Non-additive effects of alternative stable states on landscape flammability in NW Patagonia: fire history and simulation modelling evidence

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Abstract. Understanding the relationship between flammability and time since fire (TSF) is crucial for predicting ecosystem responses to changes in fire regimes. Landscapes composed of alternative stable states displaying positive fire–vegetation feedbacks are especially sensitive to these changes. We derived TSF–flammability functions (Logistic, Olson, Moisture, Weibull) from survival analysis applied to north-west Patagonian landscapes and simulated landscapes composed of different proportions of alternative stable states (shrublands and forest) and fire frequencies. We expected that landscapes dominated by shrublands would show an asymptotic growth (Logistic or Olson) and those dominated by forest would show a hump-shaped growth (Moisture). Additionally, we expected that the landscape-level flammability functions would resemble the pattern of the most abundant community. We found that shrublands tended to dominate the TSF–flammability relationship (Logistic) even when they were less abundant in the landscape (non-additive effects). The flammability function followed a hump-shaped growth (Moisture) only when the forest cover was >80%. Our results highlight that alternative stable states occur not only because of positive fire–vegetation feedbacks, but also thanks to the non-additivity of the flammability of the different states in the landscape. Non-additive effects could have an important role in accelerating landscape transformations towards more flammable states.

Additional keywords: ecosystems, temperate, fire frequency, fire history, fuel, age.

Introduction

The relationship between flammability and time since fire (TSF) modulates feedback mechanisms between fire and vegetation (Lindenmayer et al. 2011; Kitzberger et al. 2012; Tepley et al. 2018). Once a fire occurs, future fire occurrence and spread depends on the flammability of the post-fire vegetation, which can be less (negative feedback) or more (positive feedback) flammable than the pre-fire vegetation. Ecosystems that display negative feedbacks steadily increase in flammability as they age (e.g. Heinselman 1973; Johnson and Van Wagner 1985; Covington and Moore 1994). Landscapes dominated by those ecosystems display resilient, shifting steady-state mosaics, where young stands protect old stands from burning because recently burned patches are less likely to burn than patches that burned a long time ago (Bormann and Likens 1979). Conversely, in ecosystems that display positive feedbacks between the vegetation’s flammability and fire, recently burned patches are more fire prone than older post-fire patches (Cochrane 1999; Johnson et al. 2001; Beckage et al. 2009; Odion et al. 2010; Gosper et al. 2013; Paritis et al. 2015; Tepley et al. 2016; Zylstra 2018). As stands age, structural, micro-environmental and compositional changes throughout the successional sequence can lead to an initial increase in flammability followed by a decline. Landscapes dominated by these self-reinforcing positive fire–vegetation feedbacks are prone to develop alternative flammability states where pyrophytic (fire prone) communities coexist under the same environmental conditions with pyrophobic (fairly fire-free) communities (Odion et al. 2004; Wood and Bowman 2012; Paritis et al. 2015; Tiribelli et al. 2018). The coexistence of these two contrasting states generates different fire regimes and strong spatial interactions at the landscape scale. Thus, the proportion of pyrophytic v. pyrophobic states may critically influence the fire regime of these heterogeneous landscapes.

Evidence from paleoecological (McWethy et al. 2010, 2013), field (Paritis et al. 2015; Tepley et al. 2016) and simulation modelling studies (Kitzberger et al. 2012; Perry et al. 2012) suggests that landscapes dominated by ecosystems with positive feedbacks are highly vulnerable to changes in the fire regime (anthropogenic or climate driven). Their vulnerability lies in the
fact that the switch (sensu Wilson and Agnew 1992) from one alternative state to another occurs abruptly once a critical threshold is crossed, and a return to the initial state requires conditions and trajectories different from those that induced the initial transition (i.e. hysteresis; Scheffer et al. 2001; Scheffer and Carpenter 2003). A system dominated by a pyrophobic state can abruptly change to a pyrophytic state when disturbance frequency and severity exceeds a certain threshold. For instance, if fire frequency is higher than the time needed for a decrease in flammability, or if fire severity is such that it does not allow for a rapid recolonisation. By contrast, the transition from a pyrophytic to a pyrophobic state requires the absence of disturbance over a long period, and depends on the ability of the species that dominate the pyrophobic state to regenerate (seed dispersal distances, establishment rate, shade tolerance, growth rate). With high fire frequency or severity, these communities may remain in a flammable state, unable to mature and transition to a less flammable community (Kitzberger et al. 2012; Tepley et al. 2018). Thus, assessing how flammability changes with TSF is crucial to predict future-vegetation switches in response to changes in the fire regime.

In the temperate forests of southern South America and Oceania, there are several examples of landscapes displaying alternative stable states mediated by fire, which have either been studied empirically (Blackhall et al. 2012, 2017; Paritsis et al. 2015; Tepley et al. 2016) or theoretically (Perry et al. 2012; Schertzer et al. 2015). These regions share similar vegetation structure, life-history traits and environmental characteristics that allow the coexistence of pyrophytic and pyrophobic communities (Kitzberger et al. 2016). The pyrophobic communities are dominated by heliophilous, fast-growing species that produce rapid fuel build up because of their sometimes multi-stemmed architecture. By contrast, coloniser, fire-sensitive species that create closed-canopy forests with moist and dark understory are as they age, dominate the pyrophobic communities. Particularly, Patagonian landscapes present a variety of examples of alternative stable states of pyrophytic, resprouting shrublands and pyrophobic, closed-canopy forests (Paritsis et al. 2015; Kitzberger et al. 2016; Blackhall et al. 2017). In a previous study (Tiribelli et al. 2018), we found that these two communities have contrasting fuel-accumulation patterns as they age. Resprouting shrublands rapidly increase their amount of fine fuel with age until reaching an asymptote, after which fine-fuel density remains fairly constant and higher than in forests. Conversely, in closed-canopy forests, the amount of fine fuel increases the first decades after fire (~30 years) because of the resprouting understory species as well as the colonisation of obligate seeders. Once the colonising trees overtop, shade and outcompete the shrub layer, the amount of fine fuel, density and vertical continuity begin to decrease until reaching an asymptote, which is also lower than that in shrublands of the same age (‘hump-shaped pattern’). In short, the overall fuel and micro-environmental conditions of these forests make them less likely to catch fire than shrublands (see Morales et al. 2015). Adding further complexity, forests may transition to resprouting shrublands following large severe fires that eliminate fire-sensitive tree seed sources, whereas reinvocation of stable shrublands in forests is a slow accretion process mediated by long fire-free periods (Kitzberger et al. 2016).

Empirically testing landscape flammability in relation to stand age is only practically feasible by analysing past fire occurrence (e.g. TSF maps, fire-interval distributions). Survival analysis (Heinselman 1973; Johnson and Van Wagner 1985; Johnson and Gutsell 1994; Moritz et al. 2009) provides a framework to assess flammability at the landscape level and how it changes with TSF. Here flammability represents the probability of fire spreading through the landscape, given that an ignition occurred, combined with the rate of ignitions (sensu McCarthy et al. 2001). In survival analysis, the intervals between successive fires representing survival times (fire intervals) are used to fit fire interval distributions. From this fitted distribution, it is possible to derive a flammability function (or hazard function) that describes how the chance of burning changes with TSF (Johnson and Gutsell 1994; McCarthy et al. 2001).

Originally, flammability functions were derived from the Weibull model (e.g. Heinselman 1973; Johnson and Van Wagner 1985) following the idea that flammability would either increase exponentially with time or remain constant. However, this exponential growth is not suitable for every ecosystem. McCarthy et al. (1999, 2001) proposed alternative models that may be more appropriate to some ecosystem’s vegetation dynamics. In two of them, flammability increases up to an asymptote, with the ‘Logistic’ model allowing for a delay in the initial flammability increase, and the ‘Olson’ model increasing in flammability immediately after fire. In the so-called ‘Moisture’ model, flammability initially increases but then decreases following changes in vegetation structure, fuel accumulation and micro-environmental characteristics (McCarthy et al. 1999, 2001). As flammability is a function of fuel load, these different relationships between fire hazard and TSF ultimately depend on the type of community and its vegetation structure.

Survival analysis has been applied as a fire-management tool, and to test and develop management practices (Moritz 2003; Moritz et al. 2004; Van Wilgen et al. 2010; O’Donnell et al. 2011). However, it has only been used to assess fire hazard in rather homogeneous landscapes, often composed of a single community successional developing through TSF. One important assumption is that the aging elements are part of the same statistical population, meaning that the landscape is composed of the same regeneration or successional sequence that changes its flammability as it ages. In addition, it is assumed that the landscape does not change its TSF–flammability relationship between fire-return periods (Tepley et al. 2018). Clearly, landscapes displaying alternative stable states do not meet these assumptions, as they are composed of coexisting communities with contrasting flammability, or different post-fire recovery rates or pathways.

Laboratory experiments have demonstrated that the flammability of species mixtures can show non-additive effects where one of the species of the mixture has disproportionate effects on the outcome (e.g. flame length or duration). To account for this, the flammability of landscapes displaying alternative stable states may not always be inferred from the flammability of the states in isolation. Thus, performing survival analysis in such landscapes remains challenging, as the derived flammability function may represent either (a) the function of the most abundant community in the landscape or (b) one community dominating the fire regime regardless of its abundance (non-additive effect).
Assessing these alternative outcomes is crucial to predict the effects of future shifts in fire regimes and to decide on different fire-management policies, as a given management practice (e.g. fire suppression or prescribed burning), (a) may not be suitable for the entire landscape or (b) it may be only suitable for small portions of it.

The main objective of this study was to infer the TSF–flammability functions from fire-occurrence data of two contrasting vegetation types coexisting in the landscape as alternative stable states. First, we sought to assess to what extent flammability functions derived from shrublands or forests (pyrophytic and pyrophobic community types) matched those estimated from field-based assessments (Parisis et al. 2015; Tiribelli et al. 2018). To do this, we fitted fire-interval distributions to five landscapes of north-west (NW) Patagonia composed of different proportions of shrublands and forests where fire history during the 20th century was well documented. Based on previous field-based data, we expected that landscapes dominated by shrublands would show an increasing flammability with age until reaching an asymptote (Logistic or Olson model). By contrast, landscapes dominated by forests would show an increase followed by a decrease in flammability (Moisture model). Second, we used a simulation approach to assess if any TSF–flammability relationship (shrubland or forest) dominated the fire regime when both community types coexisted in the landscape. In order to do this, we first simulated fire histories in landscapes with different proportions of shrublands and forests, and fire frequencies, with known flammability functions for every community type. Then, we fitted flammability functions to those simulated fire histories in order to assess (a) if the fitted models corresponded to the most abundant community type in the landscape or (b) if one model dominated the fire regime regardless of its abundance, and if this outcome depended on the fire frequency.

**Methods**

**Study area**

The study area extends 39–43°S along the Patagonian Andes, Argentina (Fig. S1, available as Supplementary material to this paper). In this area, the vegetation varies along a steep precipitation gradient that extends from west to east (~3000 to 800 mm year\(^{-1}\)) and less markedly along a temperature gradient associated with elevation and slope exposure (Veblen et al. 1992). Here we focus on three different community types: pyrophytic closed-canopy forests dominated by tall Nothofagus spp. trees or by Austrocedrus chilensis (hereafter ‘forests’), and two pyrophytic types, tall resprouting shrublands dominated by resprouting shrubs or short trees (hereafter ‘shrublands’) and Araucaria araucana–Nothofagus antarctica woodlands (hereafter ‘woodlands’).

**Closed-canopy forests (forests)**

From west to east at mid altitudes (~800–1100 m above sea level), closed-canopy forests are dominated by the evergreen tree Nothofagus dombeyi with an understorey of bamboo Chusquea culeou, or co-dominated by the evergreen conifer Austrocedrus chilensis. At higher altitudes (~1000–1500 m above sea level), forests are dominated by deciduous Nothofagus pumilio. These three tree species have thin bark and are easily killed by fire, although large trees may survive low intensity surface fires (Kitzberger et al. 2005). In these communities, all trees are non-resprouters, do not have a persistent seed bank or exhibit fire-induced germination, and can only regenerate from unburned patches that provide seeds (hereafter coloniser trees, sensu Pausas and Keeley 2014). Nothofagus spp. trees are heliophilous, have a short post-fire regeneration window and their seeds are wind-dispersed with short dispersal distances – typically no further than 50 to 100 m. Given these characteristics, after severe, large fires they fail to regenerate and are replaced by shrublands of resprouting species that were often present in the understory before the fire (see the section below). A. chilensis is an intermediate shade-tolerant tree able to regenerate even in dense shrublands (Landesmann et al. 2015) and is capable of long distance seed dispersal (Landesmann and Morales 2018). However, it needs several decades without fire before it overtops and suppresses the shrubs (Landesmann et al. 2016).

**Tall, resprouting shrublands**

At drier sites or after severe fires, shrublands, composed of resprouting short trees (e.g. Nothofagus antarctica, Lomatia hirsuta, Maytenus boaria), tall shrubs (e.g. Embothrium coccineum, Diostea juncea) and bamboo C. culeou, dominate the landscape (Veblen et al. 2003). These shrub species are vigorous post-fire resprouters and typically dominate the early post-fire community. These pyrophytic communities are highly prone to burning because of site and fuel conditions and, because they usually occur in valley bottoms or lower-mid slopes, they are subject to frequent human-set fires. Moreover, the multi-stemmed growth form of their dominant species provides highly connected fuel ladders making them highly flammable, and their vigorous post-fire resprouting leads to rapid fuel recovery that allows for short fire-return intervals (Veblen 1992). Many of these shrublands may either be the early stages of post-fire succession that eventually result in closed-canopy forest, or maintain their species composition and functions when subjected to repeated burning and heavy livestock pressure (Blackhall et al. 2008, 2017; Parisis et al. 2015).

**A. araucana–N. antarctica woodlands**

In the northern portion of the study area, A. araucana open woodlands develop within a matrix of resprouting N. antarctica shrubs. These communities are probably the legacy of fires set in NW Patagonia by aboriginal populations before c. 1900 and by European settlers between c. 1890 and 1920 (Veblen and Lorenz 1988). Contrary to other Patagonian tall trees, mature A. araucana trees have several adaptations to survive and regenerate after fire, such as thick bark, basal epicormic buds and protected terminal buds. Its seedlings are capable of regenerating under a canopy of N. antarctica (Veblen et al. 1995). However, owing to its vigorous resprouting, N. antarctica dominates the post-fire stand for several decades and A. araucana trees require ~70 years without fire to eventually overtop N. antarctica (Veblen et al. 1995). Fire is an important disturbance in this pyrophytic community because of N. antarctica’s characteristics that promote fire conferring to the community characteristics described in the Tall, resprouting shrublands section.
Fire history in Patagonia

Modern Patagonian landscapes are the result of legacies of past human and natural stand-replacing fires. During the pre-European settlement period (pre-1890s), infrequent fires, set by native populations or lightning, allowed forest regeneration to take place. During the settlement period (1890–1920), Euro-Argentinean settlers set large, frequent fires to open land for pastures and agriculture (Moreno 1897; Willis 1914; Rothkugel 1916). Frequent forest re-burning, possibly fuelled by strong early 20th century droughts and bamboo post-flowering die-off, generated vast areas of pyrophytic shrublands dominated by resprouting shrubs and bamboo that have mostly persisted to the present day (Mermoz et al. 2005; Gowda et al. 2012). After the 1930s, the creation of National Parks and an increasingly negative, popular perception of forest fires drastically reduced fire frequency (Kitzberger et al. 1997), inducing the regeneration of many post-fire forest stands dating back to the settlement-period fires (Veblen and Lorenz 1987). After several 20th century decadal wet periods, a warming and drying trend started in the 1980s, during which large, severe fires generally burned within pyrophytic resprouting shrublands, but also affected large portions of pyrophobic closed-canopy forests (Mermoz et al. 2005; Veblen et al. 2008).

Fire-history maps

In order to fit flammability functions to landscapes with different proportions of shrublands, woodlands and forests (pyrophytic and pyrophobic communities), we gathered fire-history data from the National Parks Administration (APN), Lanin National Park (LNP) and from the Forest Management Department of Chubut Province. We sorted the fire data into five fire-history maps following National Park borders, political borders associated with different firefighting jurisdictions, natural fire breaks, such as lakes or alpine vegetation and international borders (hereafter, Lago Puelo–Lago Epyèn, Brazo Tristeza, Cerro Catedral–Lago Gutierrez, Lago Lolog, Lago Norquinco; Table 1; Fig. S1, fire-history maps for individual sites are in Supplementary material 1). For every fire within the fire-history maps, we had the year, area (ha) and, in some cases, the cause, along with a shape layer with the limits of the fire. These spatial layers were developed by the APN, LNP and the Forest Management Department of Chubut Province using Landsat satellite imagery, aerial photographs and historical fire maps (Willis 1914; Mermoz et al. 2005; Orellana 2013). We obtained the vegetation data from the World Wildlife Fund (WWF) Valdivian Forest Ecoregion map (Lara et al. 1999). The vegetation communities of this map were reclassified into three categories: forest, shrublands and woodlands.

### Table 1. Summary of the main fire history map characteristics

<table>
<thead>
<tr>
<th>Fire-history map</th>
<th>Burnable area</th>
<th>Burned area</th>
<th>Period</th>
<th>FRP (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lago Puelo–Lago Epyèn</td>
<td>161872.56</td>
<td>83903.252</td>
<td>1941–2016</td>
<td>145</td>
</tr>
<tr>
<td>Brazo Tristeza</td>
<td>10827.052</td>
<td>2496.161</td>
<td>1957–2016</td>
<td>256</td>
</tr>
<tr>
<td>Cerro Catedral–Lago Gutierrez</td>
<td>7195.096</td>
<td>3111.641</td>
<td>1914–2016</td>
<td>236</td>
</tr>
<tr>
<td>Lago Norquinco</td>
<td>16269.312</td>
<td>10262.376</td>
<td>1917–2016</td>
<td>157</td>
</tr>
<tr>
<td>Lago Lolog</td>
<td>45866.556</td>
<td>10684.3</td>
<td>1917–2016</td>
<td>269</td>
</tr>
</tbody>
</table>

The vegetation communities of this map were reclassified into three categories: forest, shrublands and woodlands.

**Fire-history map I. Lago Puelo–Lago Epyèn**

Located around Lago Puelo National Park and Lago Epyèn Provincial Reserve, this site is dominated by pyrophytic forests (90% total area) and fires burned mostly within this community (92% total area burned) (Fig. S2). Most fires affecting this landscape are human-caused (81% of area burned) from which 25% are intentional fires.

**Fire-history map II. Brazo Tristeza**

Brazo Tristeza is a southern branch of Nahuel Huapi Lake (Fig. S3). This landscape is within a restricted area of the Nahuel Huapi National Park where there are no settlements and most fires (75%) were caused by lightning. This site is dominated by pyrophytic forests (90%) and most fires run through this community (92% of area burned).

**Fire-history map III. Cerro Catedral–Lago Gutierrez**

Located on the eastern slope of Cerro Catedral, and limited by the western shore of Lago Gutierrez (Fig. S3). This landscape is composed of pyrophytic shrublands (47%) and pyrophobic forests (53%). Fires burned mostly within shrublands (62% of area burned). Many recreational activities take place in this area of Nahuel Huapi National Park, which receives thousands of visitors every year. Here all fires recorded were human-caused, albeit not intentionally.

**Fire-history map IV. Lago Norquinco**

Located on the northern limits of the Lanin Nationa Park, this landscape is subject to many rural activities, such as raising livestock, extracting firewood and Araucaria seed collection (Fig. S5). Most fires were human-caused (75%) from which at least 60% were intentional. This site is composed of pyrophytic shrublands (30%) and pyrophytic woodlands (61%). Fires burned within both woodlands and shrublands (62 and 37% of area burned respectively).

**Fire-history map V. Lago Lolog**

Located on the Northern shore of Lago Lolog in Lanin National Park (Fig. S6). This landscape is composed of pyrophytic shrublands (30%) and pyrophytic forests (70%). Fires burned mostly within shrublands (58% of area burned) also affecting adjoining forests. Most fires were caused by lightning.
Simulated fire histories

To explore how TSF interval distributions respond to variations in the proportion of shrublands and forests (pyrophytic and pyrophobic communities respectively) and variations in fire frequencies, we built a stochastic spatially explicit model implemented in SELES (spatially explicit landscape event simulator; http://www.gowlland.ca/downloads/register.htm, accessed 19 December 2018; Fall and Fall 2001). A complete model overview is in Supplementary material 2. The model simulates ignitions randomly in the landscape and fire spread, as well as plant succession. Fire spreads in the landscape given a fire-spread probability that depends on TSF and the community type (Fig. S7). Fire-spread probability increases with TSF until reaching an asymptote in shrublands (the pyrophytic community), following the pattern found in tall, resprouting shrublands (Paritsis et al. 2015; Tiribelli et al. 2018). In forest (the pyrophobic community), flammability increases and then decreases until reaching a lower asymptote (humped-shaped function, Fig. S7) (Paritsis et al. 2015; Tiribelli et al. 2018). When a cell burns, it immediately regenerates into a shrubland and succession to a forest occurs only if seeds reach the site from an unburned forest cell. Seed-dispersal probability follows an exponential decay (Fig. S8). This emulates the observed succession patterns in NW Patagonia (e.g. Paritsis et al. 2015; Landesmann et al. 2015, 2016; Tiribelli et al. 2018). Cells have a 30 × 30 m resolution (0.09 ha) and the landscape is a 3600 ha square grid (200 × 200 cells) that varies in vegetation composition and TSF. The model was wrapped or toroidal to avoid border effects. All stochastic processes occur at cell level whereas model results are assessed at the landscape level. The model simulates fires and regeneration in annual time steps and simulation runs comprise 1000 years (see Supplementary material 2 for simulation details and descriptive results). We simulated six vegetation-composition scenarios (Fig. S9) with six different initial shrubland–forest proportions (100–0, 80–20, 60–40, 40–60, 20–80 and 0–100%), and three ignition frequencies (2 ignitions per year, 1 ignition per year and 0.1 ignitions per year). We selected proportions of forest and shrubland in order to both emulate the portions of our real landscapes and to have a continuum of proportions in order to assess (a) if the fitted flammability functions corresponded to the more abundant vegetation type in the landscape or (b) if one vegetation type dominated the fire regime regardless of its abundance. For every initial proportion, we ran 10 fire-history simulations of 1000 years per scenario. We considered that an ignition propagated into a fire when it reached >0.5 ha.

TSF interval distributions

From both fire-history types (real and simulated), we calculated the fire-return period (FRP) for every study site as:

\[ FRP = \frac{N \times S}{A} \]

where \( N \) is the number of years of the study period; \( A \) is the total burnt area (ha); and \( S \) is the size of the study area (ha) (Oliveira et al. 2012). In order to calculate fire intervals in real landscapes, we rasterised the vector layers to grids of 100 m resolution and point-sampled them every 400 m to reduce spatial autocorrelation (Quantum GIS Development Team 2012). We used only grid cells that belonged to any of the vegetation categories from the WWF Valdivian Forest Ecoregion map (Lara et al. 1999) leaving out unburnable cells corresponding to water, rock and alpine vegetation. We then computed three different types of fire intervals following O’Donnell et al. (2011): (1) time to fire (TTF), (2) TSF, and (3) between-fire intervals (BFI). The first two are right-censored intervals and were treated as minimum potential fire intervals (see Polakow and Dunne 1999; Moritz et al. 2009; O’Donnell et al. 2011; Oliveira et al. 2012). For those vegetation cells that remained unburned during the observation period, we assigned a TTF value equal to the length of the study period (O’Donnell et al. 2011). Some authors decide to dismiss these double-censored intervals but when the fire-return period is smaller than the period of the study it is appropriate to include them in the analysis (Table 1) (Oliveira et al. 2012). For simulated landscapes, we only used BFI as the return period was smaller than the period of the study (1000-year simulation) and we used simulated fires > 5 ha to correspond with the minimum fire size found in our real landscapes fire histories.

With these data, we fitted four different fire interval distributions and derived flammability functions: the Weibull model that allows for an exponential increase in flammability with time, the Logistic and the Olson models where flammability increases with time up to an asymptote, and the Moisture model where flammability first increases and the decreases as the community ages. For detailed information on the cumulative and density forms of these models see Supplementary material 3. To fit these models, we used a Bayesian approach using JAGS (ver. 3.4.0, Just Another Gibbs Sampler; https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf, accessed 19 December 2018; Plummer 2003). Alternative models’ structures and prior distributions for model parameters can be found in Supplementary material 3. We checked for convergence for all model parameters and we then calculated the mean values of posterior distributions as point estimates and the 95% Highest Posterior Density (HPD) interval as a measure of uncertainty around the point estimates (Gelman and Hill 2007). The effective number of samples for each Monte Carlo Markov Chain (MCMC) can be found in Supplementary material 4. In order to select between alternative models, we calculated the WAIC (Watanabe Information Criterion, Watanabe 2012) and performed a posterior, predictive check in R (R version 3.3.1, R Foundation for Statistical Computing, Vienna, Austria).

Results

Mapped fire histories

Fire-return periods (FRP) where shorter in fire-history maps subject to frequent anthropogenic ignitions (Lago Puelo–Lago Epuyén and Lago Norquínco), and longer when most fires were natural (Brazo Tristeza, Cerro Catedral Lago Gutierrez, Lago Lolog). Flammability in fire-history maps where fires burned mostly through Nothofagus and Austracodroes forests (Table 1) followed a Moisture model (Lago Puelo–Lago Epuyén and Brazo Tristeza) (Fig. 1a, b). For these fire-history maps, WAIC was lower and the posterior predictive check revealed a better fit to this hump-shaped model. However, there were strong
differences in the shape of these flammability functions. In Lago Puelo–Lago Epuyén, where FRI was shorter (high fire frequency), flammability reached higher values and decreased faster than in Brazo Tristeza, where FRP was longer. Conversely, in fire-history maps where fires burned mostly shrublands, flammability followed either a Logistic model (Cerro Catedral–Lago Gutierrez, Lago Ñorquinco) or a Weibull model (Lago Lolog) (Fig. 1c, d). Again, there were strong differences in the shape of these flammability functions. In Lago Norquinco, where FRP was shorter (higher fire frequency) than in Cerro Catedral–Lago Gutierrez, flammability reached higher values. For model selection details see Supplementary material 4.

Simulated fire histories

The proportion of ignitions that propagated and the percentage of fires >5 ha decreased with the proportion of forests in the landscape (Fig. S10a, c), but the ignition frequency affected these variables differently for forests and shrublands. In landscapes dominated by shrublands (0% forest), as ignition frequency decreased, the proportion of ignitions that propagated, and the proportion of fires >5 ha increased (Fig. S10a, c). In landscapes dominated by forests, this relationship was reversed. As ignition frequency decreased, the proportion of ignitions that propagated and the proportion of fires >5 ha decreased.

Final forest cover was higher than initial forest cover in all scenarios, especially in those where the frequency of ignitions was low allowing for tree recolonisation (0.1 ignitions per year, Fig. S10d). However, in almost all scenarios most of the burned area corresponded to shrublands (>80%), except in the 100% forest (Fig. S10c). In terms of fire size distributions, as forest cover declined, the size of fires increased (Fig. 4). However, when landscapes were dominated by shrublands (0% forest) a reduction in ignition frequency resulted in bigger fires (median of less frequent fires; Fig. 4).

When landscapes were initially dominated by forests (>80%) and when the ignition frequency was low (0.1 ignitions per year), we were not able to fit the fire-interval distributions. The number of intervals between fires was not enough to inform the models (the models did not converge) because the number of fires >5 ha (Fig. 4) was small, and the landscapes were sampled every 400 m. Flammability in landscapes dominated by forest (80%) followed a Moisture model whereas flammability in landscapes that had <60% forest flammability followed a Logistic model (Fig. 2). When ignition frequency was low (1 ignition every 10 years) and with at least 20% initial forest cover, there was a discrepancy in the selected model among replicates, not all replicates fitted to the same model (Fig. 2, 3). Flammability reached higher values with increasing fire frequency and decreasing fire cover (Fig. 3). For model selection details see Supplementary material 2 (Table S2).

Discussion

By performing survival analysis on fire-history maps using a variety of models, we assessed fire–vegetation feedbacks for NW Patagonia that operate at the landscape scale. We found that closed-canopy forests display positive feedbacks between flammability and fire, as, in fire-history maps dominated by this vegetation type, flammability increased during the first post-fire years and then decreased following a hump-shaped pattern (Moisture model). Conversely, shrublands and woodlands displayed negative feedbacks, as, in fire-history maps dominated by shrublands, flammability increased until reaching an asymptote (Logistic model). This follows fuel-accumulation patterns,
where, in shrublands dominated by resprouting multi-stemmed shrubs, fine fuels increase very rapidly to a fairly constant value (Paritsis et al. 2015; Tiribelli et al. 2018). However, in sites where trees are able to colonise early after a fire, fine fuels first increase up to a maximum and then decrease to an intermediate level when trees cast sufficient shade to suppress the understorey vegetation (Paritsis et al. 2015; Tiribelli et al. 2018).

Our modelling exercise suggests that, when both community types coexist in the landscape, shrublands tend to dominate the relationship between flammability and TSF even when they are less abundant in the landscape. Thus, we can be confident that in landscapes comprising >20% heliophilous fast-growing species, either tall resprouting shrublands or A. araucana woodlands, flammability increases with TSF. Conversely, a landscape has to be almost exclusively dominated by closed-canopy forests (>80%) for flammability to increase in the first decades after fire and then decrease. This strongly suggests that heterogeneous landscapes have non-additive properties given by the flammability of different communities. As in the community assembly, where the most flammable species contribute...
disproportionally to the community’s flammability (see de Magalhães and Schwilk 2012; van Altena et al. 2012), we found that in heterogeneous landscapes the most flammable community can influence the fire regime well out of proportion of its abundance in the landscape.

Moreover, from our simulations, we found that there appears to be a critical amount of shrubland coexisting with forests needed before fires are able to burn through and generate a shrubland-type fire regime (between 20 and 40% of the landscape) (see Turner et al. 1989). Below this threshold, fire spread is more sensitive to fire frequency as higher ignition frequencies were needed for fires to burn through the landscape (e.g. Turner et al. 1989; Gardner et al. 1992). This may very well be the mechanism by which positive feedbacks establish in closed-canopy forests. Assuming that two fires occur sufficiently close in time so that the post-fire stand cannot develop into a less flammable community assembly (see Parissis et al. 2015; Tiribelli et al. 2018), the second fire may be able to burn through the landscape and produce a larger fire, enhancing the probability of a third, new fire, and so on. Another important mechanism is spatial contagion and neighbourhood effects. If fires tend to recur frequently in patches of shrublands and these have extensive boundaries with patches of forest, fires will tend to ‘erode’ portions of the latter faster than the capacity of seeders to recolonise and successfully develop into a forest again (Gowda et al. 2019). Provided this happens, continued erosion of the forest area will eventually pass a burn-through threshold beyond which the fire regime will be ultimately driven by the shrublands’ flammability rules (increasing flammability with time).

Therefore, in landscapes displaying alternative stable states the overall flammability cannot be easily derived from the fire history of the whole landscape. As found in the simulation model, especially in landscapes exceeding critical thresholds of communities’ composition (between 20 and 40% shrubland), survival analyses will fail to capture the flammability properties of forests and thus will not reveal the positive feedback between fire and vegetation. This has important implications for the maintenance of these ecosystems in the context of global change, as landscapes displaying positive feedbacks are especially sensitive to changes in ignition frequencies and fire severity due to changes in land use or climate (Kitzberger et al. 2012). Thus, it is crucial to be well aware of the limitations of survival analysis to capture the flammability function of these communities when coexisting with those that are more flammable. In this context, given that survival analysis are often used for management decisions (Moritz 2003; Moritz et al. 2004; Van Wilgen et al. 2010; O’Donnell et al. 2011), we need a much better understanding of community successional patterns at the landscape scale. In this way, we could assign every fire interval to a given community and fit fire-interval distributions, not to the landscape itself, but to every community separately.

Fig. 4. Fire size distribution for each landscape scenario (100 to 0% initial forest cover) and ignition frequency (logarithm of fire size absolute frequency v. fire size). Each circle, triangle and square in the graph represents the median size for a given logarithm of frequency. The dotted line marks the boundary between fires larger and smaller than 5 ha.
Our results indicate that the proportion of shrublands versus forests in combination with fire-ignition frequency strongly affected the landscape-level flammability estimates. When landscapes initially dominated by forests were subject to frequent human-ignited fires (e.g. Lago Puelo–Lago Epuyen and 80% 1 ignition per year simulations), TSF–flammability trajectories showed a strongly left-skewed peak of the Moisture model, suggesting very high flammability in young stands and a faster decrease in flammability as the stand enters intermediate ages. By contrast, forested sites with less influence of human-ignited fires and less naturally ignited fires (e.g. Tristeza, and 80% 0.1 ignition per year simulations) tended to show a more ‘rounded’ Moisture model with highest flammability at mid-age and less pronounced declines as the stand aged. When landscapes were initially co-dominated by both shrublands and forests, the flammability function increasingly resembled that of shrublands as ignition frequency increased (i.e. faster increase in flammability and higher flammability threshold). This suggests that changes in ignition frequency (human or climate driven) can strongly affect the TSF–flammability relationship and in consequence fire–vegetation feedbacks. On one hand, if there is at least 40% shrubland in the landscape, increases in ignition frequency can shift the whole landscape to shrublands, ultimately increasing the fire hazard. However, we believe that, if ignition frequency exceeds the time needed for forests to develop (disperse seeds, establish and mature), the landscape may shift to a shrubland-flammability relationship regardless of its abundance. On the other hand, decreases in ignition frequency can reduce fire hazard if >60% of forests act as natural firebreaks and reduce fire size.

In Andean Patagonia, several decades without fire are needed for the forest to return to its pre-fire composition, because its dominant species (that will potentially confer characteristic of a pyrophobic state) are at a reproductive post-fire disadvantage compared with the species conferring pyrophytic characteristics to shrublands and woodlands (resprouters). Conversely, short periods with high ignition frequency can produce abrupt changes towards the dominance of shrublands. Throughout history, human-occupation periods with intense use of fire by repeating ignitions on certain portions of the landscape (e.g. roads, towns, accessible areas, Paritis et al. 2013) had the capacity to rapidly shift pyrophobic landscapes towards more fire-prone ones (McWethy et al. 2013; Whitlock et al. 2015). This has probably been the case of the sharp landscape transformation in NW Patagonia induced by fire during the Euro-Argentinean settlement period when Nothofagus-dominated forests turned into extensive shrublands that persist to the present day in modern landscapes (Mermoz et al. 2005; Gowda et al. 2012). Moreover, amplifying the role humans play on the landscape, periods of warmer and drier conditions, which are conducive to larger and more severe fires (Holz and Veblen 2011), are further enhanced by the non-additive effects detected in this study.

In short, our results highlight that alternative stable states occur in the landscape not only due to positive feedbacks but also because of the non-additivity of the flammability of the different states. This non-additivity may exacerbate the effect of positive feedbacks given increases in ignition frequency or severity (anthropogenic or climatic). In a context of enhanced global change, where not only climate but also humans could drive shifts in fire regimes (Veblen and Lorenz 1988; Miller et al. 2005; Marlon et al. 2009; Bowman et al. 2011; McWethy et al. 2013), non-additive effects could have an important role in accelerating landscape transformations towards more flammable shrubland-dominated landscapes. Societies use fire for agriculture, ranching, forestry and wildlife management, and these ecosystem disturbances operate at shorter time scales than climatic ones. Patagonia in particular has, during the last few decades, seen severe forest loss associated to fires initiated near roads and anthropogenic activities, such as property development and pine plantations that disturb the natural establishment of forest species and bring novel, negative fire–vegetation feedbacks to Patagonian landscapes (Mermoz et al. 2005; Gowda et al. 2012). Better understanding of the resulting flammability of heterogeneous landscapes is needed to infer feedback mechanisms, identify thresholds and determine the factors that affect the resilience of ecosystems.

Authors’ contributions
F. Tiribelli, T. Kitzberger and J. M. Morales conceived the ideas and designed methodology; J. H. Gowda, M. Mermoz and F. Tiribelli developed the simulation model; M. Mermoz developed part of the fire history database; F. Tiribelli, T. Kitzberger and J. M. Morales analysed the data; F. Tiribelli led the writing of the manuscript. All authors interpreted results, contributed critically to the drafts and gave final approval for publication.

Conflicts of interest
The authors declare that they have no conflicts of interest.

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