

Changes in vegetation structure and fuel characteristics along post-fire succession promote alternative stable states and positive fire–vegetation feedbacks

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Funding information

CONICET, Grant/Award Number: PIP
11220110100058; Rufford Small Grant
Foundation

Co-ordinating Editor: Beverly Collins

Abstract

Aims: Structural and compositional changes along post-fire succession modify plant community proneness to burn (flammability). The dominant regeneration strategies and life forms, and their interactions along post-fire succession, modulate these changes by affecting density, amount and connectivity of fuels. Depending on how flammability evolves during post-fire succession it may feed back negatively, neutrally or positively into fire probability and behaviour. Negative fire–vegetation feedbacks arise when communities increase flammability as stands age, while positive feedbacks occur where early stages have higher flammability than later stages. We characterized changes in vegetation structure and fuel characteristics with time since fire in sites where either resprouters maintained dominance (shrublands), or where colonizer trees reached the sites and dominate later post-fire stages (forests).

Location: Northwestern Patagonia, Argentina.

Methods: We measured vegetation structure and characterized fine fuels with the intercept pole method in stands of different post-fire age in 18 shrublands (range 1–115 years) and 18 forests (range 7–216 years).

Results: In shrublands fuel amount quickly recovered after fire to a relatively constant value and fine fuel density remained high. Conversely, in forests, fuel amount rapidly increased during early post-fire stages (when resprouting shrubs dominate the community), peaked at c. 30–50 years (related to the co-existence of resprouters and young trees) and decreased to a relatively constant value (when tall trees dominate the community and suppress resprouters). Moreover, forest fuel density decreased with time. These changes in fuel characteristics were largely linked to changes in vegetation structure, which in turn were modulated by the dominant regeneration strategies and life forms.

Conclusions: Our results provide evidence of a positive fire–vegetation feedback for the community dominated by colonizer trees, while the community dominated by resprouter shrubs showed a neutral feedback. Given the co-existence of flammable shrublands bordering fire-sensitive forests and their low tree regeneration rates, we argue that forest communities are especially sensitive to changes in fire frequency and severity driven by global change. Anthropogenic or climate-driven changes in ignitions are threatening these landscapes, which may undergo potentially rapid transformations, as seen in other temperate ecosystems.

KEYWORDS

fine fuels, flammability, *Nothofagus*, post-fire colonizer, post-fire resprouter, pyrophobic forests, pyrophytic shrublands, time since fire

1 | INTRODUCTION

As a site develops after a fire event, changes in community structure, composition and abiotic factors affect the amount and condition of fuels, and thus its flammability or ability to burn (White & Zipperer, 2010). Depending on how flammability evolves along post-fire succession, a variety of fire–vegetation feedbacks can be produced. The nature of these feedbacks has important consequences for landscape dynamics, such as self-organization, maintenance of alternative stable states, fire regime shifts and vulnerability to changes in ignitions and climate (Kitzberger, Aráoz, Gowda, Mermoz, & Morales, 2012).

Negative fire–vegetation feedbacks occur in communities where flammability gradually increases with time since fire. Classic examples are SW North American pine-dominated communities, where flammability steadily increases with stand age due to increasing fuel loads, tree densification and vertical connectivity via “fuel ladders” (see Covington & Moore, 1994). During normal climatic conditions (when fuels control fire behaviour), these communities generate relatively resilient shifting steady-state mosaics, where young stands protect old stands from burning (Bormann & Likens, 1979; Heinselman, 1973; Johnson & Van Wagner, 1985). Conversely, positive fire–vegetation feedbacks occur in communities where flammability increases rapidly after fire and then decreases as the stand ages. Classic examples are wet sclerophyllous forests of SE Australia. There, young post-fire communities are co-dominated by shade-intolerant *Eucalyptus* and shade-tolerant rain forest species with abundant fine fuels. As these communities mature, the rain forest species gradually gain dominance and produce moister understories with coarser fuels, decreasing flammability (Jackson, 1968). Older stands may also become less flammable in communities where longer-lived trees overtop and shade the understory species, making fuels horizontally sparser and disconnected from the canopy (Gosper, Prober, & Yates, 2013; Gosper, Yates, Prober, & Wiehl, 2014; Odion, Moritz, & DellaSala, 2010; Paritsis, Veblen, & Holz, 2015). In these communities, the relationships between vegetation and fire can produce pyrophytic (fire-promoting) and pyrophobic (fire-avoiding) alternative stable states that co-exist in the landscape (Kitzberger et al., 2012; Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011; Pausas, 2015). With high fire frequency or high fire severity, these communities may remain in a flammable state, unable to mature into a less flammable community (Kitzberger et al., 2012). Despite the important consequences of fire–vegetation feedbacks on landscape resilience, flammability trajectories of communities have been commonly inferred from remote sensing (Bowman, Williamson, Prior, & Murphy, 2016; Odion et al., 2010; Taylor, McCarthy, & Lindenmayer, 2014), simulation models (Kitzberger et al., 2012; Perry & Enright, 2002; Perry, Wilshurst, McGlone, McWethy, & Whitlock, 2012) or

observations of the effects of fire on different developmental stages (Blackhall et al., 2017; Paritsis et al., 2015; Pausas, Alessio, Moreira, & Corcobado, 2012; Tepley, Veblen, Perry, Stewart, & Naficy, 2016). Field-based assessments of how flammability changes with time are rather scarce in the literature (i.e. Baeza, Santana, Pausas, & Vallejo, 2011; Gosper et al., 2013, 2014; Haslem et al., 2011; Schimmel & Granström, 1997).

Flammability can be estimated at different levels – plant parts, whole plants and communities – and is defined by four components: ignitability, sustainability, consumability and combustibility (Anderson, 1970; White & Zipperer, 2010). At the community level, flammability depends not only on the plant species present but also on their spatial arrangement and the environmental conditions (White & Zipperer, 2010). At this broader scale, components of flammability can be estimated from litter depth, relative humidity, temperature and live fuel moisture content (ignitability), bulk density, vertical and horizontal continuity of fuels (sustainability), amount of live and dead fine fuels (i.e. leaves and twigs <6-mm diameter; consumability), and fire intensity and flame height (combustibility; Behm, Duryea, Long, & Zipperer, 2004; White & Zipperer, 2010; Blackhall et al., 2017). Changes in these variables with time since fire may be modulated by the interplay between different regeneration strategies (resprouting, seeding and colonizing; Pausas & Keeley, 2014), life forms (tall trees, shrubs, herbs) and their interactions (competition or facilitation) along successional stages. Dominant regeneration strategies determine not only the vegetation's ability to recolonize or persist but also the time necessary to accumulate sufficient fuel to sustain a new fire. Resprouters or seeders (e.g. serotinous species) usually dominate the early post-fire community, quickly contributing to biomass and fuel build-up (Pausas & Keeley, 2014). Conversely, colonizers (non-resprouting species with no post-fire persistent seed bank, nor fire-induced germination) may need more time to disperse from unburned patches, establish and interact with pre-established seeding or resprouting vegetation (if present) (Bowman et al., 2016; Pausas & Keeley, 2014). Therefore, assessing how plants with different regeneration strategies and life forms interact and dominate different successional stages becomes crucial to understand changes in flammability with time.

In NW Patagonia, resprouter shrubs and colonizer trees constitute the main regeneration strategies and life forms. Shrubs and other resprouters such as bamboos (*Chusquea culeou*) create dense shrublands with an open upper canopy beneath which temperatures are high and relative humidity is low (Blackhall et al., 2017; Paritsis et al., 2015; Raffaele, Veblen, Blackhall, & Tercero-Bucardo, 2011). Colonizer trees form closed canopy forests with shady, mesic understories dominated by resprouting shrubs and bamboos of similar composition (but less vigour and dominance) as shrublands. Previous



studies on this system have found that fire spreads more readily (Morales, Mermoz, Gowda, & Kitzberger, 2015) and wildfires are more extensive in shrublands than in forests under the same conditions of rainfall and topography (Mermoz, Kitzberger, & Veblen, 2005), and that shrublands present more fine fuels and more flammable plant traits (Blackhall et al., 2017; Paritsis, Holz, Veblen, & Kitzberger, 2013; Paritsis et al., 2015). The aim of this study is to characterize changes in vegetation structure and fuel characteristics with time since fire in a community dominated by resprouting shrubs and one dominated by colonizer trees. We expect that patterns of vegetation structure and fuel accumulation along the time since fire gradient will show that communities dominated by resprouter shrubs increase in flammability with post-fire age and that communities dominated by colonizer trees will show an initial increase followed by a decrease in flammability with long time since fire.

2 | METHODS

2.1 | Study sites

The study sites are located between latitudes 39° and 43°S (Table S1, Figure S1 in Appendix S1), where vegetation varies along a steep precipitation gradient (W to E approx. 3,000–400 mm/year), and less markedly along a temperature gradient associated with elevation and aspect. At mid-altitudes (≈800–1,100 m a.s.l.) forests are dominated by the evergreen colonizer tree *Nothofagus dombeyi* (Veblen, Kitzberger, Raffaele, & Lorenz, 2003). This tree has thin bark, does not have a persistent seed bank and cannot resprout after a fire event. Rather, its' post-fire regeneration depends on neighbouring patches providing seeds (Donoso, 2006). Although there are no estimates of dispersal kernels for this species, post-fire recruitment is normally limited to the first 60 m from the fire boundaries. This tree creates closed-canopied forests with dark mesic understoreys composed of resprouting shade-tolerant shrubs and the bamboo *Chusquea culeou*. At relatively drier sites there are shrublands of the deciduous *Nothofagus antarctica* that exists as a multi-stemmed shrub and sometimes a small tree (Veblen et al., 2003). This species creates dense shrublands together with other heliophilous less dominant resprouting shrubs and the bamboo *C. culeou*. We chose *N. antarctica* shrublands as an example of a resprouting community (hereafter "shrubland") and *N. dombeyi* forests as an example of a colonizer community (hereafter "forest").

In order to test whether vegetation structure and fine fuel characteristics change differently with time since fire in shrubland compared to forest, we chose 18 post-fire shrublands (between 1 and 115 years since fire) and 18 post-fire forests (between 7 and 216 years since fire) (Table S1 in Appendix S1). We obtained the time since fire of every site from a mapped fire history developed by the National Park Administration based on Landsat images, aerial photography and tree ring-based fire history databases (Kitzberger, 1994; Mermoz et al., 2005). When selecting sites, we looked for the absence of signals of firewood collection (i.e. tree stumps), non-existent or low livestock impact (browsing signals) and the absence

of recurrent low intensity fires (fire scars) in order to minimize potential impacts of past human activities. Although northern Patagonia is subject to extensive livestock raising, we chose sites where cattle were unlikely to be present, either because they are within the most protected areas of the National Parks or because topographical conditions prevent cattle from reaching the sites (i.e. steep slopes, rivers or lakes).

2.2 | Vegetation structure and fine fuel measurements

During the summers of 2015 and 2016 we measured vegetation structure, and characterized fine fuels. In every post-fire stand we established two 60-m parallel transects at least 20 m apart from each other. In each transect, we located a sampling station every 2 m (31 per transect and 62 per stand). At every sampling station we measured maximum vegetation height in shrublands, and in forests the maximum understorey height (maximum height reached by non-*N. dombeyi* plants) and *N. dombeyi* canopy base height using a laser distance measurer. Moreover, in forests every three sampling stations (11 per transect) we chose the nearest tree and measured its crown diameter. With a 25-mm diameter and 4-m height pole, divided into 16, 25-cm intervals, we recorded intercepts between the pole and vegetation (twigs and leaves), only within the "fine fuel" category (<6-mm diameter) as rated by the National Fire Danger Rating System (NFDRS 2006). For every vegetation intercept we recorded the species and if it was dead or alive. In addition, we measured litter depth. With these data we calculated variables related to vegetation structure with the aim of describing their changes along succession and variables related to community flammability in order to test our predictions on how flammability changes with time since fire.

2.2.1 | Variables related to vegetation structure

(1) Maximum resprouting vegetation height (*MRVH* in m): maximum height reached by the vegetation in shrublands and by the understorey in forests at every sampling station. (2) *Distance between strata* (m): measured as the difference between the maximum height reached by the understorey species and the canopy base height in the forest. This variable has negative values when shrubs (understorey) are taller than the canopy base height. (3) *Crown diameter* (m): measured as the maximum distance along the longest axis from edge to edge through the crown centre in the forest dominant trees.

2.2.2 | Variables related to flammability

We considered ignitability, consumability and sustainability proxies (see Behm et al., 2004; Blackhall et al., 2017; White & Zipperer, 2010). Ignitability proxies (how easily a fuel ignites) have been associated with litter depth and fuel moisture content:

1. *Litter depth* (*Litter* cm) measured as the depth of dry leaves and twigs on the ground.
2. *Community-weighted fuel moisture*

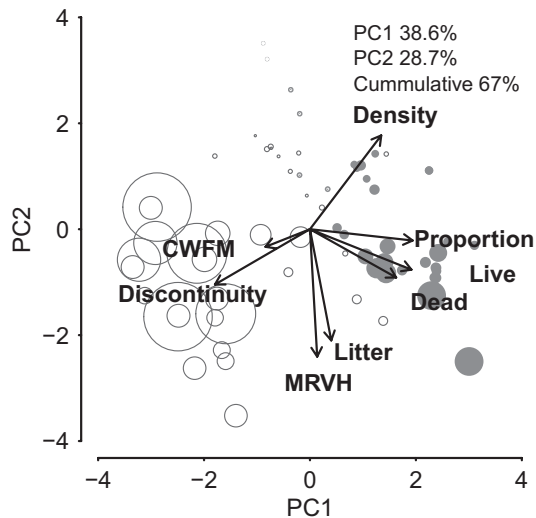


FIGURE 1 Forest and shrublands differ in their association with vegetation structure (MRVH) and fine fuel variables (proportion, density, discontinuity, dead, live, litter, CWFM) and are inversely correlated with time since fire. MRVH (m): maximum height reached by the vegetation in shrublands and by the understory in forests. Discontinuity (m): maximum distance between two consecutive vegetation intercepts. Proportion: fine fuel proportion. Dead: dead fine fuel proportion. Live: live fine fuel proportion. Density: the number of intervals with at least one intercept over the amount of intervals that constitutes vegetation maximum height. Litter (cm): depth of dry leaves and twigs on the ground. CWFM: live fuel moisture content of the dominant species. Shrubland transects ($n = 36$) ● and forest transects ($n = 36$) ○, circle size represents different time since fire. Relative loadings of the variables on the first (arrow direction; PC1) and second PC (arrow length; PC2)

content (CWFM) estimated from live leaf moisture content at the end of the dry season (H) of the most frequent species in shrublands and forest (Blackhall et al., 2017; Kitzberger unpubl data) along with their relative abundance (RA) at every transect ($CWFM = \sum_s H_s * RA_s$ where s is the species). This variable does not account for micro-environmental conditions that desiccate fuels in different communities, but rather indicates the expected live fuel moisture of the community given the intrinsic moisture contents and relative abundances of the species at each community.

Consumability proxies (consider how much of a fuel would burn):

Fine fuel proportion (Proportion) measured as the number of intervals with at least one intercept divided by the total number of intervals (16). This was calculated for all the intercepts together and separately for dead (*dead*) and live (*live*) intercepts. For forest sites, we also calculated the fine fuel proportion of resprouters and colonizer species separately.

Sustainability proxies (consider the ability of a fuel to continue burning):

1. *Fuel vertical discontinuity (Discontinuity m)* is the maximum distance between two consecutive vegetation intercepts at every sampling station. (2) *Fine fuel density (Density)* was measured as the number of intervals with at least one intercept over the number of intervals that constitute (or represent) vegetation maximum height. In contrast to fine fuel proportion, this variable considers the maximum height of vegetation, which determines how compact (or dense) is the vertical arrangement of fuels. For example, if vegetation maximum height is 2 m, the number of intervals that represent vegetation maximum height will be $2.0 \text{ m} / 0.25 \text{ m}$, which equals eight intervals. Thus, two points may have the same fine fuel proportion, say $2/16$, but different fine fuel density, e.g. $2/8$ (vegetation maximum height 2 m) and $2/10$ (vegetation maximum height 2.5 m).

2.3 | Data analysis

We performed a PCA to explore how vegetation structure (MRVH) and flammability variables (proportion, density, discontinuity, dead, live, litter and CWFM) varied between vegetation types and time since fire. To assess main sources of variation in structure and flammability, we analysed the association between the first two components of the PCA (PC1 and PC2) with time since fire (tsf) using Pearson's product moment correlation coefficient in R (R Foundation for Statistical Computing, Vienna, Austria).

We fitted hierarchical models in order to evaluate the relations between vegetation structure (MRVH, Distance between strata and Crown diameter) and tsf with the aim of describing their changes along succession. We also analysed fuel variables (Fine fuel proportion and Fine fuel density) and tsf in order to test our predictions about changes in flammability with time since fire. Hierarchical models allowed us to take into account the lack of independence among sampling stations at each site (Gelman & Hill, 2007).

Details on models' structures, hierarchies and prior distributions for all model parameters can be found in Appendix S2. For all model parameters we calculated the mean of posterior distributions as point estimates and the 95% Highest Posterior Density intervals (HPD) as measures of uncertainty around these estimates (Gelman & Hill, 2007). The effective sample size from each Monte Carlo Markov Chain (MCMC) can be found in Appendix S1. In order to select among alternative models we used DIC (Deviance information criterion) and performed posterior predictive checks (Appendix S3).

2.3.1 | Models for variables related to vegetation structure

To describe how MRVH in resprouting shrublands and tree crown diameter in forest changed with tsf we fitted a saturating exponential growth function (monomolecular), and for forests distance between strata we fitted a sigmoid function (Bolker, 2011; Appendix S2).

2.3.2 | Models for variables related to flammability

Following our predictions on how flammability may change with tsf, we expected that fine fuel proportion (total, dead and live) could either increase with time since fire or increase and then decrease. Thus, we fitted two alternative functions: a sigmoid function where we predict that fine fuel proportion would increase with tsf until reaching an asymptote, and alternatively, a hump-shaped function that is a subtraction of two sigmoids. Finally, for fine fuel density we fitted an exponential function assuming that it could remain constant or decrease exponentially due to the spatial arrangement of the vegetation (Appendix S2).

3 | RESULTS

3.1 | Principal components analysis

The first two principal components of the PCA explained 38.6% and 28.7% of the total variation in vegetation structure and fuel

variables, respectively. PC1 was positively associated with fine fuels (dead, live and total) and negatively correlated to fine fuel discontinuity (Figure 1). When communities were considered separately, PC1 showed a positive correlation with tsf in shrublands ($0.52, t = 3.57, p < .05$) and a negative correlation in forests ($-0.59, t = -4.24, p < .05$). Thus, PC1 separated shrublands from forests but only at longer tsf as young forest and shrublands tended to be more alike (centred around zero scores). Mature (but also in many cases young) resprouting shrublands were largely associated with high proportions of fine fuels (both dead and live) whereas mature forests were largely associated with highly discontinuous fuels. PC2 was positively correlated with fine fuel density and negatively correlated with litter depth, MRVH and CWFM (Figure 1). PC2 showed a negative correlation with tsf both for shrublands ($-0.71, t = -5.89, p < .05$) and forests ($-0.37, t = -2.39, p < .05$). Thus, PC2 separated early post-fire stages of both shrublands and forests from young intermediate and old-growth stages. Early stages were associated with high fine fuel density as opposed to later phases of both forests and shrublands with higher-statured vegetation and deeper litter layers.

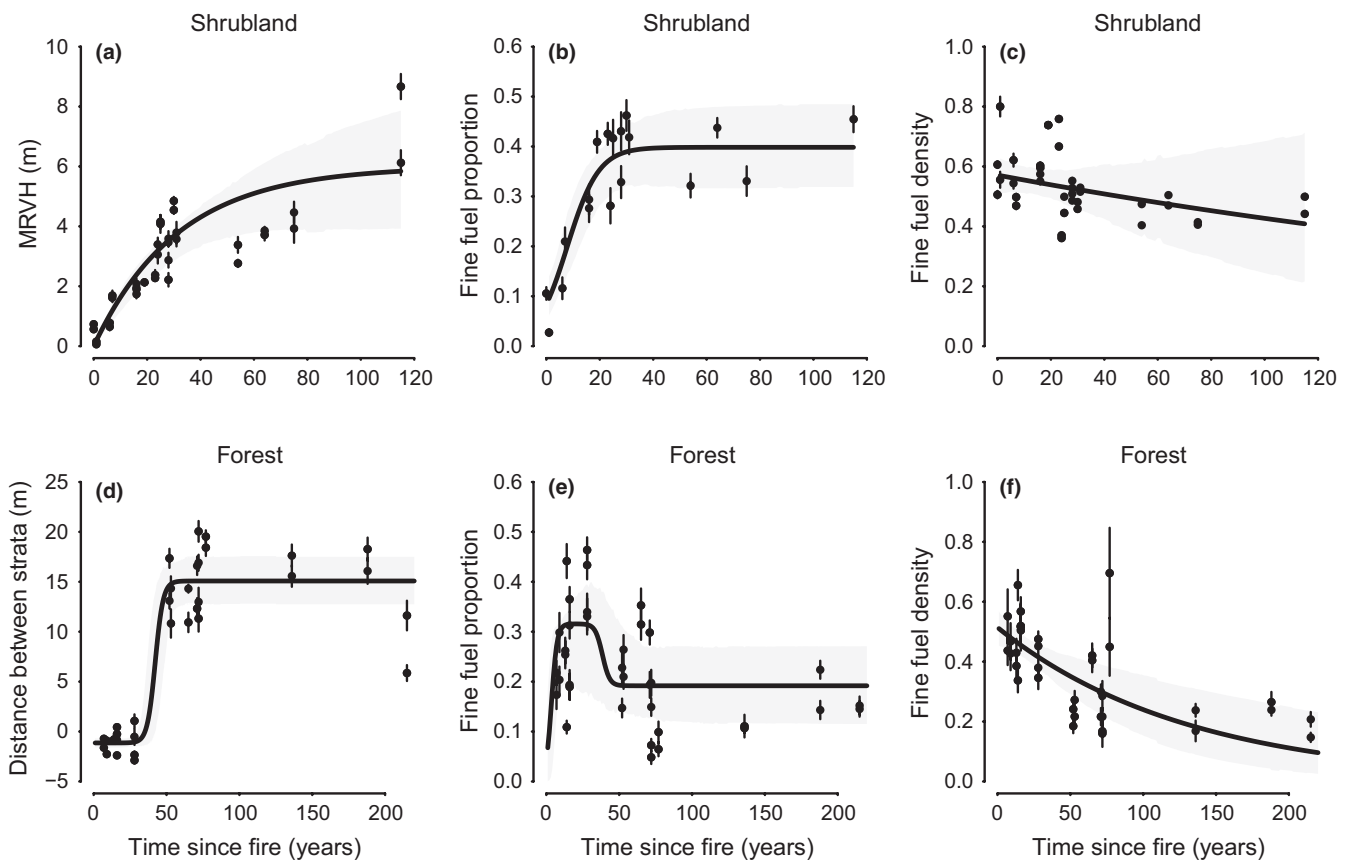


FIGURE 2 Vegetation structure variables along post-fire succession: (a) Increasing maximum resprouters vegetation height (MRVH) in shrublands, (d) Increasing vertical discontinuity between the understorey and the lower part of the canopy in forests (negative values correspond to shrubs overtopping trees). Fuel patterns along the post-fire succession: (b) Shrublands increase in total fine fuel amount, (c) and have constant fuel density, (e) while in forest total fine fuel amount follows a hump-shaped pattern (f) and fuel density decreases. ● correspond to mean values and | to standard deviation. – show the global tendency from a hierarchical regression and grey shades represent the high posterior density interval

3.2 | Regression models

3.2.1 | Variables related to vegetation structure

Resprouting shrubland maximum height increased asymptotically with tsf up to 90 years post-fire when it stabilized at about 6 m (Figure 2a). Forest presented a single stratum during the first 35 years after fire. Subsequently, forest started to show two strata separated by a gap of around 16 m by 60 years after fire (Figure 2d). Tree crown diameter increased asymptotically with tsf, reaching 8.5 m 150 years post-fire (Figure S2 in Appendix S1). Variance increased with tsf for all tree variables. See Appendix S1 for parameter posterior means and HPD intervals.

3.2.2 | Variables related to flammability

There was no difference in DIC and posterior predictive check between the two models proposed for shrublands fine fuel proportion (total, dead and live). According to the sigmoid function, fine fuel proportion increased almost immediately after fire ($a_1 = 1.325$ years) at a constant rate during the first 35 years post-fire ($b_1 = 0.170$, HPD: 0.079; 0.268) and stabilizing at 0.4 (Figure 2b; asymptote: 0.398; HPD: 0.318, 0.487). In forests, the hump-shaped

function had the lowest DIC for fine fuel proportion (total, dead and live), and the posterior predictive check revealed a better fit for this model (see Appendix S3 for model selection details). Fine fuel proportion increased faster in forests than in shrublands during the first 20 years ($b_1 = 0.374$, HPD: 0.129; 0.816) when it stabilized at 0.33 for about another 20 years. After this, it started to decrease stabilizing at a proportion of 0.2 at about 50 years post-fire (Figure 2e). Dead and live fuels followed similar patterns to that of total fine fuel in both vegetation types, but live fuels were always more abundant than dead fuels (Figure S3 in Appendix S3; see Appendix S3 for model selection details). We did not detect changes in fine fuel density with time in resprouting shrublands, as the rate of decrease was not different from zero (Figure 2c: -0.003 HPD: -0.009 , 0.003). In contrast, fine fuel density in colonizer forests decreased exponentially with time (Figure 2f, -0.008 HPD: -0.012 , -0.003). Finally, the contribution of the colonizer species *N. dombeyi* to the proportion of fine fuels in forests decreased exponentially with time (Figure S4 in Appendix S3, -0.029 HPD: -0.049 , -0.010), while the contribution of resprouter understorey species followed a hump-shaped curve (Figure S4 in Appendix S1). See Appendix S1 for parameter posterior distributions mean values and HPD intervals. Regarding changes in community-weighted fuel moisture content (CWFm), it remained constant in shrublands of

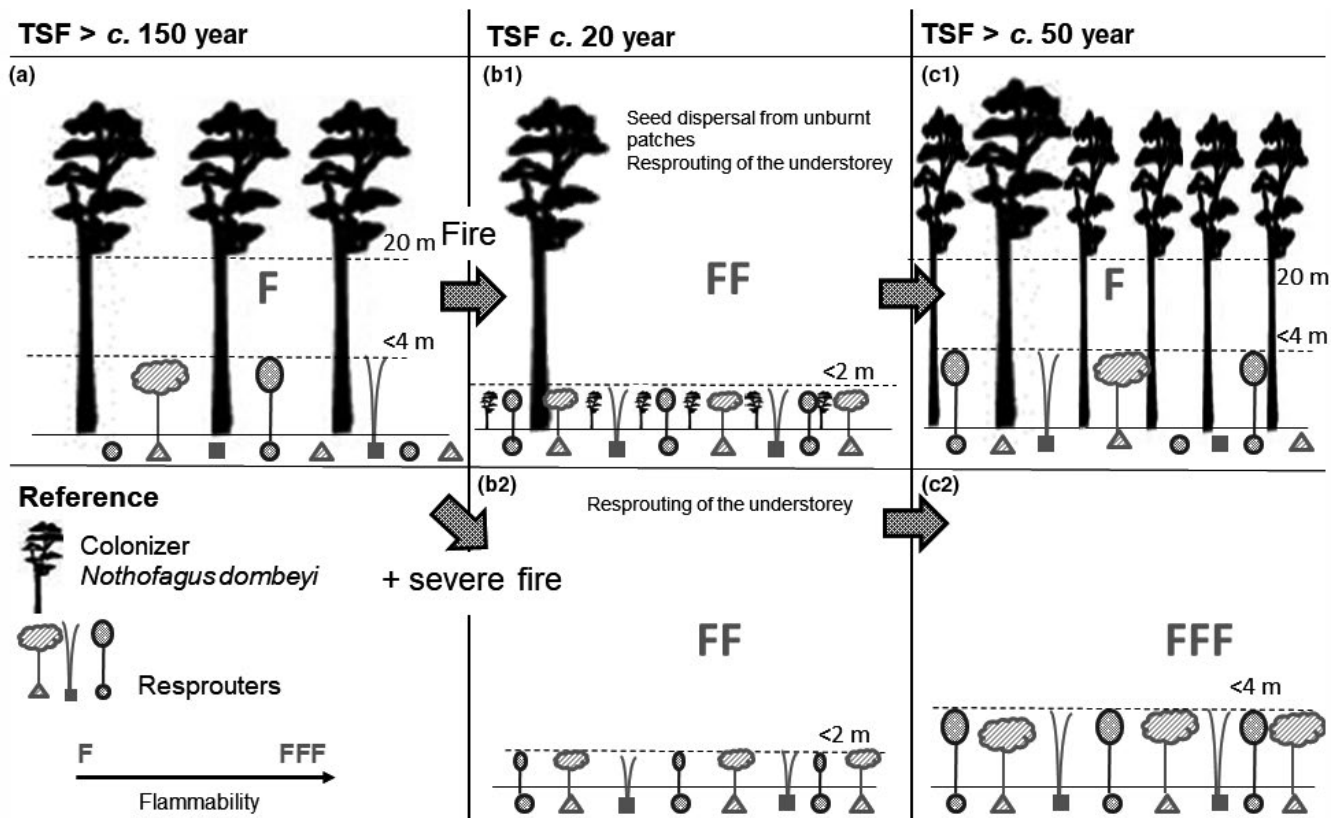


FIGURE 3 Post-fire vegetation dynamics model for a colonizer forest. (a) Pre-fire closed-canopy forest. Upper row (b1 and c1) represents a stand developing after a fire in normal fire weather and frequency conditions. Tall colonizer trees regeneration depends on seeds dispersing from unburnt patches and establishing in the matrix of resprouters. Lower row (b2 and c2) represents a stand developing after severe recurrent fires. Tall colonizer trees regeneration is difficult given the absence of near unburnt patches and the community is now dominated by resprouter species previously present in the understorey.



different post-fire ages. In forests CWF was higher than in shrublands during the first 75 years post-fire and decreased in open old-growth forests (Figure S5 in Appendix S1).

4 | DISCUSSION

During the course of succession, the interactions among species with different regeneration strategies and life forms, together with stochastic events of dispersal and recruitment, modulate changes in vegetation structure and composition, which in turn shape fire-vegetation feedbacks. Here we show that in communities dominated by resprouting multi-stemmed shrubs, post-fire flammability increased very rapidly to a relatively constant value, suggesting a rather neutral fire-vegetation feedback. In contrast, in sites where trees were able to colonize early after fire, flammability first increased to a maximum and then decreased to an intermediate level, suggesting the existence of a positive fire-vegetation feedback. In this fashion, early forest stages and shrublands fit into a pyrophytic type community with rapid fuel accumulation, and intermediate and mature forests fit into a pyrophobic community with trees that grow tall enough to cast sufficient shade to produce, under normal fire weather conditions, fire-resistant closed communities (Bond & Midgley, 2012).

During the early stages of post-fire succession, both community types (shrublands and forests) showed a rapid increase in fine fuels, high fine fuel density and no strata differentiation (higher consumability and sustainability). Thus, young forests (<30 years) bore a considerable resemblance to young resprouting shrublands, as they both presented a single rapidly developing vegetation layer. At these early successional stages the post-fire forest community was dominated by multi-stemmed resprouting shrubs that persisted from the pre-fire understorey, with *N. dombeyi* saplings embedded within the dense shrub-dominated matrix (Figure 3b1). This suggests that irrespective of whether the community will eventually become a forest or a shrubland, consumability increases during the first 10–20 years after fire, mainly driven by the presence of multi-stemmed resprouting shrubs.

At about 30 years after fire, structural and compositional changes caused flammability trajectories to diverge. In shrublands, the amount and density of fine fuels remained high, and the dominant species had low fuel moisture content even at older stages, suggesting the persistence of a pyrophytic state. In contrast, where *N. dombeyi* trees had established within the matrix of resprouters, by 30–50 years after fire, trees were tall enough to create two distinct canopy layers and overtop and overshadow the resprouting shrubs, reducing the amount and density of fine fuels, implying lower consumability and sustainability (e.g. Haslem et al., 2011; Gosper et al., 2013, 2014; Paritsis et al., 2015; Tepley et al., 2016; Figure 3c1). Moreover, the separation of understorey fuels and canopy fuels prevents the propagation of fire into the canopy, and canopy closure changes light conditions, reducing the thermal amplitude and increasing the relative humidity of the understorey, thus enhancing the difference in flammability among young and old stands (e.g. Blackhall et al., 2017; Paritsis et al., 2015; Tepley et al., 2016). Such alternative stable state dynamics are expected in systems where

species that will potentially confer characteristics of a pyrophytic state (high intrinsic flammability) persist in the pyrophobic state (Figure 3a), and species that will confer pyrophobic characteristics (tall canopy trees, moister fuels) are able to colonize and dominate the pyrophytic state (Figure 3).

Given these changes in flammability with time since fire, the timing of new fire events could severely affect the community trajectory of the study sites. Shrublands, despite being more flammable, seem to be more resilient than forests due to the resprouting capacity of their dominant species. No matter when the fire occurs they could regenerate into a similar community, provided fire intervals are not too short (i.e. Enright, Fontaine, Westcott, Lade, & Miller, 2011; Paula & Ojeda, 2006) and in the absence of other disturbances such as browsing (Blackhall et al., 2017; Raffaele et al., 2011). Thus, these resprouting shrublands do not seem to have a negative or positive feedback with fire, but a neutral one.

Conversely, in forests where dominant trees are colonizers, if fire occurs before strata differentiation, or before trees are able to produce seeds for recolonization (Figure 3b1), it would be difficult to return to a forest state and the system will likely shift to a shrubland (i.e. hysteresis; Scheffer, Carpenter, Foley, Folke, & Walker, 2001). At early successional stages, trees' crowns contribute to the amount of fuel in the understorey and have thinner trunks, making them more vulnerable to burning along with the resprouting shrubs of the understorey and thus die. At this point, the chance of shifting to a shrubland after a fire event is high. If fire intervals are sufficiently short, these forests will be unable to temporally escape fire, and large portions of the landscape will remain as shrublands (Figure 3b2, c2). For example, forests turned into extensive mid-slope bamboo-dominated shrublands in northern Patagonia during the high ignition Euro-Argentinean settlement period, when settlers set multiple fires to create pastures for cattle (1890–1920; Veblen & Lorenz, 1988). Alternatively, when fire intervals are longer (>150 years intervals), the overall local environmental conditions of the understorey are likely to facilitate the occurrence of less extensive and severe fires, with shorter distances to forest fragments allowing rapid recolonization (i.e. Mermoz et al., 2005). Moreover, when fires are of low intensity and severity, large mature *N. dombeyi* trees commonly survive (Kitzberger et al., 2016), so that colonization and later successional replacement of the resprouting shrubland community into more pyrophobic forest is possible (Figure 3b1). However, forest recovery may be delayed or limited if shrub canopy closure is fast because *N. dombeyi* trees are shade-intolerant, their seed production is limited to masting years and seed viability is low (Burschel, Gallegos, Martínez, & Moll, 1976; Veblen, Donoso, Schlegel, & Escobar, 1981). In summary, these broad-leaved forests may show positive fire feedbacks due to intrinsic factors that change community structure and environmental conditions after a fire and make them more vulnerable to re-burning (i.e. landscape trap; Lindenmayer et al., 2011).

These positive feedbacks can be exacerbated under current global change scenarios (Bowman et al., 2016; Enright, Fontaine, Bowman, Bradstock, & Williams, 2015). Warmer and drier predicted climate conditions for northern Patagonia Andean forests (CONAMA

2006) are conducive to larger and more severe *Nothofagus* forest fires (Veblen et al., 2008), increased lightning ignitions due to more frequent incursion of northeasterly subtropical air masses (Villalba, Masiokas, Kitzberger, & Boninsegna, 2005), increased *Nothofagus* tree mortality and dieback (Suárez, Ghermandi, & Kitzberger, 2004), and reduction in seed establishment and seedling growth rates (Tercero-Bucardo, Kitzberger, Veblen, & Raffaele, 2007). In northern Patagonia during extreme drought years, fire size tends to be larger than in normal years as biotic (i.e. old forest stands that act as firebreaks) and abiotic controls of fire attenuate during extreme fire weather (see Mermoz et al., 2005; Veblen & Lorenz, 1988). If fire extents are larger than the dispersal distances of colonizer species, recolonization will be unlikely at the centre of the fire. Growth rates of *Nothofagus* are lower during dry years, which could stall strata differentiation and thus delay the onset of the pyrophobic state (Suárez & Kitzberger, 2008; Suárez et al., 2004). This resembles the fire weather hypothesis (Enright et al., 2015), whereby fire-vegetation feedbacks can be severely enhanced by climate affecting fire severity, frequency and plant demographic rates.

Our study together with others show the prevalence of positive fire-vegetation feedbacks in communities dominated by taxa that did not evolve with a high fire frequency (McWethy et al., 2010; Perry et al., 2012). These systems are, in the context of climatic changes and anthropogenic increases in ignition, prone to suffer rapid landscape transformations (Bowman et al., 2011; Kitzberger et al., 2016; Marlon et al., 2009; McWethy et al., 2013; Miller et al., 2005; Veblen & Lorenz, 1988). Neglecting the effect of humans in enhancing fire-vegetation feedbacks can have catastrophic effects on fire regimes and cause irreversible changes in landscapes. Better understanding of community dynamics is needed to infer feedback mechanisms, identify system thresholds and determine biotic and abiotic factors that affect the resilience of ecosystems. Hence, more empirical work is needed to describe changes in flammability with time and the possible mechanisms governing positive feedbacks in order to predict future landscape transformations.

ACKNOWLEDGEMENTS

We thank Mónica Mermoz for assistance during fire history collection; Jennifer Landesmann and Ignacio Serra Olabuenaga for useful comments on the manuscript; Aime Iglesias, Patricia Veron, Nicolás Sanchez and the National Parks Lanin, Puelo, Nahuel Huapi and Alerces for assistance during fieldwork. Funding was provided by CONICET [PIP 11220110100058] to JMM and by the Rufford Small Grant Foundation to FT.

AUTHOR CONTRIBUTION

F.T., T.K. and J.M.M. conceived the ideas and designed the methodology; F.T. collected the data; F.T., T.K. and J.M.M. analysed the data and interpreted results; F.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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REFERENCES

- Anderson, H. E. (1970). Forest fuel ignitibility. *Fire Technology*, 6, 312–319. <https://doi.org/10.1007/BF02588932>
- Baeza, M. J., Santana, V. M., Pausas, J. G., & Vallejo, V. R. (2011). Successional trends in standing dead biomass in Mediterranean basin species. *Journal of Vegetation Science*, 22, 467–474. <https://doi.org/10.1111/j.1654-1103.2011.01262.x>
- Behm, A. L., Duryea, M. L., Long, A. J., & Zipperer, W. C. (2004). Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland-urban interface. *International Journal of Wildland Fire*, 13, 355. <https://doi.org/10.1071/WF03075>
- Blackhall, M., Raffaele, E., Paritsis, J., Tiribelli, F., Morales, J. M., Kitzberger, T., ... Veblen, T. T. (2017). Effects of biological legacies and herbivory on fuels and flammability traits: A long-term experimental study of alternative stable states. *Journal of Ecology*, 105, 1309–1322. <https://doi.org/10.1111/1365-2745.12796>
- Bolker, B. M. (2011). *Ecological models and data in R*. Princeton, NJ: Princeton University Press.
- Bond, W. J., & Midgley, J. J. (2012). Fire and the angiosperm revolutions. *International Journal of Plant Sciences*, 173, 569–583. <https://doi.org/10.1086/665819>
- Bormann, F. H., & Likens, G. E. (1979). Catastrophic disturbance and the steady state in Northern Hardwood Forests: a new look at the role of disturbance in the development of forest ecosystems suggest important implications for land-use policies. *American Scientist*, 67, 660–669.
- Bowman, D. M. J. S., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. a., D'Antonio, C. M., ... Swetnam, T. W. (2011). The human dimension of fire regimes on Earth. *Journal of Biogeography*, 38, 2223–2236. <https://doi.org/10.1111/j.1365-2699.2011.02595.x>
- Bowman, D. M. J. S., Williamson, G. J., Prior, L. D., & Murphy, B. P. (2016). The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Global Ecology and Biogeography*, 25, 1166–1172. <https://doi.org/10.1111/geb.12484>
- Burschel, P., Gallegos, C., Martínez, O., & Moll, W. (1976). Composicion y dinamica regenerativa de un bosque virgen mixto de rauli y coigüe. *Bosque*, 1, 55–74. <https://doi.org/10.4206/bosque>
- CONAMA. (2006). *Estudio de la variabilidad climática en Chile para el siglo XXI*. Departamento de Geofísica Facultad de Ciencias. Físicas y Matemáticas. Universidad de Chile (pp. 1–71).
- Covington, W., & Moore, M. (1994). Southwestern ponderosa forest structure: changes since Euro-American settlement. *Journal of Forestry*, 92, 39–47.
- Donoso, C. (Ed.) (2006). *Las especies arbóreas de los bosques templados de Chile y Argentina*. Autoecología. Santiago, CL: María Cuneo Ediciones.
- Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, 13, 265–272. <https://doi.org/10.1890/140231>
- Enright, N. J., Fontaine, J. B., Westcott, V. C., Lade, J. C., & Miller, B. P. (2011). Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecology*, 212, 2071–2083. <https://doi.org/10.1007/s11258-011-9970-7>
- Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models* (Vol. 1). New York, NY: Cambridge University Press.
- Gosper, C. R., Prober, S. M., & Yates, C. J. (2013). Multi-century changes in vegetation structure and fuel availability in fire-sensitive eucalypt woodlands. *Forest Ecology and Management*, 310, 102–109. <https://doi.org/10.1016/j.foreco.2013.08.005>



- Gosper, C. R., Yates, C. J., Prober, S. M., & Wiehl, G. (2014). Application and validation of visual fuel hazard assessments in dry Mediterranean-climate woodlands. *International Journal of Wildland Fire*, 23, 385. <https://doi.org/10.1071/WF13096>
- Haslem, A., Kelly, L. T., Nimmo, D. G., Watson, S. J., Kenny, S. A., Taylor, R. S., ... Bennett, A. F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology*, 48, 247–256. <https://doi.org/10.1111/j.1365-2664.2010.01906.x>
- Heinselman, M. L. (1973). Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research*, 3, 329–382. [https://doi.org/10.1016/0033-5894\(73\)90003-3](https://doi.org/10.1016/0033-5894(73)90003-3)
- Jackson, W. D. (1968). Fire, air, earth and water – an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia*, 3, 9–16.
- Johnson, E. A., & Van Wagner, C. (1985). The theory and use of two fire history models. *Canadian Journal of Forest Research*, 15, 214–220. <https://doi.org/10.1139/x85-039>
- Kitzberger, T. (1994). *Fire regime variation along a northern Patagonian forest-steppe ecotone: stand and landscape response*. PhD Thesis. Boulder, CO: Dept of Geography, University of Colorado.
- Kitzberger, T., Araújo, E., Gowda, J. H., Mermoz, M., & Morales, J. M. (2012). Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems*, 15, 97–112. <https://doi.org/10.1007/s10021-011-9494-y>
- Kitzberger, T., Perry, G. L. W., Paritsis, J., Gowda, J. H., Tepley, A. J., Holz, A., & Veblen, T. T. (2016). Fire-vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. *New Zealand Journal of Botany*, 54, 247–272. <https://doi.org/10.1080/0028825X.2016.1151903>
- Lindenmayer, D. B., Hobbs, R. J., Likens, G. E., Krebs, C. J., & Banks, S. C. (2011). Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 15887–15891. <https://doi.org/10.1073/pnas.1110245108>
- Marlon, J. R., Bartlein, P. J., Carcaillet, C., Gavin, D. G., Harrison, S. P., Higuera, P. E., ... Prentice, I. C. (2009). Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience*, 2, 697–702. <https://doi.org/10.1038/ngeo468>
- McWethy, D. B., Higuera, P. E., Whitlock, C., Veblen, T. T., Bowman, D. M. J. S., Cary, G. J., ... Tepley, A. J. (2013). A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography*, 22, 900–912. <https://doi.org/10.1111/geb.12038>
- McWethy, D. B., Whitlock, C., Wilmshurst, J. M., McGlone, M. S., Fromont, M., Li, X., ... Cook, E. R. (2010). Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 21343–21348. <https://doi.org/10.1073/pnas.1011801107>
- Mermoz, M., Kitzberger, T., & Veblen, T. T. (2005). Landscape influences on occurrence and spread of wildfires in patagonian forests and shrublands. *Ecology*, 86, 2705–2715. <https://doi.org/10.1890/04-1850>
- Miller, G. H., Fogel, M. L., Magee, J. W., Gagan, M. K., Clarke, S. J., & Johnson, B. J. (2005). Ecosystem collapse in pleistocene Australia and a human role in megafaunal extinction. *Science*, 309, 287–290. <https://doi.org/10.1126/science.1111288>
- Morales, J. M., Mermoz, M., Gowda, J. H., & Kitzberger, T. (2015). A stochastic fire spread model for north Patagonia based on fire occurrence maps. *Ecological Modelling*, 300, 73–80. <https://doi.org/10.1016/j.ecolmodel.2015.01.004>
- National Fire Danger Rating System (NFDRS) (2006). *Van Nostrand's scientific encyclopedia*. New York, NY: John Wiley & Sons.
- Odion, D. C., Moritz, M. A., & DellaSala, D. A. (2010). Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, 98, 96–105. <https://doi.org/10.1111/j.1365-2745.2009.01597.x>
- Paritsis, J., Holz, A., Veblen, T. T., & Kitzberger, T. (2013). Habitat distribution modeling reveals vegetation flammability and land use as drivers of wildfire in SW Patagonia. *Ecosphere*, 4(1), 20.
- Paritsis, J., Veblen, T. T., & Holz, A. (2015). Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. *Journal of Vegetation Science*, 26, 89–101. <https://doi.org/10.1111/jvs.12225>
- Paula, S., & Ojeda, F. (2006). Resistance of three co-occurring resprouter *Erica* species to highly frequent disturbance. *Plant Ecology*, 183, 329–336. <https://doi.org/10.1007/s11258-005-9043-x>
- Pausas, J. G. (2015). Alternative fire-driven vegetation states. *Journal of Vegetation Science*, 26, 4–6. <https://doi.org/10.1111/jvs.12237>
- Pausas, J. G., Alessio, G. A., Moreira, B., & Corcobado, G. (2012). Fires enhance flammability in *Ulex parviflorus*. *New Phytologist*, 193, 18–23. <https://doi.org/10.1111/j.1469-8137.2011.03945.x>
- Pausas, J. G., & Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, 204, 55–65. <https://doi.org/10.1111/nph.12921>
- Perry, G. L. W., & Enright, N. J. (2002). Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial “state-and-transition” model. *Journal of Biogeography*, 29, 1143–1158. <https://doi.org/10.1046/j.1365-2699.2002.00774.x>
- Perry, G. L. W., Wilmshurst, J. M., McGlone, M. S., McWethy, D. B., & Whitlock, C. (2012). Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. *Global Change Biology*, 18, 1609–1621. <https://doi.org/10.1111/j.1365-2486.2011.02631.x>
- Raffaele, E., Veblen, T. T., Blackhall, M., & Tercero-Bucardo, N. (2011). Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *Journal of Vegetation Science*, 22, 59–71. <https://doi.org/10.1111/j.1654-1103.2010.01233.x>
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596. <https://doi.org/10.1038/35098000>
- Schimmel, J., & Granström, A. (1997). Fuel succession and fire behavior in the Swedish boreal forest. *Canadian Journal of Forest Research*, 27, 1207–1216. <https://doi.org/10.1139/x97-072>
- Suárez, M. L., Ghermandi, L., & Kitzberger, T. (2004). Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *Journal of Ecology*, 92, 954–966. <https://doi.org/10.1111/j.1365-2745.2004.00941.x>
- Suárez, M. L., & Kitzberger, T. (2008). Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Canadian Journal of Forest Research*, 38, 3002–3010. <https://doi.org/10.1139/X08-149>
- Taylor, C., McCarthy, M. A., & Lindenmayer, D. B. (2014). Nonlinear effects of stand age on fire severity. *Conservation Letters*, 7, 355–370. <https://doi.org/10.1111/conl.12122>
- Tepley, A. J., Veblen, T. T., Perry, G. L. W., Stewart, G. H., & Naficy, C. E. (2016). Positive feedbacks to fire-driven deforestation following human colonization of the South Island of New Zealand. *Ecosystems*, 19, 1325–1344. <https://doi.org/10.1007/s10021-016-0008-9>
- Tercero-Bucardo, N., Kitzberger, T., Veblen, T. T., & Raffaele, E. (2007). A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. *Journal of Ecology*, 95, 771–779. <https://doi.org/10.1111/j.1365-2745.2007.01249.x>
- Veblen, T. T., Donoso, C., Schlegel, F. M., & Escobar, R. B. (1981). Forest Dynamics in South-Central Chile. *Journal of Biogeography*, 8, 211–247. <https://doi.org/10.2307/2844678>
- Veblen, T. T., Kitzberger, T., Raffaele, E., & Lorenz, D. C. (Eds.) (2003). Fire history and vegetation changes in northern Patagonia, Argentina. *Fire*

and *Climatic Change in the Temperate Ecosystems of the Western Americas* (pp. 265–295). New York, NY: Springer.

Veblen, T. T., Kitzberger, T., Raffaele, E., Mermoz, M., González, M. E., Sibold, J. S., & Holz, A. (2008). The historical range of variability of fires in the Andean-Patagonian Nothofagus forest region. *International Journal of Wildland Fire*, 17, 724. <https://doi.org/10.1071/WF07152>

Veblen, T. T., & Lorenz, D. C. (1988). Recent vegetation changes along the forest/steppe ecotone of Northern Patagonia. *Annals of the Association of American Geographers*, 78, 93–111. <https://doi.org/10.1111/j.1467-8306.1988.tb00193.x>

Villalba, R., Masiokas, M., Kitzberger, T., & Boninsegna, J. (2005). Biogeographical consequences of recent climate changes in the southern Andes of Argentina. In U. M. Huber, H. K. M. Bugmann & M. A. Reasoner (Eds.), *Global change and mountain regions: An overview of current knowledge* (pp. 157–168). Advances in Global Change Research. Dordrecht, The Netherlands: Springer. <https://doi.org/10.1007/1-4020-3508-X>

White, R., & Zipperer, W. C. (2010). Testing and classification of individual plants for fire behaviour: plant selection for the wildland–urban interface. *International Journal of Wildland Fire*, 19, 213–227. <https://doi.org/10.1071/WF07128>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1 Figures and Tables

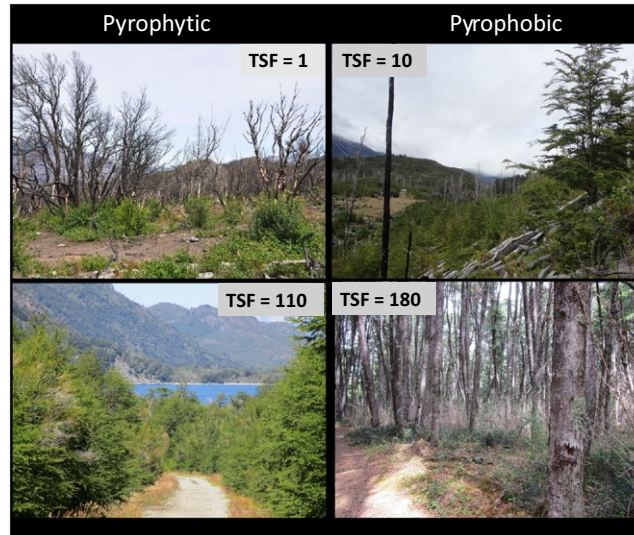
APPENDIX S2 Alternative models for vegetation structure and fine fuel variables

APPENDIX S3 Model selection and posterior predictive checks

How to cite this article: Tiribelli F, Kitzberger T, Morales JM. Changes in vegetation structure and fuel characteristics along post-fire succession promote alternative stable states and positive fire–vegetation feedbacks. *J Veg Sci*. 2018;00:1–11. <https://doi.org/10.1111/jvs.12620>

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only.
It will not be published as part of main article.



Understanding post-fire flammability trajectories is crucial to predict fire-vegetation feedbacks. We studied changes in vegetation structure and fuel characteristics along post-fire succession in two communities of NW Patagonia: resprouting shrublands and closed-canopy forests. We found a neutral feedback for shrublands and a positive one for forests, making the later especially sensitive to changes in fire regimes driven by global change.