress of heavy herbivory.

An effect of time since fire was also observed on the vertical distribution of fuel properties: all species growing in recently burned sites showed higher fine fuel biomass (live and/or dead) in at least two of the four height intervals (specifically all of them varying at medium height intervals: 50–100-cm and 100–150-cm height classes), in comparison to plants of the same species growing at unburned sites. Although varying widely according to species identity, total live and dead fine biomass across all height intervals increased on average between 215% and 900%, respectively, for plants growing at recently burned sites in comparison to plants growing in the understories of forests

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not burned for at least 50 yrs. A greater availability of fine fuel biomass favours the occurrence of more intense and severe fires (Rundel 1981).

In contrast to the effect of time since fire on fine fuel vertical distribution, the effect of cattle herbivory was to considerably decrease live and dead fine biomass, particularly for moderately and highly palatable species. *M. boaria* and *R. magellanicum* even showed a lack of vertical continuity of fuel biomass in the upper height intervals, reducing the probability of surface fire reaching the canopy (i.e. ladder effect) at heavily browsed sites (Papió & Trabaud 1991; Flannigan et al. 2009). However, in the presence of cattle the fine fuel biomass of the aggregated four moderately or non-palatable species remained high from the ground surface to 200 cm, providing continuous vertical fuel continuity. Overall, time since fire and cattle herbivory had a strong effect on fine fuel vertical distribution, and cattle presence most severely reduced vertical fuel continuity of the most palatable species.

The effect of fire and cattle on flammability will largely depend on species presence, and on which species tend to dominate burned or browsed communities. The six species examined account, on average, for almost 40% of the total cover of woody species of the communities studied, and their cover is only exceeded by that of the bamboo *Chusquea culeou* at some sites (Blackhall 2012; Blackhall et al. 2012). All species studied resprout vigorously after fire, and are likely to continue to dominate post-fire shrublands for many decades (Raffaele et al. 2011). Overall, cattle effect on community diversity and composition will depend on the palatability of the species that form the community. Our results show that at heavily browsed sites, highly palatable species such as *M. boaria* and *R. magellanicum* provide relatively little biomass for burning (i.e. lowest values of live and dead fine fuel across height strata, and nearly absent at higher strata, in comparison to the other species), and are almost absent under heavy livestock pressure (Veblen et al. 1992; Raffaele et al. 2011; Blackhall 2012). On the other hand, moderately palatable species such as *N. antarctica* and *S. patagonicus* are able to withstand high levels of herbivory, and are abundant in heavily browsed areas (Raffaele et al. 2011), providing much of the fuel at these sites. Finally, non-palatable species such as *L. hirsuta* and *D. juncea* are not affected by cattle or can even be positively affected (i.e. as seen in the higher bulk density of *D. juncea* at sites with cattle). Both species, which are abundant despite cattle presence, showed the highest values of fine fuel loading in comparison to the other studied species at all sites, and particularly *D. juncea* was the species that by far showed the highest percentage dead fine fuel, distributed across all height strata.

Conclusions

Under the moderate to heavy cattle pressure typical of the sites included in the current study, cattle consistently reduced the vertical continuity (0–200 cm in height) of fine fuel biomass only for the two most palatable species. For the moderately palatable or non-palatable species, however, the biomass of fine fuel was actually higher in some 50-cm height intervals within the browse zone in the presence of cattle. In aggregate for all species combined, fine fuel biomass was continuously distributed from the ground surface to the upper limit of the browse zone both in the absence and the presence of cattle.

Although the responses of flammability traits to fire and cattle depend on species identity, the majority of the six abundant species of shrubs and small trees studied in northwest Patagonia show higher fuel flammability at recently burned sites affected by introduced cattle. When changes are observed in relation to fire, our results show that for most species, relatively short time since fire (<15 yrs) is associated with plant characteristics that potentially increase structural flammability. Specifically, all changes observed for four out of six species are in the direction of increased flammability at recently burned sites (i.e. for one or two traits for each species). Two species (*N. antarctica* and *R. magellanicum*) showed ambiguous results, since some changes in traits would increase and others would decrease flammability in relation to time since fire. Furthermore, direct and indirect effects of cattle presence are associated with plant-level fuel properties that may potentially increase plant flammability. Specifically, among the five species showing an effect of cattle on the four traits measured (fine fuel load, plant bulk density, percentage fine fuel and percentage dead fine fuel), all observed changes were in the direction of increased flammability at sites with cattle (i.e. for one, two or three studied traits for each species). The two most palatable species showed changes towards enhanced flammability for two or three of the four plant traits per species, whereas the non-palatable or moderately palatable species showed flammability enhancing changes for one trait for two species and two traits for one species.

The current study adds essential information to a previous study that observed higher foliar flammability at recently burned sites for the same species included in the current study (Blackhall et al. 2012). Following the burning of fire-resistant tall forests, variations in foliar properties, fuel load and flammability-related plant traits appear to contribute to enhanced community-level flammability in northwest Patagonian shrublands. The findings of the current study suggest that in other ecosystems consisting of fire-prone shrublands juxtaposed with less flammable, closed canopy forests, domestic livestock, by increasing the flammability of post-fire vegetation, may be key agents in altering fire regimes in forest–shrubland mosaics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Results of 2 × 2 × 6 factorial ANOVAs (fire (F) = recently burned/unburned; cattle (C)= presence/absence; species (Spp) = six studied species) for biomass of Live Fine Fuel and Dead Fine Fuel across four 50 cm-height intervals (0-50 cm, 50-100 cm, 100-150 cm, 150-200 cm). * $P < 0.05$, ** $P < 0.01$.

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