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

Journal:	<i>Journal of Ecology</i>
Manuscript ID	JEcol-2016-0701.R1
Manuscript Type:	Standard Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Blackhall, Melisa; INIBIOMA-Universidad Nacional del Comahue, CONICET, Laboratorio Ecotono Raffaele, Estela; INIBIOMA-Universidad Nacional del Comahue, CONICET, Laboratorio Ecotono Paritsis, Juan; INIBIOMA-Universidad Nacional del Comahue, CONICET, Laboratorio Ecotono Tiribelli, Florencia; INIBIOMA-Universidad Nacional del Comahue, CONICET, Laboratorio Ecotono Morales, Juan; INIBIOMA-Universidad Nacional del Comahue, CONICET, Laboratorio Ecotono Kitzberger, Thomas; INIBIOMA-Universidad Nacional del Comahue, CONICET, Departamento de Ecología - Laboratorio Ecotono Gowda, Juan ; INIBIOMA-Universidad Nacional del Comahue, CONICET, Laboratorio Ecotono Veblen, Thomas; University of Colorado, Department of Geography
Key-words:	ecological memory, livestock effects, non-resprouting species, <i>Nothofagus</i> spp., plant-herbivore interactions, plant population and community dynamics, pyrophobic forests, pyrophytic shrublands, resprouting

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

3

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

13

14 **Summary**

15 1. Ecological memory, often determined by the extent and type of retained biological
16 legacies present following disturbance, may produce persistent landscape patterns.

17 However, after fire, the persistence or switch to an alternative state may depend on the
18 complex interplay of ecological memory (biological legacies) and potential effects of
19 new external factors influencing the post-fire environment. The current study assesses
20 both the strength of ecological memory resulting from biological legacies of pre-burn
21 vegetation types as well as post-fire effects of livestock.

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

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

35 4. We show that herbivores may produce antagonistic effects on flammability by
36 decreasing tissue ignitability, total fine fuel and litter depth, and disrupting the vertical
37 and horizontal fine fuel continuity, therefore reducing the probability of fire
38 propagation. However, cattle can increase ratios of dead to live fine fuels, reduce soil

39 moisture, and inhibit tree height growth to canopy size, consequently impeding the
40 development of a closed pyrophobic forest canopy.

41 5- *Synthesis*. Our results support the hypothesis that biological legacies, most
42 importantly the dominance by **pyrophytic** woody plants that resprout vigorously versus
43 the dominance by **pyrophobic** obligate seeders, favour fuel and flammability
44 characteristics at the community level which reinforce the mechanisms maintaining
45 pyrophytic shrublands versus pyrophobic forests. Herbivory by introduced cattle can
46 partially blur sharp pyrophobic/pyrophytic state boundaries by promoting the
47 development of novel post-fire transitional states.

48

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

52

53 **Introduction**

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

70 Alternative stable states occur when assemblages of different species coexist
71 side by side in apparently the same environment, and are often separated by sharp
72 boundaries which in general do not correspond to any underlying environmental
73 condition (Petraitis & Latham 1999; Odion, Moritz & DellaSala 2010). In recent
74 decades, there has been a growing awareness of the co-existence of fire-maintained
75 alternative states in a broad range of biomes (Wilson & Agnew 1992; Bond & van
76 Wilgen 1996; Warman & Moles 2009; Odion, Moritz & DellaSala 2010; Hoffman *et al.*
77 2012; Pausas 2015). Fire-driven alternative vegetation communities may switch

78 between a pyrophobic ecosystem which rarely burns, commonly forest, and a fire-prone
79 system, commonly savannas, grasslands, sclerophyll woodlands or dense shrublands,
80 which are subjected to frequent fire occurrence. Such fire-maintained alternative stable
81 states are recognized for forest and shrubland communities in the Andean-Patagonian
82 region of Southern South America (e.g. Mermoz, Kitzberger & Veblen 2005; Kitzberger
83 *et al.* 2012; Paritsis, Veblen & Holz 2015; Kitzberger *et al.* 2016). Shrublands and
84 forests of the northern Patagonian-Andean landscape have been the object of a series of
85 studies over the past three decades that have identified key elements and mechanisms of
86 fire-driven alternative states reflected by juxtaposed pyrophytic tall shrubland and
87 pyrophobic forests dominated respectively by resprouting versus obligate seeding tree
88 species (Veblen & Lorenz 1988; Mermoz, Kitzberger & Veblen 2005; Paritsis *et al.*
89 2013). In this landscape, herbivory by introduced animals may influence post-fire
90 vegetation recovery and therefore the potential to shift from one alternative state to
91 another (Veblen *et al.* 1992; Raffaele *et al.* 2011). The current study assesses both the
92 strength of ecological memory resulting from biological legacies of the pre-burn
93 vegetation types (e.g. pyrophytic woody plants that resprout vigorously versus the
94 dominance by pyrophobic obligate seeders) as well as the post-fire effects of livestock
95 which potentially could exacerbate or attenuate differences associated with biological
96 legacies.

97 In northwest Patagonia, plant community structure and landscape pattern have
98 been historically determined by natural and anthropogenic fire (Veblen *et al.* 2003).
99 Large areas of Andean Patagonia are occupied by either pyrophobic subalpine
100 deciduous forests dominated by the non-resprouter tree *Nothofagus pumilio* (hereafter
101 subalpine forest), or tall shrublands characterized by the dominance of resprouting
102 pyrophytic shrubs, bamboos and small trees like *N. antarctica* (hereafter tall

103 shrublands). *Nothofagus pumilio*, typically forms dense monospecific stands and
104 constitutes the most extensive forest type in southern Argentina and Chile (Veblen *et al.*
105 1996). Bordering these forests, 3-5 m tall shrublands of woody species are all capable of
106 vigorously resprouting after cutting, browsing or burning. In general, fires start at low to
107 mid-elevation in shrublands and spread upslope but may stop when they reach mature
108 *N. pumilio* forests (Paritsis, Veblen & Holz 2015). Only during extreme drought years
109 do fires burn large areas and spread into the less flammable *N. pumilio* forests (Veblen
110 & Lorenz 1988; Mermoz, Kitzberger & Veblen 2005). Three main mechanisms may
111 contribute to the lower flammability of *N. pumilio* forests as compared to adjacent
112 shrublands (Paritsis, Veblen & Holz 2015): scarcity of fine fuels near the ground surface
113 (i.e. 0-2 m height class), absence of vertical fuel continuity from the understory to the
114 canopy and a cooler and moister microclimate that reduces the rate of fuel desiccation.
115 In comparison to unburned tall forests, flammability of shrublands is promoted by
116 reduced foliar moisture, greater structural connectivity due to the architecture of
117 resprouting species, and a microclimate characterized by high solar radiation, low
118 humidity and high mean air temperatures (Blackhall, Raffaele & Veblen 2012, 2015;
119 Blackhall, Veblen & Raffaele 2015). Scarcity of remnant trees in severely burned
120 patches, limited seed dispersal, absence of seed banks, unfavourable post-fire
121 microclimatic conditions and herbivory may restrict post-fire regeneration of *N. pumilio*
122 to a narrow belt of only a few tens of meters from fire edges (Kitzberger *et al.* 2005;
123 Tercero-Bucardo *et al.* 2007; Raffaele *et al.* 2011). Species in the adjacent tall
124 shrublands and in the understories of subalpine forests resprout quickly and vigorously
125 after fire providing within a few years abundant fuel to support a subsequent fire
126 (Raffaele *et al.* 2011; Blackhall, Veblen & Raffaele 2015).

127 Herbivore impacts have been documented as major determinants of post-fire
128 vegetation trajectories in Patagonia (Veblen *et al.* 1992; Kitzberger *et al.* 2005; Tercero-
129 Bucardo *et al.* 2007) as well as in many other biomes across the globe (e.g. Vandvik *et*
130 *al.* 2005; Fuhlendorf *et al.* 2009; Perry *et al.* 2015). However, the capacity of large
131 herbivores to modify fuel or flammability characteristics of post-fire vegetation has only
132 recently been highlighted in Patagonia (e.g. Raffaele *et al.* 2011; Blackhall, Raffaele &
133 Veblen 2012) and elsewhere (e.g. Kirkpatrick, Marsden-Smedley & Leonard 2011;
134 Trauernicht *et al.* 2013; Johansson & Granström 2014; Williamson, Murphy & Bowman
135 2014; Evans, Ellsworth & Litton 2015). Continued and prolonged herbivory may alter
136 post-fire flammability and successional trajectories through a broad range of
137 mechanisms, including but not limited to selective browsing of plants with particular
138 chemical or morphological properties which in turn may modify vegetation structures
139 and/or alter competitive hierarchies (Rundel 1981, Bond & van Wilgen 1996).
140 Numerous studies have documented important influences of introduced herbivores (e.g.
141 cattle, boar, European hare and red and fallow deer) on the floristic composition and
142 structure of vegetation of a wide range of community types in Northwest Patagonia (e.g.
143 Martin, Mermoz & Gallopín 1985; Veblen *et al.* 1992, Relva & Veblen 1998;
144 Kitzberger *et al.* 2005; Blackhall, Raffaele & Veblen 2008). However, cattle effects on
145 vegetation properties specifically related to fuel and flammability at a community scale
146 have only been inferred from indirect observations (e.g. reduced quantities of surface
147 fuels; Paritsis, Veblen & Holz 2015) or from studies conducted at an individual plant
148 scale (e.g. increased foliar flammability –reduced leaf size and foliar strength, or shorter
149 time to ignition of tissues– or reduced vertical fuel continuity of palatable species;
150 Blackhall, Raffaele & Veblen 2012; Blackhall, Veblen & Raffaele 2015).

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

176 that cattle **herbivory** will contribute to the post-fire shift from burned pyrophobic forest
177 and pyrophytic shrubland to a homogenised novel pyrophytic state.

178 **Materials and methods**179 Study area

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

197 The intensity and timing of livestock use of the study sites represents the
198 common pattern of livestock use of *N. pumilio* subalpine forests and *N. antarctica* tall
199 shrublands in the National Reserve zone of Nahuel Huapi National Park where limited
200 livestock use is permitted (Raffaele *et al.* 2011). Cattle have been present in moderate
201 numbers at the sample sites for at least 30 years prior to the 1999 fire, as reported by the
202 owner of the livestock and local officials of the National Park. Since the 1999 fire, cattle

203 forage at the site mainly from spring to autumn (October to April) and a few wild cattle
204 remain at the site all year (approximately 0.03 head of cattle/hectare for the area;
205 Seoane 2015). Similarly, the introduced European hare (*Lepus europaeus*) is abundant
206 at the study sites but its effect on the vegetation is less severe than that of the livestock
207 (Raffaele *et al.* 2011). During the periodic re-measuring of permanent plots at the site,
208 we did not observe evidence of presence of any native mammalian herbivores.

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

215

216 Experimental design, data collection and variables

217 To conduct this analysis, we collected data in long-term livestock exclosures
218 installed in 2001 in a post fire subalpine forest and in a juxtaposed tall shrubland. For
219 each vegetation type, we randomly installed five fenced cattle exclosure plots and five
220 permanent unfenced control plots (each 25 m × 25 m). All the plots were located
221 following a paired plot experimental design (Sokal & Rohlf 1981) and placed in
222 severely and homogeneously burned areas lacking surviving aboveground vegetation
223 (Raffaele *et al.* 2011). In summer 2015, 16 years after fire and 14 years after we
224 installed permanent plots, we measured fuel characteristics, collected samples for
225 flammability experiments and monitored micro-environmental conditions at both sites.

226

227 *Fuel characterization*

228 At each fenced and unfenced permanent plot, stand structural fuel data were
229 collected following the point-intercept method (Mueller-Dombois & Ellenberg 1974). In
230 each plot we systematically located a grid of 5×5 points separated 3 m from each other
231 (25 points per plot, 125 per fenced or unfenced treatment at each post-fire habitat). At
232 each point we recorded all species of vascular plants that intercepted a 4 m vertical pole,
233 which was divided into 16 intervals (strata) of 0.25 m height. Species intercepts were
234 recorded only for fine fuel material (< 0.6 cm in diameter) and additionally we
235 classified these into dead and live tissues. Proportion of fine fuel material may be the
236 best correlate of overall surface area:volume ratio; the greater the surface area in
237 relation to the fuel volume, the faster the fuel will be heated and burned during a fire
238 (Countryman and Philpot 1970). At each measuring point we also recorded litter depth
239 (cm).

240 To relate fuel amounts and distribution to vegetation type and cattle pressure we
241 evaluated the following variables through the analysis of vegetation intercepts:
242 percentage of total fine fuel, percentage of dead/total fine fuel, vertical distribution of
243 total and dead fine fuel, litter continuity (%), and mean horizontal fine fuel continuity
244 (%) across the vertical distribution of fuel intervals. For estimating the percentage of
245 total fine fuel, at each measuring point (25 points per fenced or unfenced plot), mean
246 fuel intercepts at each height interval were estimated by pooling all species intercepts
247 recorded within each strata and then computing the percentage of height intervals
248 intercepted by fine fuel per measured point. The same procedure was used for
249 estimating percentage of dead fine fuel. Vertical distribution of fuel was estimated by
250 adding all intercepts per strata per plot and then calculating means per plot type. Fuel
251 horizontal continuity was estimated by calculating for each measuring point in the 5×5
252 grid, the proportion of next-measuring point (3 m distance) that intercepted the same

253 fuel type; these values were estimated for each height interval, and one value per strata
254 was calculated per plot and then averaged per type of plot. The same procedure was
255 used for estimating the proportion of litter continuity. We estimated litter depth (cm) by
256 averaging values per plot.

257

258 *Foliar moisture and plant-level flammability measurements*

259 Five species were selected for foliar moisture and flammability tests based on
260 their importance in previous vegetation measurements at the sites (i.e. from 2001 to
261 2014; Raffaele *et al.* 2011). All the species selected are native woody or semi-woody
262 species and are abundant in each type of community, comprising together on average
263 more than 63 % of total woody and semi-woody species intercepts per type of habitat
264 (reaching in some plots more than 80% of fuel intercepts for these life-form groups).
265 The species sampled at both sites were the spiny shrub *B. buxifolia* (Berberidaceae), the
266 semi-woody bamboo *C. culeou* (Poaceae) and the shrub or shrubby tree *S. patagonicus*
267 (Anacardiaceae). We also sampled individuals of the shrubby tree *N. antarctica*
268 (Nothofagaceae) at the shrubland site and saplings of the tree *N. pumilio*
269 (Nothofagaceae) at the subalpine forest. Fifteen individuals per type of plot and per
270 species in each community type (i.e. three individuals per plot) were sampled for
271 flammability tests during the same days of field fuel data collections. Samples included
272 leaves and small twigs (< 2.5 mm in diameter). From each sampled plant, we randomly
273 harvested approximately 10 g of fresh well developed, fully expanded non-senescing
274 and healthy leaves attached to the small twigs (i.e. no evidence of pathogens or
275 herbivory), corresponding to the last growing season. All the material was enclosed in
276 air tight plastic bags and stored in coolers until its analysis in the laboratory.

277 In the laboratory and immediately after field sampling, approximately 1 g of
278 fresh material of six individuals per species and condition (three individuals from two
279 plots per condition) were used to measure leaf moisture percentage using an OHAUS
280 Moisture Analyzer (Model MB25). The device was set for calculating leaf moisture
281 based on dry mass as follows = $[(\text{fresh mass} - \text{dry mass})/\text{dry mass}] \times 100$. At the same
282 time, 3.5 g of leaves attached to the small twigs per each sample collected in the field
283 (15 individuals per species and condition) were used to perform the flammability tests
284 using an infrared quartz-silica epiradiator (500 W; Helios Italquartz ®, Milan, Italy),
285 following the protocol in Blackhall, Raffaele & Veblen (2012) and Pausas *et al.* (2012).
286 The epiradiator consists of an electric heating resistance that reaches a standard surface
287 temperature of 420 °C. Samples were placed on a 10-cm diameter silica disk once the
288 electric radiator was well heated. A thermocouple (Type K, range: 50°C - 1000 °C)
289 connected to a data-logger (TES Model 1384; Time resolution: 2 s) was placed 8 cm
290 above the epiradiator disk for recording flame and heat temperature during complete
291 combustion. Flammability experiments were conducted in a closed environment to
292 prevent any drought disturbance (temperature controlled, 20-22°C). For each sample the
293 following parameters were recorded using the digital timer from the thermocouple data-
294 logger: (1) time to ignition, in seconds, measured as the time from placement of the
295 sample on the silica disk to appearance of the first flame, and (2) flame duration, in
296 seconds, determined by flame extinction. In general the ignition frequency (percentage
297 of samples that ignited) was 100 %, except for few samples of *C. culeou* and *S.*
298 *patagonicus* (6.7 % and 13.3 % failed ignitions, respectively); these failed tests were not
299 considered for computing flammability variables.

300 Leaf moisture and results from flammability tests for all species were pooled per
301 plot for each cattle treatment and habitat type (pool of four species per condition for

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

314

315 *Micro-environmental conditions*

316 From December 2014 to March 2015 we monitored air temperature (C°) and
317 relative humidity (%) by placing a Hygrochron iButton data logger (DS 1923, Maxim
318 Integrated) at three plots per type of plot, programmed to record values at 1-h intervals.
319 Data loggers were placed at 1.0 – 1.5 m above the ground and protected from direct
320 sunlight and precipitation using a covering roof. To examine microclimatic
321 characteristics from different vegetation types and cattle treatments and under
322 conditions most likely to be associated with fire, we calculated mean maximum air
323 temperature per day (°C) and mean minimum relative humidity per day (%) for
324 December and March (i.e., early and late fire season). In addition, in December 2014
325 and in March 2015 we recorded surface and 20 cm depth soil moisture (g H₂O/g soil) at
326 each fenced and unfenced plot (three to five measuring points per plot and three

327 replicates per point) with a Theta Probe type ML2X (Delta-T devices) and following the
328 protocol in Kitzberger *et al.* (2005). Microclimatic and soil parameters were averaged
329 per plot.

330

331 Data analysis

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

347 To relate the laboratory measurements of flammability to vegetation types and
348 cattle presence we analysed the following variables: leaf moisture and time to ignition
349 (to assess ignitability), flame duration (to assess sustainability) and the trend over time
350 of the temperature during the three phases of the complete combustion (assessing
351 combustibility). As previously described, the general linear mixed model was

352 independently **applied to the** data analysis of leaf moisture, time to ignition and flame
353 duration, **with vegetation type (subalpine forest/tall shrubland) and cattle**
354 **(fenced/unfenced) as categorical fixed predictors and blocks as a random effect** (except
355 for leaf moisture). The differences between cattle treatments and between each
356 **vegetation type** with reference to the temperatures at which the flammability phases
357 arose were analysed **by performing a general linear mixed model** with repeated
358 measures, considering blocks **as a random factor**. Between-subject factors were
359 **herbivory** treatments (fenced/unfenced plots) and vegetation type (subalpine forest/tall
360 shrubland), and we considered the flammability phase as the within-subject factor (with
361 three levels). We determined if differences between factors in trends over time in the
362 response variables were statistically significant.

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

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

377

378 **Results**379 Fuel amounts and distribution

380 Total fine fuel varied depending on vegetation type and the fencing treatment
381 (Fig. 1a; see Table S1 in Supporting Information for details of **statistical** analysis; cattle
382 × **vegetation type**: $P < 0.01$). Fine fuel amount was almost 250 % higher in shrubland
383 fenced plots in comparison to unfenced shrubland plots and fenced and unfenced
384 subalpine forest plots. Unfenced plots were associated with reduced total amount of fine
385 fuel in both types of vegetation, but unfenced and fenced did not differ significantly in
386 the subalpine forest. On average for both vegetation types unfenced plots showed more
387 than six fold lower litter depth **in comparison to fenced plots** (Fig. 1c; Table 1S; cattle:
388 $P < 0.01$), **and this litter depth reduction** was greater at the shrubland site, (cattle ×
389 **vegetation type**: $P = 0.05$). Overall and regardless of cattle presence, total fine fuel and
390 litter depth were considerably greater at tall shrubland sites in comparison to subalpine
391 forest (Fig. 1a,c; **vegetation type**: $P \leq 0.05$). **On average, proportion of dead / total fine**
392 **fuel was almost twofold greater at unfenced plots in comparison to fenced plots for both**
393 **vegetation types (Fig. 1b; Table 1S; cattle: $P < 0.01$).**

394 Even though in unfenced plots we observed a greater amount of fine fuel in the
395 first 0.25 m height interval at the shrubland site, plots with cattle showed significantly
396 lower amounts of total fine fuel across all other height classes (Fig. 2; $KS\ 0.56$, $P <$
397 0.02). Cattle had no significant effect over the distribution of dead fuel amounts in fuel
398 height strata in *N. antarctica* shrubland plots ($KS\ 0.44$, $P < 0.1$). At the subalpine forest
399 site distribution of total fine fuel in height classes was similar between fenced and
400 unfenced plots ($KS\ 0.38$, $P < 0.2$), whereas the amount of dead fine fuel **in** the first 1.5
401 m height classes was greater in the unfenced plots in comparison to fenced plots (KS
402 0.63 , $P < 0.01$).

403 Mean horizontal continuity of fine fuel varied between cattle treatments in the
404 tall shrubland (Fig. 3; $KS\ 0.63$, $P < 0.01$) and in the subalpine forest ($KS\ 0.5$, $P < 0.05$).
405 In the tall shrubland, unfenced plots were characterized by lower horizontal continuity
406 in all height classes, except for the 0.25 m interval which showed almost no differences,
407 **in comparison to fenced plots**. In the unfenced plots of the subalpine forest horizontal
408 fuel continuity was zero above a height of 1.25 m (Fig. 3). In the post-fire subalpine
409 forest, taller strata include mostly *N. pumilio* whereas in the shrubland these higher
410 strata include numerous resprouting species, such as *N. antarctica* and *C. culeou*, which
411 can tolerate heavy cattle browsing. **Despite** the strong difference between fenced and
412 unfenced plots, vertical distribution and horizontal continuity of fine fuel 16 years after
413 fire are considerably greater at the tall shrubland site in comparison to the subalpine
414 forest (Figs 2 and 3).

415

416 Fuel flammability

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

427

428 Micro-environmental conditions

429 In December mean maximum temperature was 18.2 °C (\pm 0.4) and mean
430 minimum relative humidity per day was 45.1 % (\pm 0.5) on average for all plots (Fig. 5).
431 Microclimate conditions were warmer and drier in March, at the end of summer season,
432 in comparison to December records, with a mean maximum temperature of 21.9 °C (\pm
433 0.3) and mean minimum relative humidity of 32.1 % (\pm 0.5) for all plots in March.
434 Sixteen years after fire occurrence and regardless of cattle presence, no significant
435 differences were observed across summer season for mean maximum air temperature
436 and mean minimum relative humidity per day between the two post-fire vegetation
437 types (Table S4; **vegetation type**: $P > 0.05$). However, in both vegetation types mean
438 maximum temperature per day in March was slightly higher in unfenced plots in
439 comparison to fenced plots (on average 0.7 °C; **cattle**: $P < 0.05$). This difference was
440 not observed in the December records (**cattle**: $P > 0.05$).

441 **We did not observe differences in soil moisture between vegetation types in**
442 **December (vegetation type: $P > 0.05$). In March, at the end of summer, soil surface**
443 **moisture was similar in all plots (cattle and vegetation type: $P > 0.05$), but soil moisture**
444 **at 20 cm depth was lower in *N. antarctica* shrubland plots in comparison to *N. pumilio***
445 **forest (vegetation type: $P < 0.01$). In December for both vegetation types soil surface**
446 **moisture and soil moisture at 20 cm depth were on average 55 % and 34 % lower,**
447 **respectively, at unfenced plots in comparison to fenced plots (Fig. 6; Table S4; **cattle**: P**
448 **< 0.01).**

449 **Discussion**450 Biological legacies affect fuel and flammability characteristics

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

462 The four components of flammability analysed in this study showed important
463 differences between the two vegetation types. A higher total fine fuel (i.e. % of total
464 intercepts of live and dead fine fuel; an indicator of potential consumability) and a
465 higher vertical and horizontal continuity of fine fuel (an indicator of sustainability) at
466 shrubland site in comparison to subalpine forest are consistent with previous studies
467 documenting rapid vegetation (and fuel) recovery in *N. antarctica* shrublands following
468 burning (Raffaele *et al.* 2011; Paritsis, Veblen & Holz 2015). Unburned *N. antarctica*
469 tall shrublands are characterized by abundant fine fuel loads and greater continuity of
470 fine fuels due to vigorous resprouting of woody species in comparison to the
471 understorey of unburned *N. pumilio* subalpine forest (Paritsis, Veblen & Holz 2015).
472 Following fire at both vegetation types, buried rhizomes, roots and lignotubers from
473 resprouting species are capable of rapid regeneration. In the shrublands, this pre-

474 disturbance legacy allows quick accumulation of abundant fuels in only a few years. In
475 contrast, regeneration of the dominant species of *N. pumilio* forests is a slow process
476 dependent on seed dispersal from unburned forest edges or in some cases from scarce
477 survivors of the fire in the burned patch. In the subalpine forest woody fuel recovery is
478 limited to rare *N. pumilio* seedlings and resprouts of woody species recorded in both
479 vegetation types, but in low abundances under the closed canopies of unburned *N.*
480 *pumilio* forests (Raffaele *et al.* 2011; Paritsis, Veblen & Holz 2015).

481 In our study, regardless of cattle presence we found higher litter depth in the
482 shrubland compared to the subalpine forest sites. Larger leaf size and low fuel bed
483 compactness favour better ventilation (Scarff & Westoby 2006), so that deeper litter of
484 fine and dry flammable fuel may contribute to greater ignitability and also promote
485 more rapid horizontal propagation and greater sustainability of fire once fuel is ignited
486 (Anderson 1982; Curt *et al.* 2011). The two-fold difference in mean litter depth is
487 consistent with the more than two-fold higher amount of standing live fine fuel at
488 shrubland fenced plots in comparison to fenced subalpine forest plots. Another
489 condition promoting differences in potential fire behaviour between the two post-fire
490 communities included higher soil moisture at 20 cm depth during March (the period of
491 higher hydrological stress) in subalpine forest plots in comparison to tall shrubland.
492 During a fire, the water loss of the upper layers of the soil is strongly influenced by the
493 water content of the underlying soil and is likely to influence temperatures attained
494 during the fire (Campbell *et al.* 1995). In general, the presence of surface organic layers
495 and dry soil conditions retard soil heating, while wet and bare mineral-soil surfaces can
496 be heated rapidly (Neary *et al.* 1999). Post-fire regeneration may be strongly influenced
497 by pre-disturbance litter characteristics and inherent soil properties since temperatures

498 reached in soil layers during a fire can affect belowground resprouting organs and
499 responses of seeds to heat (Keane & Finney 2003).

500 Fuel combustibility (i.e. the intensity with which plant material burns in
501 experimental assays) was higher for plants growing in the tall shrubland in comparison
502 to plants growing in the burned subalpine forest. Regardless of cattle presence, the
503 temperatures reached during tissue combustion were higher for plants from the
504 shrubland site in comparison to plants from the subalpine forest. This was observed for
505 the pool of species (means weighted according to species frequency) sampled in each
506 vegetation type and also for individual species and non-weighted means. **Although** *N.*
507 *antarctica* showed lower foliar moisture in comparison to *N. pumilio* (M. Blackhall, E.
508 Raffaele, J. Paritsis & F. Tiribelli, unpublished data), foliar moisture **of the four pooled**
509 **species** was similar between both sites. Higher temperatures during complete
510 combustion indicate higher amounts of heat released and therefore higher probabilities
511 of triggering ignition in neighbour plants by driving moisture out of living and dead
512 tissues (Rundel 1981; Pausas *et al.* 2012). Previous studies in Patagonian post-fire
513 vegetation have shown that more flammable foliar traits (foliar moisture, leaf size, leaf
514 strength or time to ignition of artificially dried leaves) are more frequent at the warm
515 dry micro-climate associated with recent burns in comparison to unburned sites
516 (Blackhall, Raffaele & Veblen 2012). In the present study, post-fire shrubland and post-
517 fire subalpine forest showed similar values for mean maximum air temperatures, mean
518 minimum relative humidity and soil surface moisture, 16 years after the strong
519 homogenizing effect of fire. Therefore, except for the two *Nothofagus* species which
520 clearly showed differences in foliar moisture, the heat released by the combustion of
521 plants growing in a particular site may be inherently determined by other intra-specific
522 factors than micro-environmental conditions.

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

530

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

532 Our fencing experiment showed that 14 years after cattle exclusion there were
533 important attributable to presence or absence of cattle, yet their implications for
534 flammability were complex and sometimes antagonistic. We observed that introduced
535 livestock can strongly affect the amounts, structural distribution and flammability of
536 fuels, and thus potentially modify fire behaviour at each vegetation type. Although
537 cattle increased the proportion of dead / total fine fuel in the community, livestock
538 presence also drastically decreased total fine fuel and litter depth, and disrupted the
539 vertical and horizontal fine fuel continuity. The latter two changes are consistent with
540 the interpretation that at shrubland sites cattle may reduce the probability of fire
541 propagation. However, in addition to increasing the proportion of dead / total fine fuel,
542 cattle also impede the regeneration of the subalpine forest to a non-flammable mature *N.*
543 *pumilio* community by dwarfing tree saplings and preventing the attainment of a tall
544 closed vegetation canopy (Raffaele *et al.* 2011). Through these different mechanisms,
545 cattle not only may alter flammability and the potential for fire but also the resilience of
546 the systems driving them into different alternative states.

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

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

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

594

595 *Integrating the effects of biological legacies and herbivores*

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

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

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

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

629 A conceptual and simplified model of the subalpine forest and tall shrubland
630 landscapes is shown in Fig. 7, where we synthesize results of the current research and
631 findings from previous studies (e.g. Raffaele *et al.* 2011; Blackhall, Raffaele & Veblen
632 2012; Blackhall, Raffaele & Veblen 2015; Paritsis, Veblen & Holz 2015, Kitzberger *et*
633 *al.* 2016). In a scenario without herbivory by introduced cattle, strong ecological
634 memory contributes to the maintenance of the sharp boundaries dividing fire-driven
635 alternative states. In a landscape under moderate cattle pressure, inhibition of the
636 pathway from pyrophytic to pyrophobic vegetation after fire also is expected.
637 Furthermore, herbivory by livestock, depending on timing and intensity of pressure,
638 may contribute to the blurring of the alternative state boundaries, partially decreasing
639 the effect of biological legacies on the system regeneration and homogenizing the post-
640 fire degraded landscape.

641 **Conclusions**

642 **Our results show** that biological legacies of burned plant communities
643 characterized by woody plants that resprout vigorously, as opposed to those dominated
644 by obligate seeders, favour fuel and flammability properties at the community level
645 which reinforce mechanisms maintaining pyrophytic shrublands versus pyrophobic
646 forests. Characteristics measured to indicate flammability components—ignitability,
647 sustainability, combustibility and consumability—indicate **in general** greater
648 flammability of post-fire vegetation following the burning of tall shrublands in
649 comparison to burning of tall closed canopy forests (**i.e. greater values for total fine
650 fuel, litter depth, fuel vertical distribution, horizontal fuel continuity, and maximum
651 temperatures reached during combustion of tissues samples**). The experimental removal
652 of cattle from both vegetation types indicates that cattle have significant but in some
653 cases antagonistic influences on flammability. Total fine fuels, vertical and horizontal
654 fuel continuity and tissue ignitability are reduced by cattle. However, increased ratios of
655 dead to live fine fuels, reduced litter depth and therefore **reduced** soil moisture, and
656 inhibition of tree height growth which impedes the development of a closed forest
657 canopy are important **ways by** which cattle contribute to a shift from less flammable
658 forest to more fire-prone shrublands. Thus, control of livestock access to recently
659 burned forests **or at least individual protection of *N. pumilio* saplings** is essential for
660 post-fire **pyrophobic** forest recovery.

661

662 **Acknowledgments**

663 Research was supported by PIP Grant No. 112 201101 00058, PICT Grants 2012-2371
664 and 2012-0949, Awards 0956552 and 0966472 from the United States National Science
665 Foundation, and Universidad Nacional del Comahue (UNC B172). We thank the
666 Administración de Parques Nacionales for permitting the research. Author
667 contributions: ER, TK, TTV, MB and JP conceived the ideas and designed
668 methodology; ER, JP, FT, TK, JHG collected the data; FT, MB, JP and JMM analysed
669 the data; MB, FT and TK prepared the Figures and Tables; MB and TTV led the writing
670 of the manuscript. For their assistance in different instances of this study we thank
671 Anahí Pérez, Antonio Locria and Manuel de Paz. All authors contributed critically to
672 the drafts and gave final approval for publication.

673

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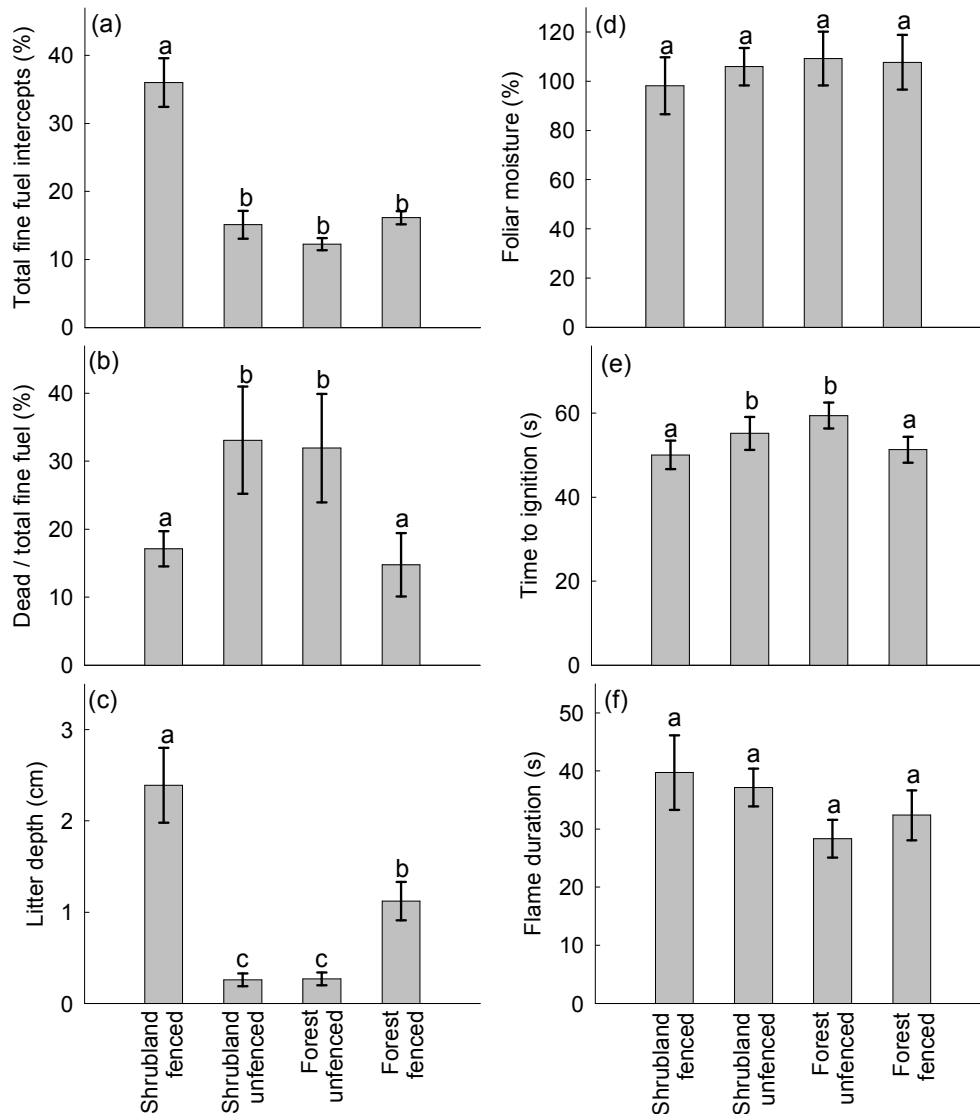
890 **Table 1:** Definitions of the four flammability parameters first described by Anderson
 891 (1970) and modified by White & Zipperer 2010. For each parameter a few examples of
 892 associated characteristics of the vegetation are given, detailing the scale of study: field
 893 studies (patch or stand scale) or laboratory assays (typically conducted at the scale of
 894 plant parts). The specific variables analyzed in our study for each flammability
 895 parameter are highlighted in bold letters. References: Anderson 1970; Anderson 1982;
 896 Gill & Zylstra 2005; Behm et al. 2004; White & Zipperer 2010; Blackhall, Raffaele &
 897 Veblen 2012; Cobar-Carranza et al. 2014; Bianchi & Defossé 2015; Blackhall, Veblen
 898 & Raffaele 2015.

899

<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	litter depth ; height to lowest branch	ignition delay time, moisture content , thickness of tissues
Sustainability	The ability to sustain fire once ignited	plant bulk density, vertical and horizontal continuity of fuel , surface area burned	heat of combustion, duration of combustion , total heat released
Combustibility	Measures the rapidity of combustion or how well plant material burns	fire intensity, length of flame	peak temperature , rate of temperature increase, the flame length
Consumability	Considers the proportion of the original mass consumed by the combustion	amount of live and dead fine fuel biomass in an individual or in the community	mass loss rate in combustion tests

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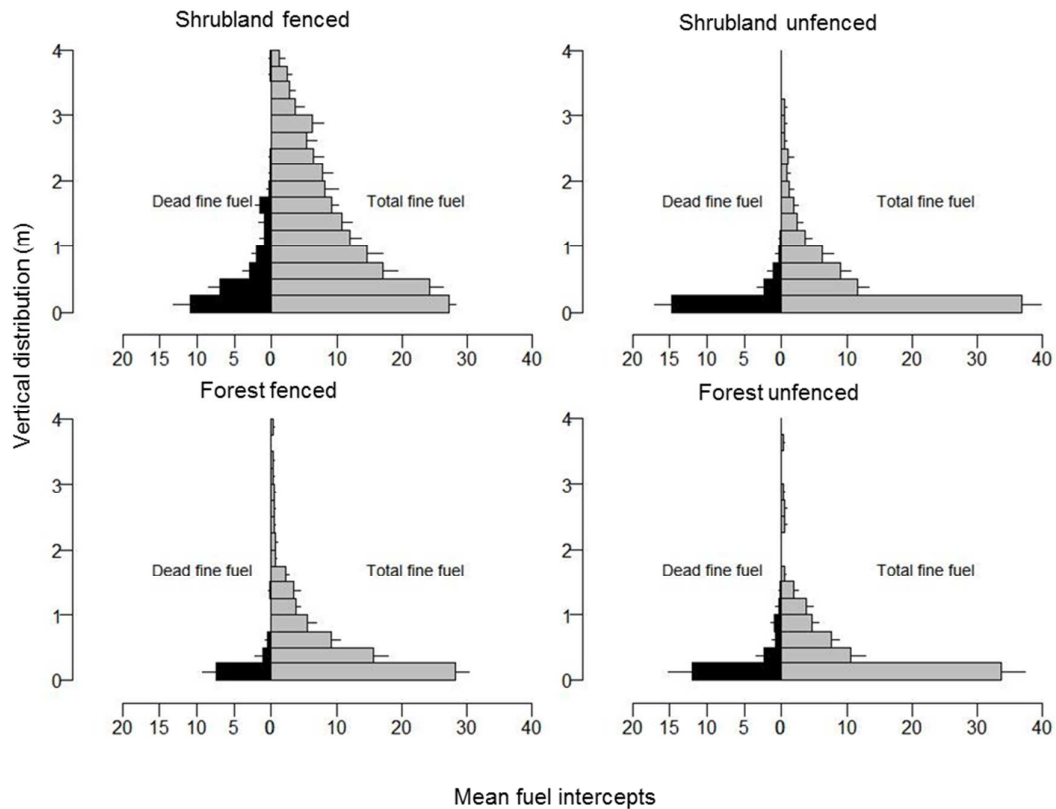
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903 **Fig. 1:** Means (\pm SE) for fuel and flammability characteristics: (a) percentage of total
 904 fine fuel intercepts (%), (b) proportion of dead/total fine fuel (%), (c) litter depth (cm),
 905 (d) foliar moisture (%), (e) time to ignition (s)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

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909 are shown for variables with significant differences between site or cattle effects ($P <$
910 0.05).

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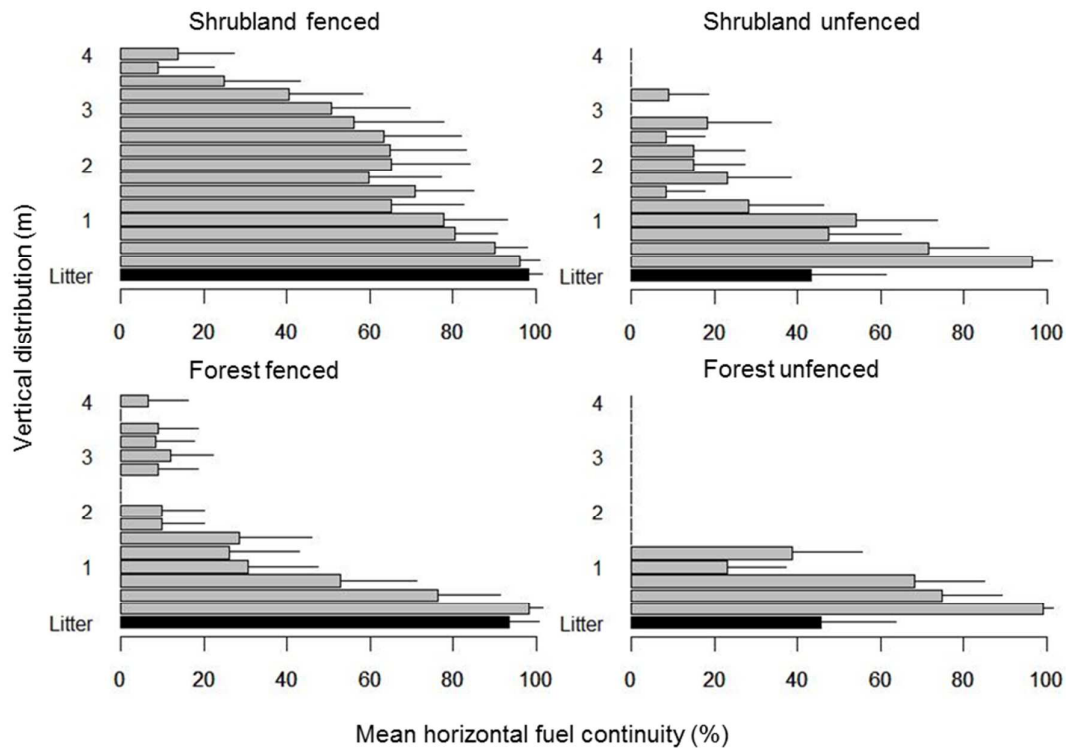


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914 **Fig. 2:** Mean fuel intercepts of fine fuel in 0.25 m height classes used for assessing fuel
 915 vertical distribution at post-fire *Nothofagus pumilio* subalpine forest and post-fire *N.*
 916 *antarctica* shrubland sites, for unfenced and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

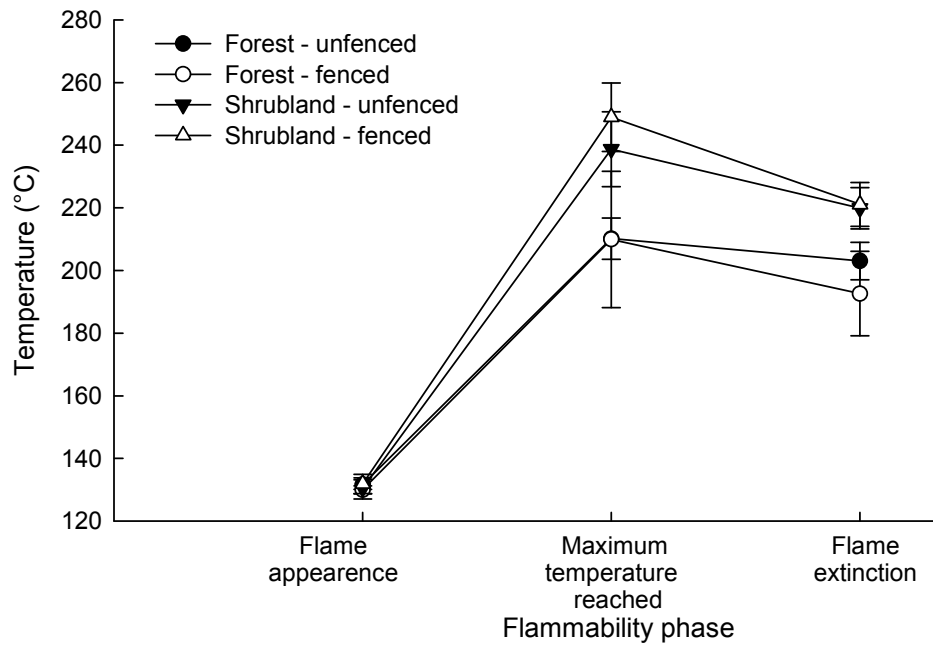
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920 **Fig. 3:** Mean horizontal fuel continuity (expressed as percentages; see Methods for
 921 details) for litter (surface level) and for each 0.25 m height class (\pm SE) at post-fire
 922 *Nothofagus pumilio* subalpine forest and post-fire *N.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

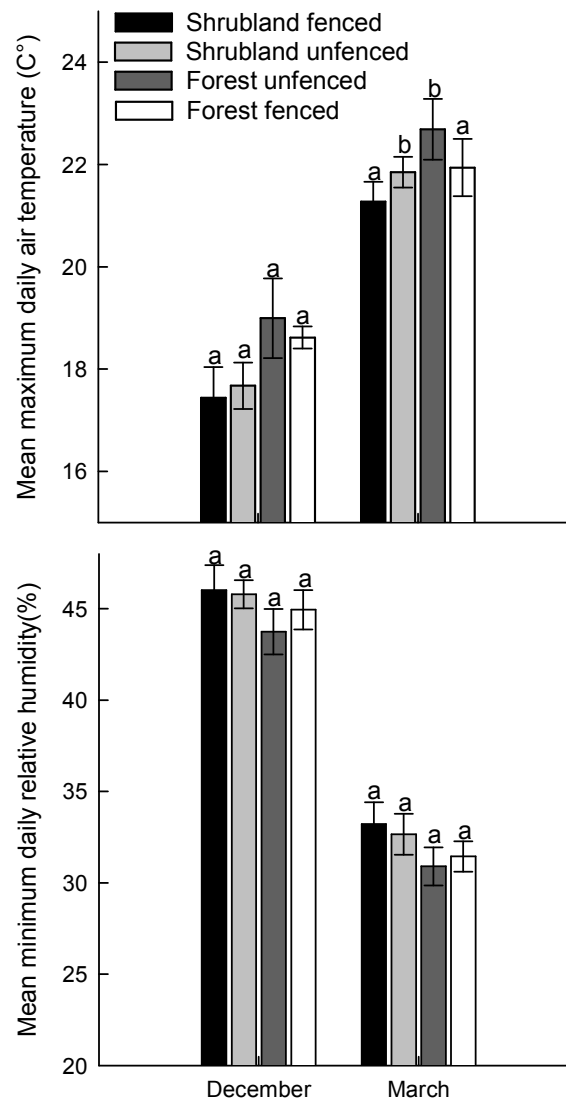
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926 **Fig. 4:** Mean (\pm SE) of temperature recorded in the following phases of the complete
 927 combustion: flame appearance, maximum temperature reached and flame extinction.
 928 Curves are shown for post-fire *Nothofagus pumilio* subalpine forest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

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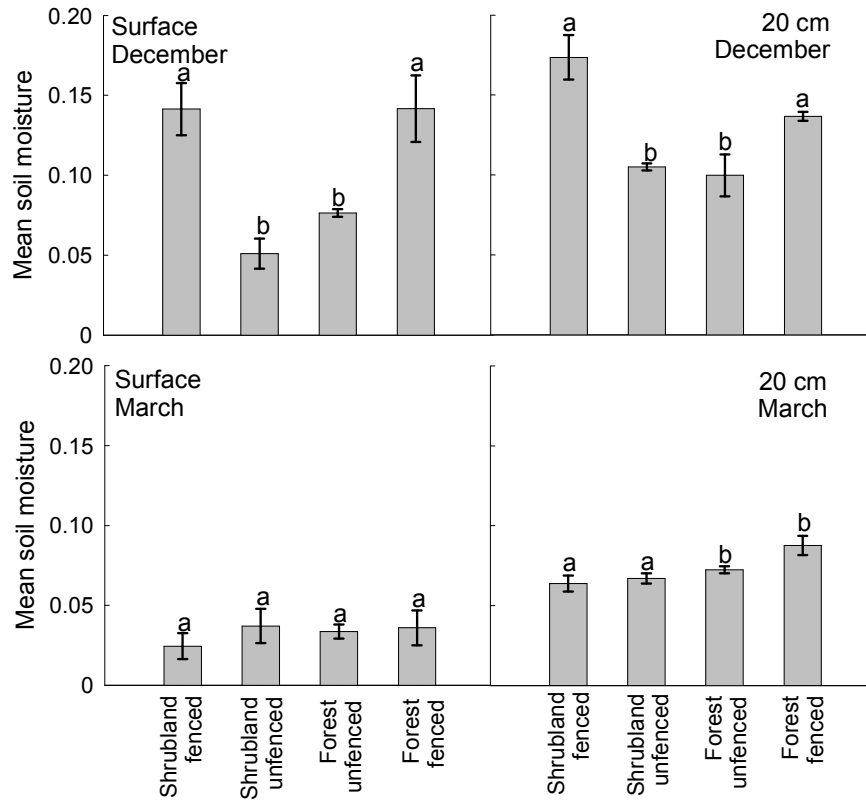


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934 **Fig. 5:** Mean maximum daily air temperature (C°) and mean minimum daily relative935 humidity (%) (\pm SE) for December 2014 and March 2015, at post-fire *Nothofagus*936 *pumilio* subalpine forest and post-fire *N. antarctica* shrubland sites in unfenced and

937 fenced plots. Different letters are shown for variables with significant differences

938 between site or cattle effects ($P < 0.05$).



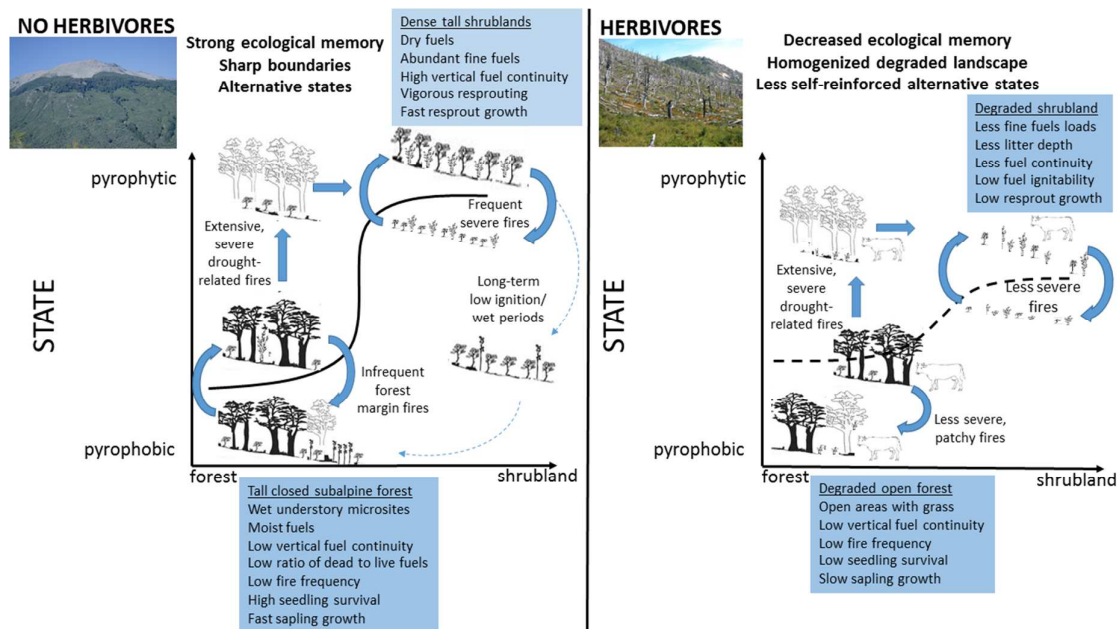
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941 **Fig. 6:** Mean (\pm SE) soil moisture (g H₂O / g soil) at the soil surface and at 20 cm depth
 942 in December 2014 and March 2015 at post-fire *Nothofagus pumilio* subalpine forest and
 943 post-fire *N. antarctica* shrubland sites, for unfenced and fenced plots.

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

48

1 **Supporting Information**2 **Table S1**

3 Results of the general linear model considering the influence of two categorical
 4 predictors (cattle= fenced/unfenced plots; vegetation type (VG) = *Nothofagus pumilio*
 5 subalpine forest/*N. antarctica* tall shrubland) and their interaction, on fine fuel
 6 variables: total fine fuel, dead/total fine fuel and litter depth. See Fig. 1 for the mean
 7 values. * $P \leq 0.05$, ** $P \leq 0.01$.

Effect	DF	Total fine fuel (%)		Dead /total fine fuel		Litter depth (%)	
		F	P	F	P	F	P
Cattle	1	32.73	<0.01**	12.02	<0.01**	54.07	<0.01**
VG	1	27.43	<0.01**	0.06	0.82	4.89	0.06
Cattle × VG	1	15.38	<0.01**	0.02	0.90	5.62	0.05*

8

9

10 **Table S2**

11 Results of the general linear model considering the influence of two categorical
 12 predictors (cattle= fenced/unfenced plots; vegetation type (VG) = *Nothofagus pumilio*
 13 subalpine forest/*N. antarctica* tall shrubland) and their interaction, on laboratory
 14 flammability variables: foliar moisture, time to ignition and flame duration. See Table 1
 15 for the mean values. * $P \leq 0.05$, ** $P \leq 0.01$.

Effect	DF	Foliar moisture (%)		Time to ignition (s)		Flame duration (s)	
		F	P	F	P	F	P
Cattle	1	0.20	0.66	7.86	0.02*	0.86	0.38
VG	1	0.38	0.55	0.43	0.53	2.35	0.16
Cattle × VG	1	0.09	0.76	0.40	0.54	0.04	0.84

16

17

18 **Table S3**

19 Results the general linear mixed model with repeated measures, where between-subject
 20 factors were grazing treatments (cattle=fenced / unfenced plots) and vegetation type
 21 (VG= *N. pumilio* subalpine forest/*N. antarctica* tall shrubland) and we considered the

22 flammability phase as the within-subject factor (with three levels: temperature needed to
 23 achieve flame appearance, maximum temperature reached and temperature during flame
 24 extinction). See Fig. 4 for the mean values. * $P \leq 0.05$, ** $P \leq 0.01$.

Temperatures reached during phases of combustion (°C)			
<i>Effect</i>	<i>DF</i>	<i>F</i>	<i>P</i>
Cattle	1	0.002	0.99
VG	1	11.58	<0.01**
Phase (time)	2	112.23	<0.01**
Cattle × VG	1	0.57	0.45
Cattle × Phase	2	0.25	0.78
VG × Phase	2	3.13	0.05*
Cattle × VG × Phase	2	0.06	0.94

25

26

27 **Table S4**

28 Results of the general linear model considering the influence of two categorical
 29 predictors (cattle= fenced/unfenced plots; vegetation type (VG) = *Nothofagus pumilio*
 30 subalpine forest/*N. antarctica* tall shrubland) and their interaction, on micro-
 31 environmental conditions (mean maximum daily air temperature and mean minimum
 32 daily relative humidity for December 2014 and March 2015). See Figs 5 and 6 for the
 33 mean values. * $P \leq 0.05$, ** $P \leq 0.01$.

34

<i>Effect</i>	<i>DF</i>	Mean maximum air temperature (°C)				Mean minimum relative humidity (%)			
		December		March		December		March	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cattle	1	0.31	0.61	8.39	0.04*	1.07	0.36	1.41	0.30
VG	1	5.14	0.09	1.41	0.30	1.17	0.34	1.56	0.28
Cattle × VG	1	0.02	0.90	0.14	0.73	0.50	0.52	0.01	0.98

<i>Effect</i>	<i>DF</i>	Soil surface moisture				Soil 20cm moisture			
		December		March		December		March	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cattle	1	30.48	<0.01**	0.46	0.51	29.48	<0.01**	1.97	0.20
VG	1	0.82	0.39	0.16	0.70	4.72	0.06	11.33	<0.01**
Cattle × VG	1	0.79	0.40	0.98	0.35	2.63	0.14	4.45	0.07

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