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Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia

Juan Paritsis, Thomas T. Veblen & Andrés Holz

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Alternative stable state; Fire ecology; Fuel; Flammability; *Nothofagus*; Obligate seeders; Positive feedbacks; Resprouting shrubs

Nomenclature
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Paritsis, J. (corresponding author, j.paritsis@gmail.com): Laboratorio Ecotono, INIBIOMA, CONICET–Universidad Nacional del Comahue, 8400 Bariloche, Argentina
Veblen, T.T. (veblen@colorado.edu): Department of Geography, University of Colorado, Boulder, CO 80309, USA
Holz, A. (andres.holz@pdx.edu): School of Plant Sciences, University of Tasmania, Hobart, Tas. 7001, Australia & Department of Geography, Portland State University, Portland, OR 97207, USA

Abstract

Question: Under climate change and increased ignitions by humans, burning of forests in which severe fires were naturally infrequent may result in environmental changes that increase the probability that they will burn again. On the eastern slopes of the northern Patagonian Andes, after fire-resistant *Nothofagus pumilio* forests burn they are typically replaced by fire-prone shrublands dominated by resprouting shrubs. We examine fuel properties and microclimatic conditions at the community level as potential fire feedback mechanisms mediating switches from fire-resistant *N. pumilio* forests to fire-prone shrublands.

Location: Northwestern Chubut province, Patagonia, Argentina.

Methods: We characterized the volume and vertical distribution of fine fuels, understorey woody and semi-woody plant composition, stand structure and microclimatic conditions in unburned and burned *N. pumilio* forest and shrublands 14–29 yr after severe fire.

Results: Fuel amount and arrangement in unburned *N. pumilio* forests are unfavourable for fire activity compared with post-fire *N. pumilio* forests and shrublands. Unburned *N. pumilio* forests presented vertical discontinuities in fine fuel distribution and lesser amounts of fine fuels near the ground in comparison to fuels in shrublands. Floristic understorey composition of unburned and burned shrublands was very similar, while composition of unburned and burned *N. pumilio* forests showed clear differences. Additionally, microclimatic conditions following burning of *N. pumilio* forests and shrublands were significantly warmer and drier than in the unburned forest, and more frequently exceeded thresholds associated with fire activity in this region.

Conclusions: Positive feedbacks from initial burning of otherwise fire-resistant *N. pumilio* forest will accelerate the rate of fire-induced conversion of forests to non-forest assemblages. Once transformed to the alternative state of shrublands, return to a forest cover is unlikely due to increased probability of burning in shrublands, as well as the unfavourable effects of warmer and drier conditions on tree establishment.

Introduction

Alternative stable state theory is often applied to explain the co-existence in the same landscape of highly flammable plant communities with those that rarely burn, where changes in fire regimes and fire feedbacks mediate switches in the vegetation (Wilson & Agnew 1992; Petraitis & Latham 1999). Alternative community states, often separated by sharp boundaries, in the same underlying site conditions are often triggered by initial burning in the less flammable plant community and then maintained by positive fire feedbacks from the post-fire ecosystem (e.g. Cochrane et al. 1999; Odion et al. 2010; Lindenmayer et al. 2011). Climate change together with increased ignitions by humans and rapid changes in land use appear to be enhancing these vegetation switches by promoting the burning of otherwise fire-resistant vegetation (Flannigan et al. 2009; Hoffmann et al. 2012). Once more fire-prone

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community states are established, the self-perpetuating effects of fire by pyrogenic plants may make it extremely difficult to return to the previous less flammable state (Perry & Enright 2002; Odion et al. 2010; Lindenmayer et al. 2011). Documenting and understanding the biotic and physical mechanisms responsible for the inferred positive feedbacks is crucial for improving predictions of fire-driven changes in vegetation in the context of climate change and land-use practices such as fire suppression and introduction of invasive species (Flannigan et al. 2009; Veblen et al. 2011; Hoffmann et al. 2012).

A variety of approaches have been used to detect and evaluate positive feedbacks between fire and vegetation flammability, including the use of remote sensing to document spatial associations of fire with particular vegetation types (Odion et al. 2010), simulation modelling to understand potential successional and landscape trajectories (Beckage et al. 2009; Kitzberger et al. 2012; Perry et al. 2012) and laboratory and field experiments of fire effects on plant traits (Gómez-González et al. 2011; Pausas et al. 2012). Direct evidence of the mechanisms involved in generating and maintaining these positive feedbacks is limited, and is often based on inference from general observations of different fire behaviour in repeated fires or in different vegetation types (Cochrane et al. 1999; Nepstad et al. 2001). However, empirical studies are needed that clearly identify negative fire feedback mechanisms in communities of lower flammability and positive feedback mechanisms in fire-prone communities (Knox & Clarke 2012).

Burning of forests in which fires are typically infrequent may result in environmental changes that enhance the probability that they will burn again. Severe fires kill most canopy trees so that increased insolation results in higher maximum temperatures and more rapid drying of surface fuels (Nepstad et al. 2001; Silveira et al. 2009; Knox & Clarke 2012). Although such studies have documented enhanced favourability of post-fire microclimates for fuel drying and probability of fire over short time periods (i.e. <10 yr), the longer-lasting microclimatic influences of altered vegetation structures have received less research attention. Assuming adequate fuel quantity and continuity, the higher solar radiation and lower relative humidity associated with more open and shorter vegetation canopies will reduce fine fuel moisture content, which is a primary factor controlling flammability (Perry 1998; White & Zipperer 2010). In fact, comparison of tall tropical forest with adjacent sites of shorter vegetation stature and open canopies has documented lower fuel moisture content that allowed ignition of surface fires in the latter (Uhl et al. 1988).

In the temperate forests of southern South America the deciduous southern beech, *Nothofagus pumilio*, typically forms dense monospecific stands, which on the easternmost slopes of the Andes often border 2- to 5-m tall dense shrublands or steppe vegetation of grasses and low shrubs. Photographic evidence documenting the stability of sharp boundaries between these forests and tall shrublands over >80-yr periods initially lead to the hypothesis that vegetation-mediated differences in flammability of these juxtaposed communities maintained these sharp boundaries (Veblen & Lorenz 1988). It was suggested that the more mesic conditions of the tall forests and the lack of vertical fuel continuity reduced their flammability. In contrast, in the tall shrublands crowning of fires was enhanced by the vertical fuel continuity of multi-stemmed branching of the shrubs from the ground surface to the canopy and by the abundance of fine fuels from *Chusquea culeou* bamboos (Veblen & Lorenz 1988). At a centennial time scale, tree-ring dating of fire history across an extensive landscape mosaic revealed higher levels of fire activity in tall *Nothofagus antarctica* shrublands than in adjacent *N. pumilio* forests (Veblen et al. 1992). At a time scale of ca. 30–50 yr, time series of remotely sensed imagery over large areas (tens of thousands of km^2) have shown that fires are less likely to ignite in or spread into *N. pumilio* forests than in the neighbouring tall shrublands (Mermoz et al. 2005; Paritsis et al. 2013). *N. pumilio* forests normally burn only during extreme drought years, whereas fires in the shrublands also occur under less extreme drought (Mermoz et al. 2005). Most fires start at low to mid-elevation in shrublands and burn upslope into the zone of subalpine *N. pumilio* forests (Mermoz et al. 2005). Only during extreme drought conditions can fires burn large areas (hundreds of hectares) of fire-resistant *N. pumilio* forests (Mermoz et al. 2005). Post-fire regeneration of *N. pumilio* is limited to a narrow belt of only a few tens of meters from the forest edge due to limited seed dispersal, as well as unfavourable microclimatic and edaphic conditions and sometimes herbivory by livestock and other introduced animals (Kitzberger et al. 2005; Tercero-Bucardo et al. 2007; Raffaele et al. 2011). Hence, burned *N. pumilio* forests are typically replaced by fire-prone shrublands dominated by vigorously resprouting shrubs that provide rapid fuel recovery in these fire-prone habitats. Relative to adjacent tall forests, the shorter fire return intervals in the shrublands favour continued dominance by the bamboos and shrubs, all of which vigorously resprout, whereas the juveniles of *N. pumilio* (an obligate seeder) are eliminated by repeated burning (Kitzberger et al. 2005; Raffaele et al. 2011; Fig. 1).

The scenario described above has been widely observed in northwestern Patagonia (Veblen & Lorenz 1988; Kitzberger et al. 2005; Raffaele et al. 2011; Veblen et al.

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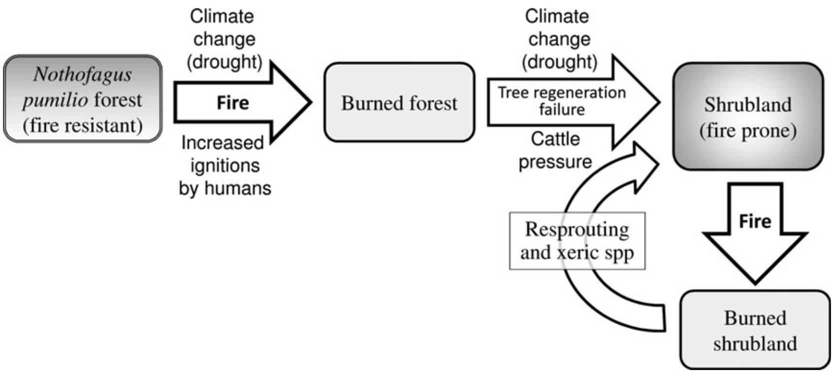

Fig. 1. Conceptual model showing the proposed positive feedback between vegetation and fire and some of the key variables responsible for it.

2011). Spatio-temporal simulation of landscape dynamics assuming that flammability is initially high after forest burning and then declines to lower levels suggests that in such landscapes, the less flammable forests are likely to rapidly decline in extent under scenarios of relatively slight increases in ignitions and fire-enhancing weather (Kitzberger et al. 2012). However, the mechanisms contributing to the high flammability of young post-fire communities relative to low flammability of the tall *N. pumilio* forests have not been fully identified and quantified. Differences in vegetation structure and microclimate have long been hypothesized to increase the flammability of tall shrublands compared to *Nothofagus* forests (Veblen & Lorenz 1988). Recent research has shown that at the individual plant level, recently burned (i.e. within the last 15 yr) sites are characterized by plants with flammability-enhancing traits, such as higher retention of dead fine fuel, larger amounts of live fine fuels and lower foliar moisture (Blackhall et al. 2012). The current research complements those findings for individual species by examining fuel properties and microclimatic conditions at the community level as potential fire feedback mechanisms mediating switches from fire-resistant *N. pumilio* forests to fire-prone shrublands. Our overall objective is to quantify fuel properties (amount and vertical distribution), vegetation structure and microclimate in unburned forests and in post-fire plant communities as mechanisms that might explain flammability differences between these communities. We quantify and compare fine fuel amounts (volume) across height classes, stand structure (tree size structure and crown base heights) and species composition in unburned and burned *N. pumilio* forests and in burned and unburned shrublands. We compare microclimatic conditions (air temperature and relative humidity) among unburned *N. pumilio* forests and burned forests and shrublands, and evaluate the frequencies with which temperature and relative humidity thresholds associated with wildfires in northwestern Patagonia are exceeded.

Methods

Study area

The study area extends from ca. 42°50′ S to 44°20′ S and from ca. 71°15′ W to 71°35′ W on the east side of the Andes in Chubut province, Argentina (Fig. 2). The topography in the western portion of the area is mountainous, whereas low foothills and plains dominate the easternmost areas (Fig. 2). Mean annual precipitation decreases from >2000 mm at the Andean divide to ca. 500 mm in the east of our study area (i.e. ca. 50 km east of the divide; Hijmans et al. 2005). Most precipitation occurs during May–September, both as rain and snow, whereas December–March is predominantly dry. Mean monthly temperatures vary from 4 °C for July (winter) to 15 °C for January (summer), but differ greatly with elevation (Hijmans et al. 2005). Maximum summer temperatures reach up to 35 °C in the region (Esquel Aerodrome weather station; http://www.tutiempo.net). High elevations are characterized by deciduous forests of *N. pumilio*, which is the dominant of the most extensive forest type in southern Argentina and Chile (Veblen et al. 1996). The eastern foothills are characterized by tall and dense shrublands and woodlands of the shrubby resprouting tree *N. antarctica* and other small trees and shrubs, such as *Schinus patagonicus*, *Berberis microphylla* and *Ribes cucullatum* (Veblen et al. 2008; Quinteros et al. 2010). The easternmost areas are dominated by Patagonian steppe, with tussock grasses (*Stipa* spp., *Festuca* spp.) and low shrubs such as *Mulinum spinosum*.

Sources of fire ignitions include both lightning and humans, but in most years humans are the more common cause of wildfires (Veblen et al. 2008). Indigenous people have burned the forest-steppe ecotone mostly for hunting purposes and the mesic forest zone for clearing transportation routes (Veblen & Lorenz 1988). Euro-American settlers caused large-scale forest burning during the 1890s and early 1900s to open the landscape for livestock raising (Willis 1914). Extensive livestock raising and fuelwood

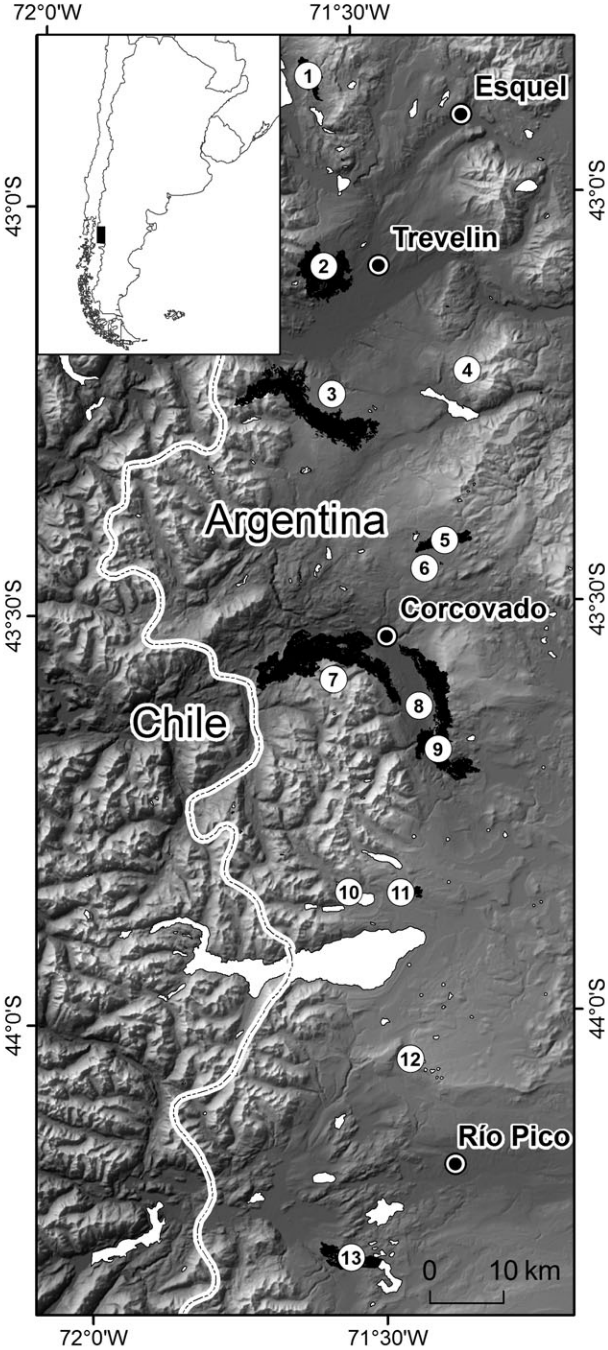

Fig. 2. Location and extent of the 13 fire events (black polygons) sampled. See Table 1 for names and characteristics of the sites sampled.

production continue to be the main uses of *N. antarctica* tall shrublands in the study area (Reque et al. 2007). Higher elevation *N. pumilio* forests receive less anthropogenic use than shrublands in the study area because they are generally less accessible and on steeper slopes. With the creation of national parks in the region in the 1930s, a fire suppression policy was implemented, with variable success (Veblen et al. 2008; Sagarzazu & Defossé 2009). Currently, most fires are human-ignited and respond to a variety of causes, from fire mismanagement to intentionally set wildfires as a means to express social tension (De Torres Curth et al. 2012; Marini 2012; Mundo et al. 2013).

Study design and data collection

We used Landsat TM imagery, digital vegetation maps (Lara et al. 1999) and field surveys to select 13 accessible high-severity fires that burned between 1983 and 1998 in *N. pumilio* forest and/or shrubland (Table 1). Eight of these fires burned in both *N. pumilio* forest and shrubland, and were adjacent to tall (i.e. >15 m) unburned *N. pumilio* forest. The remaining five fires burned in either *N. pumilio* forest (three fires) or shrubland (two fires). To determine pre-burn vegetation, we used a combination of Landsat imagery, vegetation cover maps and field observations. During the summers of 2011–2013, we characterized the volume and vertical distribution of fine fuels, stand structure and understorey plant composition in five different vegetation types representing the following fire histories: (1) tall *N. pumilio* forest unburned for ≥100 yr (UnFo; 11 sites); (2) post-fire tall *N. pumilio* forest 14 to 29 yr after fire that converted to short shrubland and grass cover (BuFo/Sh; 11 sites); (3) post-fire tall *N. pumilio* forest 14 to 29 yr after fire with abundant *N. pumilio* juveniles (BuFo/Fo; six sites); (4) tall shrubland unburned for ≥50 yr (UnSh; ten sites); and (5) tall shrubland burned within the last 14 to 29 yr that recovered back to shrubland (BuSh/Sh; ten sites) (Fig. 3, Table 1). Many of the shrublands probably originated from earlier burning of tall *N. pumilio* forests (e.g. Fig. 3d). All sampling areas in both BuFo/Fo and BuFo/Sh were within 20 to 60 m from the unburned forest edge of UnFo sites. All vegetation types within each fire perimeter were located on similar slope aspects, but due to their natural distribution UnFo, BuFo/Sh and BuFo/Fo were at slightly higher elevations compared to UnSh and BuSh/Sh vegetation types (difference = 77.6 ± 24.3 m; mean ± SE). All sites experienced some degree of use by cattle, but the most intense impact of livestock was in the BuFo/Sh type where in some cases bunchgrasses, which naturally occur in both burned and unburned shrublands, had been largely replaced by herbaceous turfs.

Fire dates were obtained from documentary records (Sagarzazu & Defossé 2009) as well as from Landsat images. For fires for which we did not have precise documentary records of the fire year and where there were fire-scarred *N. pumilio* trees (i.e. six sites), we collected a minimum of three fire-scarred partial cross-sections per site. Samples were processed following standard dendrochronological procedures (Stokes & Smiley 1968), and fire

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Table 1. Characteristics of the sampled sites. Sampled vegetation types at each fire site are indicated with an 'x'. Reported fire years preceded with a 'ca.' can be up to 5 yr earlier than the indicated year and an asterisk indicates that the year was determined using fire scars (±1 yr).

Map Code	Fire Name	Fire Year	Estimated Extent (ha)	UnFo	BuFo/Sh	BuFo/Fo	UnSh	BuSh/Sh	Elevation Range (m)	Slope Aspect (°)
1	La Torta	1983	740	x	x		x	x	830–1120	220–240
2	IFONA	1987	2680	x	x			x	1040–1080	120–140
3	El Blanco	1996	4150	x	x		x	x	860–940	280–340
4	Rosario	*1991	50	x	x		x		980–1190	270–300
5	Loma Grasa A	*1989	880	x	x	x	x	x	1010–1030	280–300
6	Loma Grasa B	ca. 1992	65				x	x	900–910	Flat
7	Carrenleufú	1988	5020	x	x	x	x	x	450–1100	0–20
8	Corcovado	*1998	2040	x	x			x	870–1080	260–270
9	Palenque	ca. 1992	1290				x	x	460–470	Flat
10	Engaño	*1987	130	x	x	x	x	x	950–980	220, flat
11	Guacho	*1986	410	x	x	x	x		990–1050	160–180
12	Vinter sur	1984	120	x	x	x	x		1090–1240	260, flat
13	Lago 2	*1988	1060	x	x	x		x	810–820	90–120

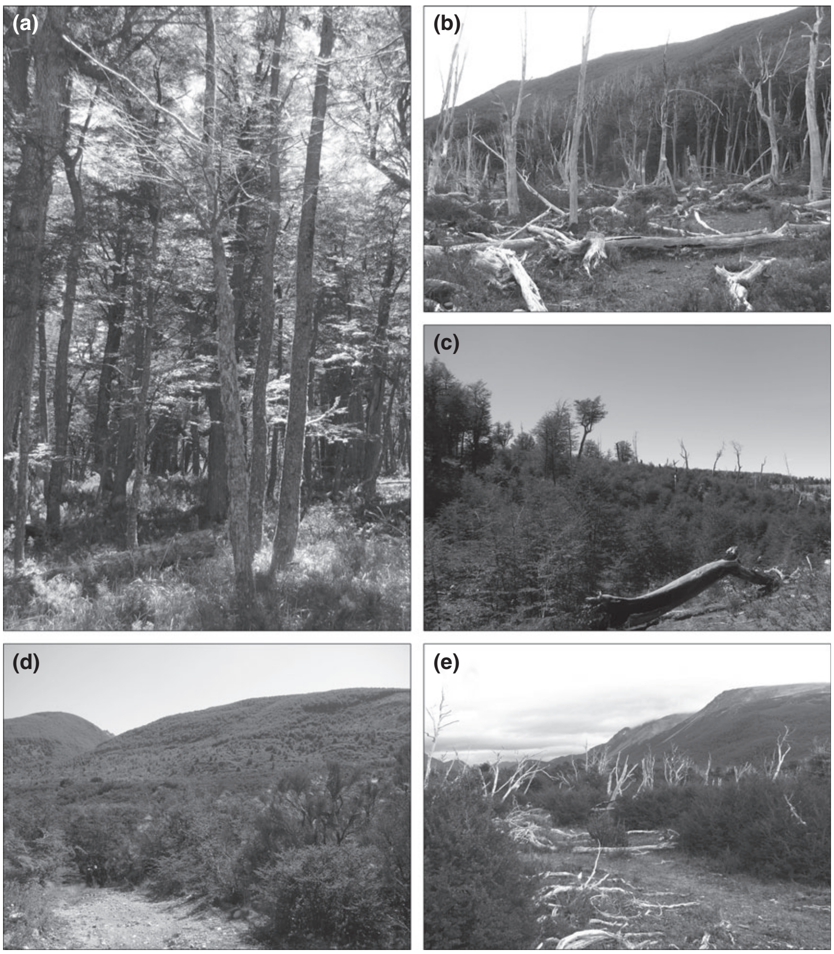

Fig. 3. Five vegetation types characterized in this study: (**a**) unburned *N. pumilio* forest (UnFo); (**b**) burned *N. pumilio* forest converted to short shrubland (BuFo/Sh; 1987 fire); (**c**) burned *N. pumilio* forest with dense regeneration of juveniles (BuFo/Fo; 1986 fire); (**d**) unburned shrubland (UnSh) and (**e**) burned shrubland that recovered back to shrubland (BuSh/Sh; 1987 fire). The sharp boundaries between tall forest and tall shrubland in the background of (**d**) reflect burns older than ca. 30 yr.

years were determined following procedures used in Veblen et al. (1999). We also collected increment cores from at least three trees in the UnFo vegetation type to obtain the approximate minimum age of the stand. No collection of increment cores was conducted in UnSh due to the large proportion of rotten centres in *N. antarctica* trees.

To quantify fine fuel volume and its vertical distribution at each vegetation type, we set three 50-m long transects parallel to the fire boundary and within 10 to 50 m from it, containing ten equally distributed 2-m^2 circular plots each. We defined fine fuel as foliage and all plant material, dead or alive, <0.6-cm diameter. In each 2-m^2 plot, we visually estimated fine fuel volume (%) at three different portions of a projected vertical cylinder (i.e. 0–2, 2–5, 5 m to the highest point in the canopy). Volumes were obtained by combining visual estimations of fine fuel cover in the horizontal and in the vertical dimensions. Our aim was not to estimate a packing ratio but rather a consistent estimation of the bulk density of fine fuels (i.e. fuel volume plus the inter-particle void volume with a 10-cm^3 grain) useful for comparative purposes among the surveyed vegetation types. Volume was recorded as six discrete percentage classes (<1%, 1–5%, 5–25%, 25–50% 50–75% and 75–100%) that were subsequently transformed into single percentage values using the median percentage value for each class (Pellissier et al. 2004). For the 0–2 m portion, the <1% class represents an almost bare soil with a few dispersed and short forbs and/or grasses, whereas the 75–100% class represents dense and continuous leaves and twigs with few gaps. Estimations of fuel volume were conducted by the same observer for all the sites and vegetation types. Nevertheless, to test for the accuracy of our estimations, we compared these data with a pole intercept method at eight sites (i.e. 240 plots). For the pole intercept method, a 2-m pole with divisions every 25 cm was placed vertically in the centre of the plot, and we recorded how many segments were in contact with fine fuels. We conducted the pole intercept method only for the 0–2 m portion of the cylinder. Results obtained with both methods were positively correlated ($r = 0.85$, $P < 0.01$).

We also characterized understorey woody and semi-woody species composition and cover in all vegetation types, except in BuFo/Fo due to the near absence of woody and semi-woody plants beneath the dense layer of *N. pumilio* regeneration in this vegetation type. We used the same plots as for the fuel volume estimations, and we recorded species identity and percentage cover up to 2-m height (using the same percentage classes described above). To characterize the height of the understorey layer, we recorded the maximum height of woody and semi-woody species in the plot. As with fuel volume values, we transformed the cover class values into single percentage values. Along each 50-m transect and where trees (>4-cm DBH) were present, we characterized the structure of the stands by recording tree density, DBH, tree height and crown base height. Transects varied in width in order to include a minimum of ten trees. Due to the high stem density, in the BuFo/Fo type we tallied the number of seedlings (<1 cm DBH and <1.4 m height), saplings (<4 cm DBH and >1.4 m height) and trees in 2-m^2 plots. Because trees were rarely present in BuFo/Sh we did not characterize the tree structure of this vegetation type.

To assess variation in environmental variables relevant to fire activity among vegetation types, we monitored air temperature and relative humidity (RH) during the summer season in UnFo and BuFo/Sh vegetation types at eight fire sites. We placed one temperature and RH data logger (Hygrochron iButton DS1923, Maxim Integrated) per vegetation type at each site, programmed to record values at 4-h intervals starting at 12:00 h. Data loggers were placed at 1.0–1.5 m above the ground and covered with a small protective roof away from direct sunlight, and were active in the field for 61 days in all sites simultaneously (i.e. 25 Jan to 25 Mar 2012).

Data analysis

Fine-fuel volume was compared among the five vegetation types for the first two height intervals (0–2 and 2–5 m) using a Kruskal–Wallis one-way ANOVA by ranks test with Mann–Whitney post-hoc tests due to the lack of normally distributed variables. We did not make statistical comparisons for fuel volume at the >5 m interval because of the high variability in height among vegetation types. We explored the variation in woody and semi-woody plant species composition among vegetation types using the Bray-Curtis similarity index (Bloom 1981). We used the mean percentage species cover at each vegetation type and constructed a matrix with all the possible comparisons among vegetation types. We also determined the six most frequent woody and semi-woody species per vegetation type and visually compared their ranks. Statistical differences in stand structure variables between UnFo, UnSh and BuSh/Sh were tested with one-way ANOVAs and post-hoc Tukey tests for those variables that were normally distributed (i.e. DBH, tree height and crown base height), and with a Kruskal–Wallis one-way ANOVA by ranks test followed by Mann–Whitney post-hoc tests for those variables that did not have a normal distribution (i.e. basal area). All statistical tests were conducted using site means as replicates.

To examine microclimatic parameters under conditions most likely to be associated with fire, we computed mean temperature and mean RH for the 10% of the days with the highest daily temperature and the 10% of the days with the lowest RH in UnFo, BuFo/Sh and BuSh/Sh. We

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also calculated the mean maximum temperature and mean minimum RH per vegetation type. Finally, to assess the frequency of days with high probability for fire ignition based on meteorological conditions during ignition of past fires in the region (Sagarzazu & Defossé 2009), we computed the number of days with both maximum temperatures >25 °C and minimum RH < 25%. Statistical differences in temperature and RH between vegetation types were analysed with one-way ANOVAs and post-hoc Tukey tests.

Results

Fuels and species composition

In the UnFo sites fine fuels are vertically discontinuous, with relatively low volumes in the 0–2 m height class and a near absence of fine fuels in the intermediate height class of 2–5 m (Fig. 4). Most of the fine fuel volume in these unburned tall forests is in the >5 m height class (Fig. 4). Although the BuFo/Sh sites show no significant difference in the volume of fine fuels in the lowest height class (0–2 m) compared with UnFo, the BuFo/Sh fuels in higher classes (>2 m) are practically absent. UnFo and BuFo/Sh have lower fuel amounts in the lowest height class (0–2 m) compared to all other vegetation types. Volume and vertical distribution of fine fuel are relatively similar between UnSh and BuSh/Sh, with abundant fuel in the lowest height class and a gradual decline in fuel volume in upper height classes (Fig. 4). BuFo/Fo has a similar vertical fuel load and distribution as UnSh and BuSh/Sh but with additional fuel volume in the intermediate height class (2–5 m; Fig. 4).

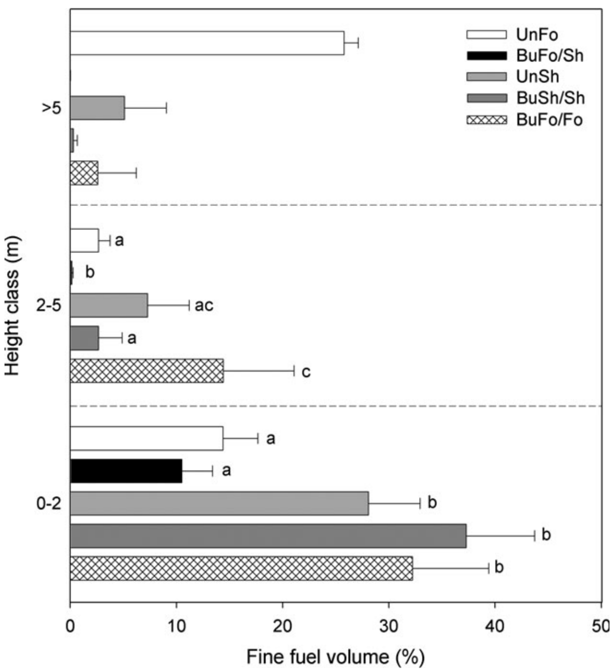

Fig. 4. Fine fuel volume (%) in three height classes for the five vegetation types. Values within the same height class followed by different letters are significantly different ($P < 0.05$). Statistical comparisons for the >5-m interval were not performed because the variable maximum height of this interval class among vegetation types precluded comparability of fuel volumes. Vegetation types and codes are: unburned *N. pumilio* forest (UnFo); burned *N. pumilio* forest converted to short shrubland (BuFo/Sh); unburned shrubland (UnSh); burned shrubland that recovered back to shrubland (BuSh/Sh); and burned *N. pumilio* with dense *N. pumilio* regeneration (BuFo/Fo).

Bray-Curtis similarity matrix (Table 2) and abundances of the most common species (Table 3) indicate important differences in species composition and abundance between unburned and burned forest sites (UnFo and BuFo/Sh) in contrast to the floristic similarity of unburned and burned shrublands (UnSh and BuSh/Sh). BuFo/Sh is more similar in species composition to UnFo than to UnSh and BuSh/Sh. However, similarity indices between BuFo/Sh and UnSh or BuSh/Sh are higher than those between UnFo and UnSh or BuSh/Sh (Table 2). The UnFo vegetation type is characterized as having trees of larger DBH and basal area compared with the UnSh and BuSh/Sh vegetation types (Fig. 5a,b). Tree height in UnFo is significantly higher than in UnSh and BuSh/Sh, but there is no significant difference in tree height between UnSh and BuSh/Sh (Fig. 5c). Crown base height and understorey height indicate a vertical discontinuity of ca. 6 m in fine fuels in UnFo (Fig. 5d). In contrast, fine fuel layers are vertically continuous in the UnSh and BuSh/Sh vegetation types, where the crown base height is lower than the height of the understorey layer (Fig. 5d). BuFo/Fo is characterized as having dense seedlings and saplings (5400 ± 1606 and 7433 ± 2568 ha^{-1}, respectively) and moderate tree density (1500 ± 637 ha^{-1}) of *N. pumilio*, reflecting the belts of post-fire tree regeneration immediately bordering the unburned forests (i.e. UnFo sites).

Microclimate

Temperature and RH data indicate that microclimatic conditions in UnFo are generally cooler and moister than in

Table 2. Bray–Curtis similarity matrix using the mean species percentage cover for the four vegetation types. Vegetation types and codes are: unburned *N. pumilio* forest (UnFo); burned *N. pumilio* forest converted to short shrubland (BuFo/Sh); unburned shrubland (UnSh); and burned shrubland that recovered back to shrubland (BuSh/Sh).

	UnFo	BuFo/Sh	UnSh	BuSh/Sh
UnFo	1			
BuFo/Sh	0.47	1		
UnSh	0.24	0.34	1	
BuSh/Sh	0.24	0.36	0.82	1

Table 3. Mean (±SE) frequency expressed as percentage for the six most common woody and semi-woody species in each vegetation type. Species codes are: *M.c.* (*Maytenus chubutensis*), *B.s.* (*Berberis serratodentata*), *N.p.* (*Nothofagus pumilio*), *C.c.* (*Chusquea culeou*), *V.n.* (*Vicia nigricans*), *C.r* (*Chiliotricum rosmarinifolium*), *S.s.* (*Senecio* sp.), *R.c.* (*Ribes cucullatum*), *B.m.* (*Berberis microphylla*), *R.m.* (*Ribes magellanica*), *N.a.* (*Nothofagus antarctica*), *S.p.* (*Schinus patagonicus*).

Rank	UnFo		BuFo/Sh		UnSh		BuSh/Sh	
1	*M.c.*	62.7 (9.0)	*S.s.*	29.1 (8.8)	*N.a.*	53.7 (12.1)	*N.a.*	59.7 (10.8)
2	*B.s.*	48.8 (13.2)	*R.c.*	21.8 (7.2)	*B.m.*	46.3 (9.1)	*B.m.*	43.7 (8.9)
3	*N.p.*	35.8 (8.5)	*M.c.*	20.0 (5.4)	*R.c.*	37.3 (9.3)	*R.c.*	26.7 (8.2)
4	*C.c.*	19.1 (10.4)	*V.n.*	18.8 (10.6)	*S.p.*	24.7 (11.2)	*M.c.*	20.7 (5.4)
5	*V.n.*	15.8 (10.6)	*B.m.*	17.6 (7.7)	*M.c.*	17.7 (6.7)	*S.p.*	14.7 (6.7)
6	*C.r.*	11.5 (5.6)	*R.m.*	17.0 (6.5)	*C.c.*	15.7 (10.7)	*C.c.*	12.0 (9.9)

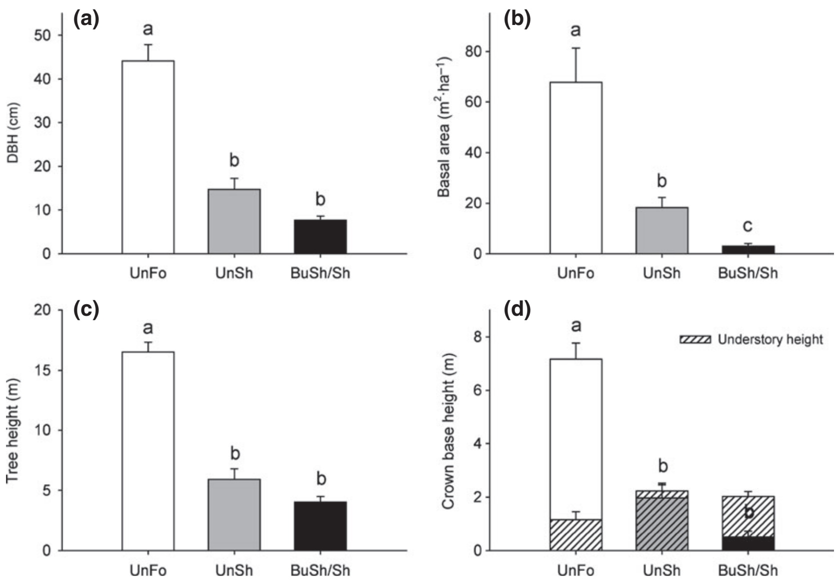

Fig. 5. Stand structure variables for unburned *N. pumilio* forest (UnFo); unburned shrubland (UnSh); and burned shrubland that recovered back to shrubland (BuSh/Sh). Data on tree sizes and density were not collected for the BuFo/Fo and BuFo/Sh vegetation types. Different letters indicate significant differences with one-way ANOVA and post-hoc Tukey tests ($P < 0.05$) for (**a**), (**c**) and (**d**), and with Kruskal–Wallis one-way ANOVA by ranks tests followed by Mann–Whitney post-hoc tests ($P < 0.05$) in (**b**). In (**d**), mean understorey maximum heights are also depicted to visually compare them with the crown base heights.

BuFo/Sh and BuSh/Sh. The warmest 10% of days for the eight recorded sites (mean ± SE) was significantly cooler ($P < 0.05$) in UnFo (20.4 ± 0.5 °C) than in BuFo/Sh and BuSh/Sh (24.4 ± 0.7 and 24.9 ± 0.4 °C, respectively; Fig. 6a). The driest 10% of days in UnFo (32.3 ± 1.9%) was significantly moister ($P < 0.05$) than in the other vegetation types (BuFo/Sh = 26.0 ± 1.2% and BuSh/Sh = 25.2 ± 1.0%; Fig. 6b). Mean maximum temperature in UnFo (22.2 ± 0.5 °C) was significantly lower than in BuFo/Sh and BuSh/Sh (27.4 ± 0.9 and 27.5 ± 0.7 °C, respectively; Fig. 6c), and mean minimum RH in UnFo (25.3 ± 1.3%) was significantly moister than in BuFo/Sh and BuSh/Sh (20.9 ± 1.7% and 18.4 ± 1.0%, respectively; Fig. 6d). Mean maximum temperature difference recorded between vegetation types on a given day was 7.6 ± 1.0 °C between UnFo (cooler) and BuSh/Sh (warmer), followed by 6.7 ± 0.8 °C between UnFo (cooler) and BuFo/Sh (warmer; Fig. 6e). Mean maximum RH difference recorded was 29.5 ± 3.7% between UnFo (moister) and BuSh/Sh (drier), followed by 24.0 ± 4.3% between UnFo (moister) and BuFo/Sh (drier; Fig. 6f). None of the microclimatic parameters differed significantly between the BuFo/Sh and BuSh/Sh sites, implying similarly warm and dry microsites even when the burned shrubland was dominated by ca. 2–4-m tall shrubs. Finally, number of days with temperatures >25 °C and RH < 25% (i.e. optimal conditions for fire ignition in the region) was zero in UnFo for the summer of observation (i.e. 61 days). In contrast, in BuFo/Sh and BuSh/Sh mean number of days per summer with these conditions was 1.1 ± 0.4 and

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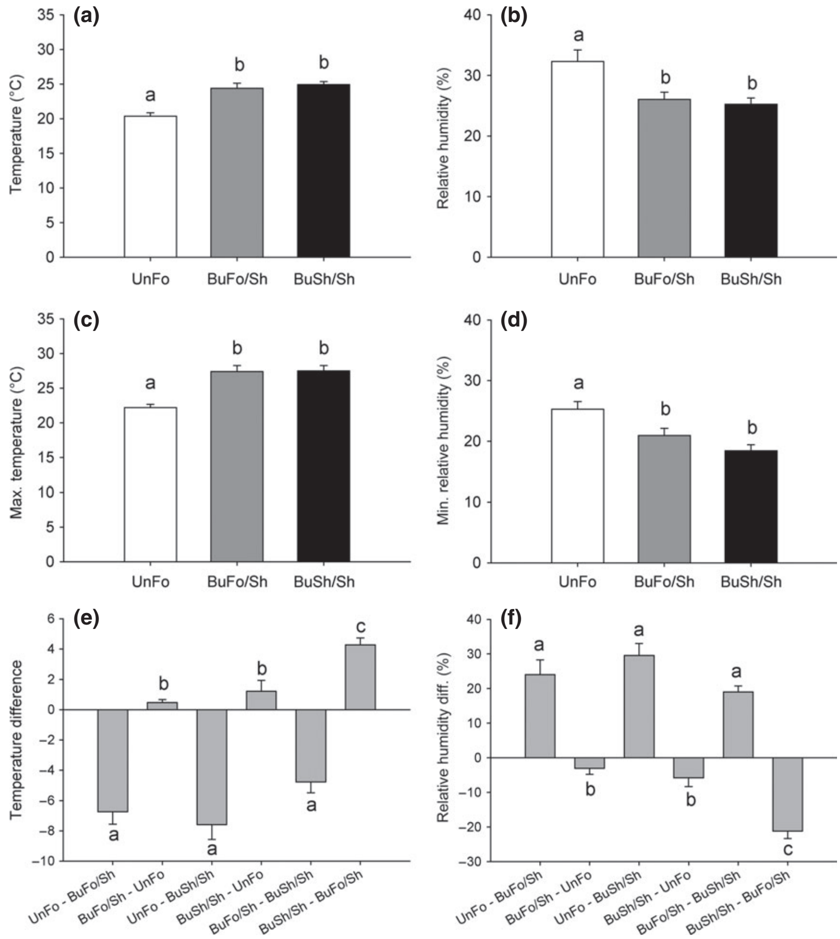

Fig. 6. Microclimatic summer conditions (mean ± SE) in unburned *N. pumilio* forest (UnFo), burned *N. pumilio* forest converted to short shrubland (BuFo/Sh) and burned shrubland that recovered back to shrubland (BuSh/Sh). (**a**) Daytime air temperature for the 10% of warmest days at each vegetation type. (**b**) Daytime relative humidity (RH) for the 10% of driest days at each vegetation type. (**c**) Maximum air temperature and (**d**) minimum air RH per vegetation type. (**e**) Maximum air temperature differences and (**f**) maximum air RH difference recorded for all the possible comparisons among vegetation types for all sites. Different letters indicate significant differences with one-way ANOVA and post-hoc Tukey tests ($P < 0.05$).

1.0 ± 0.4, respectively. Moreover, in BuFo/Sh sites there were up to two consecutive days that met these conditions.

Discussion

Our results are consistent with the hypothesis that following burning of low flammability *N. pumilio* forests, the fuel arrangements and environmental conditions of the succeeding shrublands increase the likelihood of subsequent burning. Prior research on these Patagonian ecosystems using time series of remotely sensed images and mapping of pre- and post-fire vegetation types has documented the greater propensity for shrublands to burn and the lower likelihood of fires to occur in tall *N. pumilio* forests (Mermoz et al. 2005; Paritsis et al. 2013). Previous research has also shown that fine fuel properties and foliar flammability of individual species in post-fire shrublands are more conducive to fire spread (Blackhall et al. 2012). In the current study, we quantified the following mechanisms contributing to the lower flammability of *N. pumilio* forests in comparison to adjacent shrublands: (1) lower amounts of fine fuels near the ground surface, (2) lack of vertical fuel continuity from the understorey to tree canopy, and (3) cool and moist microclimate that would reduce the rate of drying of sub-canopy fuels.

The volume of fine fuels in the 0–2 m height class was significantly less in the unburned *N. pumilio* forest in comparison with burned or unburned vegetation dominated by tall shrubs or by dense populations of *N. pumilio* saplings. The abundance and greater continuity of fine fuels near the ground surface would favour surface fire spread in all these non-forest vegetation types. The only vegetation type with surface fuel volumes similar to

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unburned forest was the burned forest converted to short shrubs and grass cover (BuFo/Sh), which had the most intense impacts from cattle. Here, fine fuel reduction would probably inhibit surface fire spread unless herbivore pressure is reduced. In an intermediate height class of 2 to 5 m, fine fuel volumes were low in the unburned forest, resulting in a discontinuity of vertical distribution of fine fuels from the understorey to the fine fuels of the tree canopy. In the unburned forest, on average there was a gap of ca. 6 m between the maximum heights of the understorey shrubs and the crown base height of canopy trees. In contrast, in unburned and recovering burned shrublands, both percentage fine fuels and low crown base heights provided continuous vertical distributions of fuel from the surface to the top of shrub crowns. Thus, the density and vertical continuity of fuels in these shrublands would be expected to favour the spread of surface fires into a continuous layer of intermingled shrub canopies.

Microclimates in unburned *N. pumilio* forest, compared to shrub-dominated sites where the forest had been burned 14 to 29 yr earlier, were characterized by significantly lower maximum temperatures and significantly higher RH for the 10% of the warmest and the driest days, respectively. Documented fire and weather records show that threshold temperatures and RH optimal for fire occurrence in this region are >25 °C and RH < 25% (Sagarzazu & Defossé 2009). Over the 61-day period of our study, these thresholds were never exceeded in the unburned forest, while in both the burned forest developing into a shrubland and in the burned shrubland there was 1 day on average among sites that exceeded this threshold. Overall, these microclimatic conditions indicate that the plant communities that develop following burning of tall *N. pumilio* forests are likely to experience more rapid drying of dead and live fuels, as has been found in other studies of angiosperm-dominated forests (Nepstad et al. 2001; Silveira et al. 2009; Knox & Clarke 2012). Furthermore, these results are consistent with the previous research in Patagonia documenting lower foliar moisture content of the dominant shrubs at post-fire sites (<15 yr after fire) in comparison to unburned forests (Blackhall et al. 2012).

Our study documented two divergent successional pathways following the burning of tall *N. pumilio* forests, both of which are characterized by fuel and environmental conditions more conducive to fire than the unburned tall forest. In the first pathway, narrow (<50 m) strips bordering unburned forest with seed sources are dominated by dense populations of *N. pumilio* seedlings and saplings that provide a continuous surface fuel load that, in the absence of a protective tree canopy, is exposed to the drying effects of high insolation. This initial phase of post-fire tree regeneration is likely to be more susceptible to the spread of surface fires than the adjacent tall forest for at least the 29-yr post-fire period included in our study. The alternative pathway is forest conversion to a short shrubland, as reflected both by the absence of tree seedlings and the shift in floristic composition towards dominance by shrubs not common in the understorey of the tall forests (e.g. *N. antarctica*, *R. cucullatum*). In the absence of future fires, the latter community could eventually succeed to tall *N. pumilio* forest, as suggested by the occasional presence of tree seedlings, especially at more mesic microsites and sites of difficult access for livestock (i.e. steep gullies and sites protected by piles of logs). However, given the slow dispersal of *N. pumilio* seed from unburned forest edges or scarce survivors of the fire, succession from shrubland back to forest is a slow process requiring at least several to many decades (Veblen et al. 1996). Thus, there is a lengthy window during which the more flammable shrublands could burn again, killing the juveniles of the obligate seeder *N. pumilio* but favouring continued dominance of the resprouting shrub species.

The current study is the first attempt in northwestern Patagonia to evaluate community-level fuel properties and microclimate conditions at a stand scale as potential explanations for the observed increased propensity of tall shrublands to burn in comparison with less flammable *N. pumilio* forests. However, future research is required to test the generalities of our findings across a larger range of site conditions and vegetation attributes. For instance, research conducted to the north of our study area has shown that *N. pumilio* forests on north-facing slopes are more likely to burn than stands on more mesic aspects (Mermoz et al. 2005), and slope aspect probably also affects the success of post-fire regeneration of *N. pumilio* which is highly sensitive to drought (Tercero-Bucardo et al. 2007). Further research is needed to determine the effects of both coarse-scale and fine-scale topographic variation on fuel structures, as well as post-fire tree regeneration. Additionally, detailed studies evaluating moisture content of dead and live fine fuel in the different vegetation types are necessary. Although microclimate is key in determining fuel moisture (Uhl & Kaufmann 1990), fuel moisture content in different species and in contrasting conditions (e.g. dead vs. alive) may respond differently to microclimate. Our study documents stand-level fuel, vegetation structure and microclimate conditions that provide mechanistic explanations for the higher levels of fire activity in shrublands in comparison to tall *N. pumilio* forests in northwestern Patagonia. Our quantification of fuel and vegetation structure and microclimates supports a longstanding hypothesis that shrublands are more flammable than adjacent *N. pumilio* forests due to differences in vegetation structure that facilitate spreading of crown fires in the shrublands (Veblen & Lorenz 1988; Veblen et al. 2011). The juxtaposition of fire-resistant forests with more

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flammable non-forest assemblages is often explained in terms of alternative stable state theory, where state shifts are triggered by severe fire (Petraitis & Latham 1999; Knox & Clarke 2012). Maintenance of the shrubland alternative stable state in Patagonia is facilitated by the enhancement of fire potential through the changes in fuel structures and microclimates identified in the current study. These positive feedbacks resulting from the initial severe burning of *N. pumilio* forests increase the probability of subsequent fire and reduce the probability of shifting back to the forest state. Once shifted into a self-reinforcing landscape condition, positive fire feedbacks may trap this landscape into a long-lasting new configuration.

Simulation modelling has shown that the susceptibility of landscapes shifting into fire-mediated alternative states is highly sensitive to changes in stand-level flammability with time since last fire (Kitzberger et al. 2012; Perry et al. 2012). A common assumption is that with increasing time since last fire fuel accumulation and increasing presence of dead fuels will result in a gradual increase in flammability (e.g. as in some conifer forests in North America; Johnson & Van Wagner 1985). This assumption, however, is not consistent with observed changes in flammability with time since last fire in many ecosystems worldwide (Beckage et al. 2009; Odion et al. 2010; Lindenmayer et al. 2011). In ecosystems where fire-resistant forests are replaced by fire-prone non-forest assemblages after initial burning, flammability may increase up to a certain age and then decline, resulting in a hump-shaped age–flammability relationship (Perry et al. 2012). Our results add to the body of knowledge that challenges the generalization that all plant communities increase their flammability and/or fire risk with time since fire. Simulation studies suggest that systems in which flammability at first rises and then declines with post-fire stand age are vulnerable to dramatic and rapid shifts to alternative stable states (Kitzberger et al. 2012; Perry et al. 2012). The findings of our study support such scenario simulations by quantifying the fuel and microclimatic conditions responsible for initially increasing and then declining flammability with time since fire in *N. pumilio* ecosystems. Our empirical results identify both the negative fire feedbacks due to vertical fuel discontinuities and moister microclimates in unburned *N. pumilio* forests, as well as the positive feedbacks due to continuity and abundance of fine fuels and enhanced rates of fuel drying in the alternative stable state of shrublands.

Recent and projected future trends towards a warmer climate are increasing the potential for wildfire activity in Patagonia (Holz & Veblen 2011; Veblen et al. 2011). The results of the current research suggest that positive feedbacks from initial burning of otherwise fire-resistant *N. pumilio* forest will accelerate the rate of fire-induced transformation of forests to non-forest assemblages. Once transformed to the alternative state of shrublands, return to a forest cover is likely to be impeded both by increased probability of burning in shrublands as well as by unfavourable effects of warmer and drier conditions on tree establishment (e.g. Tercero-Bucardo et al. 2007). These feedback processes, along with inhibitory influences on tree regeneration due to livestock impacts (e.g. Raffaele et al. 2011), are likely to result in more rapid rates of conversion of *N. pumilio* forests to shrublands than could be predicted from statistical models based on past fire–climate relationships alone.

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