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# Burn severity in *Araucaria araucana* forests of northern Patagonia: tree mortality scales up to burn severity at plot scale, mediated by topography and climatic context

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**Abstract** Climate change is forcing shifts in wildfire regimes, altering post-fire processes, and threatening the persistence of species and ecosystems. Key to assessing the potential for post-fire conversion to an alternate vegetation type is understanding drivers of burn severity, which in turn influence the material legacies that determine post-fire recovery. In Andean Patagonia, pyrophytic (fire promoting) shrublands juxtaposed with pyrophobic (fire inhibiting) forests of fire-sensitive species are well documented as drivers of fire spread and burn severity. However, the capacity of the highly fire- resistant *Araucaria araucana* to either promote or dampen burn severity has not previously been examined. This study uses field and remotely sensed data to examine which variables control burn severity at tree-, plot- and fire event-scales in large fires that burned *A. araucana*-dominated vegetation in four large fire events from 1987 to 2014. Logistic models were developed for each of the three scales to test for the factors influencing burn severity. Our results show that at the level of the individual tree, crown connectivity, tree size, and species strongly affect probability of death of individual trees. At a plot level, stand stocking parameters are less strongly predictive of burn severity. At a landscape-scale, vegetation type and topography, along with climatic and weather conditions are strong drivers of burn severity. These findings quantify the importance of greater tree size in the survival of the fire-resistant *A. araucana* and reinforce the regional pattern of greater fire severity being associated with tall shrubland vegetation in comparison to forests.

**Keywords** *Araucaria araucana* · Burn severity · Fire · Patagonia · Argentina

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## Introduction

Wildfire regimes across the world are shifting as a consequence of climate change, raising questions about the resilience of ecosystems under altered fire activity (Keeley and Syphard 2016; Pansing et al. 2020; Tubbesing et al. 2020). Projected changes in fire regimes (e.g., increased frequency, intensity, severity and extent of fires; Rogers et al. 2011; De Groot et al. 2013; Rocca et al. 2014), in concert with altered rates of tree establishment, growth, and survival (Allen et al. 2010; Carnicer et al. 2011), may reconfigure species' distributions and threaten the persistence of some ecosystem types. This is particularly relevant for species with a narrow distribution range, as in the case of *Araucaria araucana,* and in ecosystems where fire-vegetation feedbacks shape the landscape and regulate fire-induced forest conversion as is common in Andean Patagonia (Kitzberger et al. 2016). Positive feedbacks derived from the initial burning of *Nothofagus pumilio* forests accelerate the rate of forest conversion into shrublands and, once transformed into this alternative state, the increased likelihood of burning prevents return to a forest cover (Paritsis et al. 2015). The combined effects of a warmer and drier climate increasing fire frequency and reducing new recruitment may lead to an "interval squeeze" syndrome (sensu Enright et al. 2015), increasing the risk of species extirpation and ecosystem change. Fire-driven conversion of forests to a different forest type or a non-forest ecosystem occurs when resistance and resilience are overcome (Johnstone et al. 2016). Recovery of forests following high severity fire may be impeded by insufficient seed sources, unfavorable climate, or shortened-intervals between fires (Coop et al. 2020). The risk of conversion to non-forest vegetation may be amplified or dampened depending on how fire-initiated vegetation changes feedback into altered fire risk and behavior (Tepley et al. 2018). Key to assessing the potential for post-fire conversion to a different ecosystem type is an improved understanding of how pre-fire vegetation attributes may affect burn severity which in turn influences the material legacies (sensu Johnstone et al. 2016) that can determine the rate and success of post-fire recovery.

While climate and short-term weather conditions are widely recognized as key determinants of burn severity (i.e., % of trees killed) in forests, the effects of bottom–up controls such as vegetation attributes and terrain-related factors are also crucial, especially for fire events occurring under less than the most extreme weather conditions (Parks et al. 2012; Birch et al. 2015; Taylor et al. 2021). Terrain-related factors influence burn severity by controlling fire spread (e.g., slope, elevation, topographic position, ruggedness), fuel desiccation (heat load and potential radiation), and fuel load interactively with vegetation type. Drivers of burn severity can be assessed at different scales, revealing influences of top-down and bottom–up controls (sensu Mckenzie et al. 2011). Broad-scale climatic patterns can explain regional similarities in fire behavior (Krawchuk and Moritz 2011), whereas local drivers induce fine-scale heterogeneity (Povak et al. 2020). Vegetation attributes have been identified as driving factors of burn severity at different scales: vegetation type or size of flammable patches at a landscape-scale, plant density or dominance at a community scale, and tree species and size at an individual tree scale (Carlson et al. 2011; Wu et al. 2013; Belote et al. 2015). Along with species composition, vegetation structure controls burn severity by shaping fuel load and connectivity, generally linking higher stem densities with higher severity (Lentile et al. 2006; Prichard and Kennedy 2014). Stand structure may limit the type of fire possible in a stand: in comparison to multilayered, dense stands, active crown fire may not occur in open woodlands with low horizontal continuity of tree crowns, or in stands with a single layer of large trees with intermediate horizontal continuity but low vertical continuity (Alvarez et al. 2012). Thus, crown connectivity at the tree level may modify fire-induced mortality and scale-up to drive burn severity at a plot scale. Nevertheless, steep slopes or high wind speeds can overcome the effect of stand structure and cause fire to spread through the canopy. However, research explicitly examining drivers of burn severity across a range of scales is limited (Contreras et al. 2012).

Research conducted across a range of forest ecosystem types suggests that the relative roles of vegetation attributes and terrain-related factors in driving burn severity vary across ecosystem types, with spatial scale, and with the state of top-down (i.e., fire weather) drivers of burn severity (Wu et al. 2013; Parks et al. 2018; Povak et al. 2020). Thus, site-specific studies of vegetation and topographic influences on burn severity are required to improve our understanding of fire and vegetation interactions. This is particularly the case in the context of a warming climate and the potential for fire-induced conversion from forest to non-forest vegetation in Andean Patagonia (Veblen et al. 2011; Kitzberger et al. 2016). In this region, wildfires have long shaped the landscape, with varying frequencies and extents associated with land use and climatic drivers (Veblen et al. 2008; Mundo et al. 2013, 2017), creating a landscape mosaic of pyrophytic (more flammable, fire promoting) tall shrublands, and pyrophobic (less flammable, fire inhibiting) forests (Kitzberger and Veblen 1999; Mermoz et al. 2005; Tiribelli et al. 2018). Forest conversion occurs when moderate to high severity fires eliminate the tree cover and shift dominance to resprouting shrubs thereby enhancing community-level flammability and creating a positive fire feedback favoring the persistence of fire-prone communities (Landesmann et al. 2021). In this area of Patagonia, previous research demonstrating how moderate- to high-severity fires lead to positive feedbacks promoting conversion from forest to more fire-prone shrublands has been conducted in forests dominated exclusively by fire-sensitive trees lacking fire resistance traits and resprouting capacity (i.e., *Nothofagus dombeyi*, *N. pumilio* and *Austrocedrus chilensis*; Paritsis et al. 2015; Blackhall et al. 2017; Landesmann et al. 2021). In contrast, the current study was conducted in forests dominated by the conifer *Araucaria araucana* which due to its thick bark (commonly 14 cm thick on mature trees; Tortorelli 1942) and post-fire resprouting ability has a high capacity to survive fire (Veblen et al. 1995). This long-lived species occurs in both Argentina and Chile in a range of vegetation types from relatively open woodlands to mosaics of forest versus shrubland patches to continuous dense forests mixed with *Nothofagus* species (Veblen et al. 1995). Throughout its range, fire (both natural and anthropogenic) plays a dominant role in shaping stand and landscape-level forest patterns (Burns 1993; Blanck et al. 2013; Mundo et al. 2013). Previous research on spatial variability of burn severity in *A. araucana*-dominated vegetation has been conducted at a 30-m pixel scale using Landsat imagery (Assal et al. 2018; Franco et al. 2020). However, in our study area, the structure of *A. araucana*-dominated vegetation is highly complex ranging from single trees surrounded by shrubland, small to large patches of trees intermingled with shrubs to relatively continuous tree cover. Thus, the likelihood that these varied structures and especially varied tree crown connectivity may induce different burn severities calls for a fine-scale analysis of potential drivers of burn severity.

The current study examines variables that control fire severity at tree-, plot- and fire event-scales in large fires that occurred in forests dominated by the fire-resistant *A. araucana*. Specifically, we analyze (i) how tree size, species identity, and canopy connectivity affect probability of fire-induced tree death; (ii) how tree attributes scale up as forest structure to drive plot-level burn severity; and (iii) how topography and vegetation type (derived from satellite imagery) determine severity at a fire event scale. By studying four fire events that occurred under contrasting climatic conditions, we include climatic context in our interpretations of drivers of burn severity.

## Methods

### Study area

The study sites are located between latitudes 39° 0′ and 39° 50′ S, on the eastern side of the Andes mountain range (Argentina; Fig. 1), where dry summers favor the occurrence of wildfires. Precipitation, in the form of rain and snowfall, occurs between May and September along a steep west-to-east gradient of declining precipitation (4000–500 mm/year; De Fina 1972). Summer maximum temperatures reach up to 35 °C, and mean monthly temperatures range from 4 °C to 15 °C. Fire risk is high during the warm, dry summers, and periods of extreme drought are conducive to widespread fires (Mundo et al. 2013). Human-ignited fires are the most common, but lightning is also a significant ignition source (Veblen et al. 2008).

The dominant trees in the study area include the fire-resistant *A. araucana* as well as the fire-sensitive *N. pumilio*. *A. araucana* is a fire-resistant species, with thick bark and capability of resprouting from epicormics buds along the trunk and roots and protected terminal buds in the crown (Veblen 1982; Fuentes-Ramírez et al. 2019). It grows in stands of variable density: from open formations at dry sites to dense stands at mesic sites, where individuals are often grouped around female trees as a consequence of the narrow dispersion range of the large seeds. The flammability of *A. araucana* individuals is known to be low (Cóbar-Carranza et al. 2014), but stand flammability is expected to vary according to stand structure. Some forest stands are dominated or co-dominated by *N. pumilio* which is a deciduous broadleaf and fire-sensitive species, with thin bark. *N. pumilio* lacks any ability to resprout and its post-fire regeneration is dependent on seedling establishment (Veblen et al. 1996; Kitzberger et al. 2012; Paritsis et al. 2015). Shrublands are dominated by the post-fire resprouter *Nothofagus antarctica*, most typically

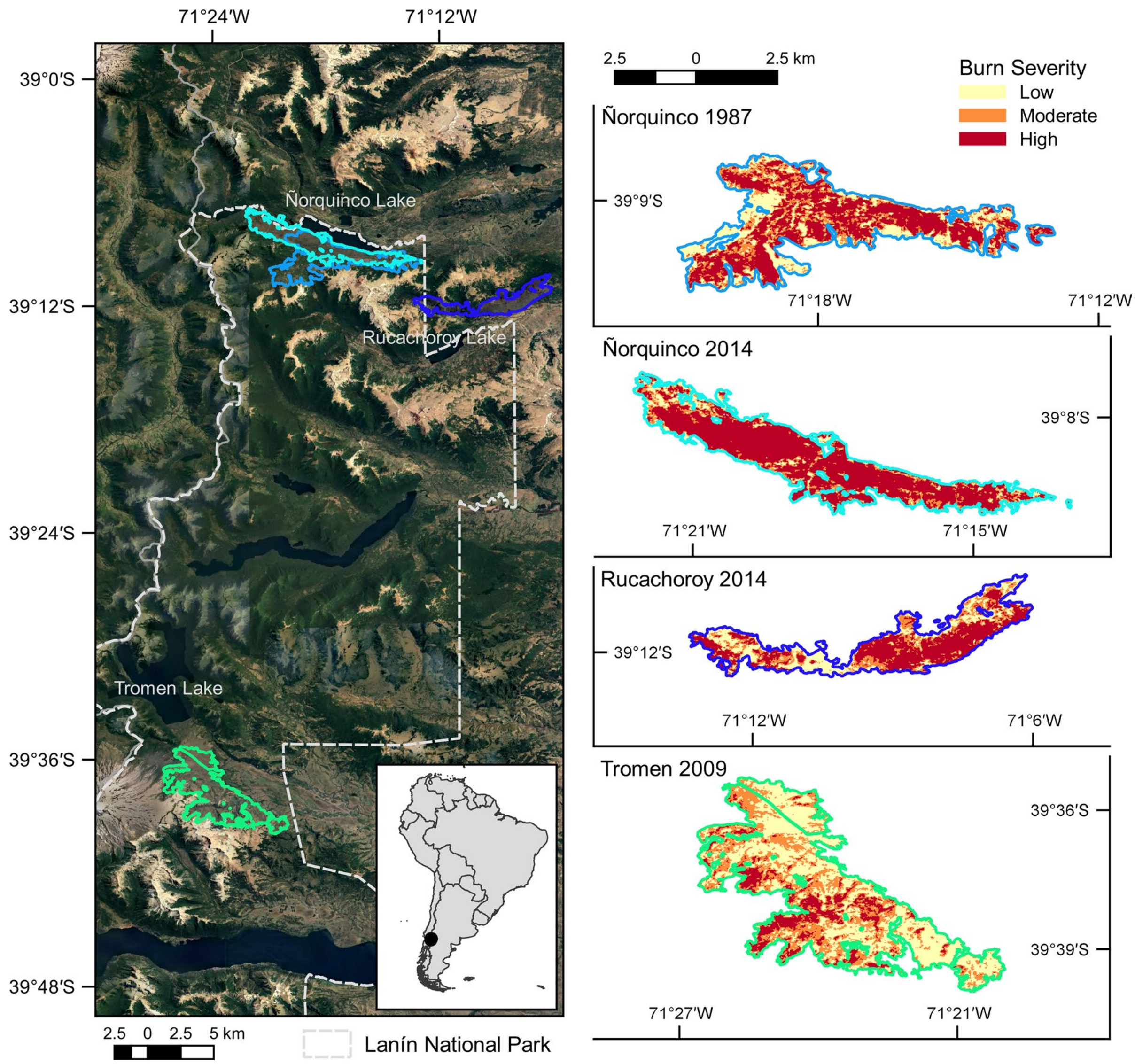


**Fig. 1** Study area map showing the locations of the four fire events. Fire perimeters are delimited by colors in left panel and burn severity classes are shown in the right panel. Burn severity classes were defined following Franco et al. (2020): low (dNBR < 300), moderate (300 < dNBR < 500), and high (dNBR > 500)

found as multi-stemmed individuals of 2–5 m height growing in dense highly flammable stands (Veblen et al. 2003; Tiribelli et al. 2018). For this study, we identified five vegetation types: tall forest dominated by broadleaved *N. pumilio* (tB) or conifer *A. araucana* (tC), mixed forest (tCB), shrublands dominated by broadleaved *N. antarctica* (sB), and tall conifer forest with a shrubby broadleaved stratum (tCsB).

For this study, four large fire events that burned *A. araucana* vegetation in the recent past (i.e., over the period of availability of satellite imagery) were selected, two of them having affected the same area (Fig. 1). The oldest one occurred between January and March 1987, burning across the Arroyo Coloco valley that flows into Ñorquinco Lake and its southern shore (Burns 1993); the ignition cause of the 1987 fire is unknown. However, the weather conditions during that summer (from January onwards) were dry; mean temperatures were close to typical values but precipitation was below the mean in January and February (data from Temuco, nearest weather station, available at https://explorador.cr2.cl). The other three events were ignited by humans and burned under severely dry conditions; one occurred near Tromen Lake in March 2009 and two others burned almost simultaneously in two contiguous valleys near Lake Ñorquinco and Lake Rucachoroy from December 2013 to January 2014.

## Data collection

Field data on vegetation structure were collected in February–March 2019. For analyses at the tree- and plot-level, 36 variable radius (from 8 to 20 m) capturing 30 trees (total surviving plus dead individuals) were located in pure *A. araucana* and mixed *A. araucana-N. pumilio* stands, representing tC and tCB vegetation types (Fig. 2). Circular plots of 30 trees (individuals of woody species with diameter at breast height equal or greater than 5 cm) have previously been used to describe the structure of these forests (Mundo 2011). The sampling protocol included 3 plots per burn severity class (high, moderate, and low) per fire year (1987, 2009, 2014) + 3 plots per burn severity in the area of the 1987 fire that reburned in 2014. At each plot for each tree (DBH ≥ 5 cm), we recorded DBH, species, status (live, death caused by fire, death before fire), sociological position (dominant/codominant, intermediate, or suppressed), and crown horizontal connectivity, along with a general description that included vertical connectivity of the canopy. Fuel continuity is known to influence fire behavior as it affects the potential of fire to spread across different strata. Due to the lag between fire

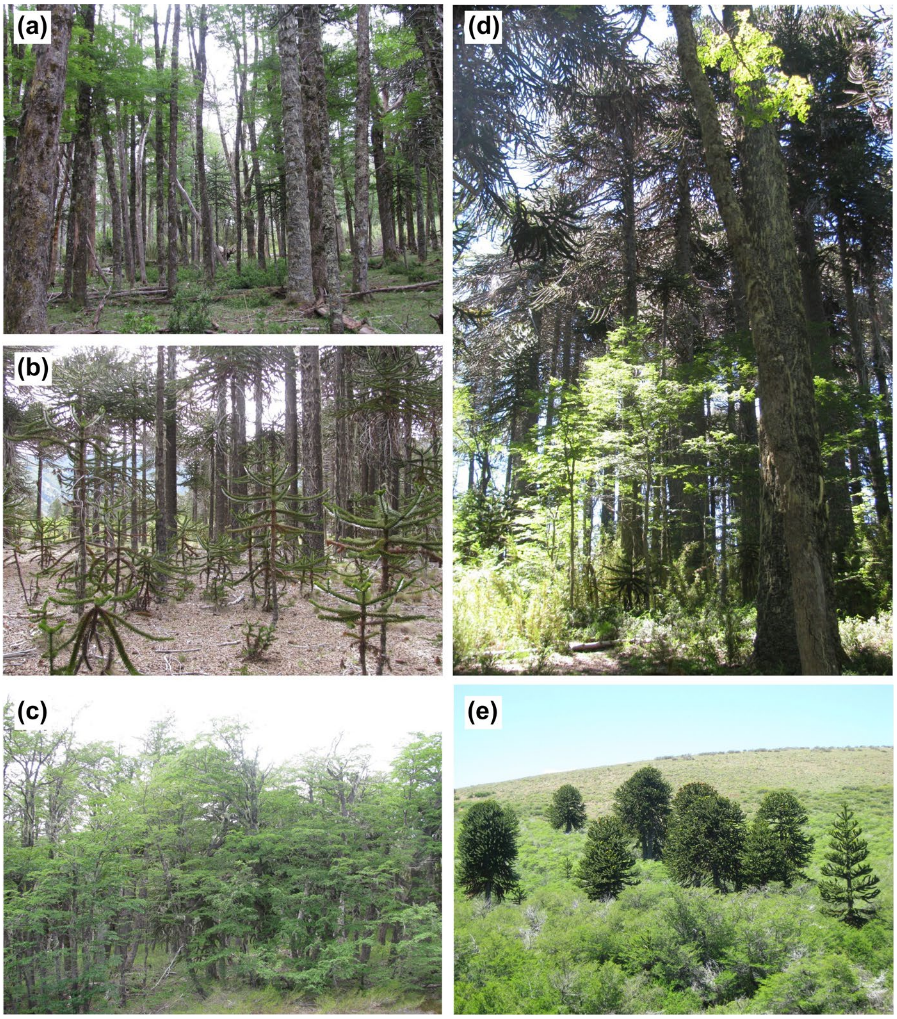


**Fig. 2** Images of vegetation types of the study area: **a** tall Broadleaved, tB, dominated by *Nothofagus pumilio*; **b** tall Conifer, tC, dominated by *Araucaria araucana*; **c** short Broadleaved, sB, dominated by *Nothofagus antarctica*; **d** mixed Conifer and tall Broadleaved, tCB; and **e** mixed Conifer and short Broadleaved, tCsB

dates and date of sampling, estimates of fuel continuity were restricted to the tree canopy and no attempt was made to reconstruct understorey fuel characteristics at the time of the fire, but legacies indicating pre-fire presence of shrubs were recorded in plot descriptions. Crown horizontal connectivity refers to the number of quadrants of the crown of a tree that overlap other crowns (0–4), following Righetto Cassano et al. (2014). This method, being simple and independent of the number of neighbors, provides reliable crown connectivity estimates even in the reburned plots, where some trees that were dead before the fire may have been completely consumed. However, this variable was only evaluated for standing trees (not for downed ones) in plots burned with low and moderate severity in the 1987 event, to avoid underestimation due to loss of evidence in areas burned with high severity. Thus, neither horizontal nor vertical connectivity was assessed in plots burned in 1987 because of the incomplete record of crown connectivity. Based on the depth and stratification of the canopy, vertical connectivity was classified as low (1, shallow and elevated canopy), moderate (2, deep but stratified canopy), or high (3, deep and continuous canopy). To support the description of vertical connectivity, total tree height and crown base height were measured for one suppressed, one intermediate, and one dominant tree. In the reburned plots, special effort was put into identifying standing trees that were dead before the fire and in recognizing pre-fire stumps that were partially consumed by the fire. Nevertheless, it is possible that some trees that died in the 1987 fire were totally consumed in the 2014 event and were not recorded; thus, pre-fire density and basal area may be underestimated. Field data were summarized to describe plot-scale pre-fire variables: stocking, composition, and canopy connectivity (i.e., mean crown horizontal connectivity including all trees) (Table 1).

For analyses conducted at the fire event scale, vegetation and terrain-related variables were derived from remotely sensed data at 645 points where values were obtained from the underlying pixel. Sample size reflects the maximum number of points that could be randomly distributed within the fire perimeters with a minimum sampling distance of 200 m to assure statistical independence of the response variable, derived from the analysis of the maximum distance of burn severity spatial autocorrelation in each event using semi-variograms. Remote sensing data included burn severity maps derived from classification of delta Normalized Burn Ratio (dNBR) values calculated from Landsat TM 5 and Landast OLI 8 images following Franco et al. (2020), vegetation maps provided by the Administración de Parques Nacionales (National Parks Administration of Argentina), and digital elevation maps available at the Instituto Geográfico Nacional of Argentina database. Topographic indices generally included in similar studies were derived from the DEM: topographic position index (TPI; Weiss 2001), topographic ruggedness index (TRI; Riley et al. 1999), heat load index (HLI; McCune 2007), potential direct incident radiation (PDIR; McCune 2007), and folded aspect (McCune 2007). Vegetation types for the 1987 event derived from the National Parks map were inspected and corrected based on visual comparison of high-resolution images available in Google Earth. All vegetation types were collapsed to fit the previously described classes (see "Study area", Table 1). All these variables were derived from 30-m resolution datasets, and TPI and TRI were calculated using a moving window of 60 m radius (5 cell square grid, centered on the focal cell).

### Data analyses

The effect of the selected variables on burn severity was evaluated by logistic models: binomial models at tree (live/dead) and fire event (high/low severity) scales and multinomial models at plot scale (high/moderate/low severity; Table 2). Logistic models have been used for similar purposes in previous studies (Bradstock et al. 2010; Murphy and Russell-Smith 2010; Belote et al. 2015; Holsinger et al. 2016) and were chosen for this study because they do not require large datasets which would been impractical for the plot-scale analysis.

Models with additive and interactive effects were fit, including all possible combinations of non-correlated factors (tested by means of Spearman correlation and $Chi^2$ tests for continuous and categorical variables, respectively, with $\alpha = 0.05$); each variable, as well as the interactions, is associated with a prediction (Table 2) that was tested by means of the significance of the term in the models. Significance of each factor was assessed by ANOVA or Likelihood Ratio tests in binomial and multinomial models, respectively; the Likelihood Ratio (LR) test was used for

**Table 1** Summary of data at tree-, plot- and fire event-scale: number of samples, name and code of each variable, and range of the data

| | Variable | Code | Range |
|---|---|---|---|
| Tree scale (692 trees in 33 plots) | | | |
| Size | Diameter at breast height (cm) | DBH | 5–205 |
| | Basal area (cm$^2$) | BA | 20–33,006 |
| | Crown dominance | CD | Suppressed/intermediate/dominant |
| Crown | Crown connectivity | CC | 0–4 |
| Species | Species | SP | *A. araucana/N. pumilio* |
| Severity | Plot severity | SEV | High/moderate/low |
| Plot scale (27–36 plots) | | | |
| Stocking | Density (ind/ha) | D | 136–1492 |
| | Basal area (m2/ha) | BA | 23–218 |
| Composition | Density of *A. araucana* (%) | Daa | 0.2–1 |
| | Basal area of *A. araucana* (%) | BAaa | 0.36–1 |
| Canopy connectivity | Mean horizontal connectivity | CC | 1.3–3.4 |
| | Min. horizontal connectivity | mCC | 0–2 |
| | Max. horizontal connectivity | MCC | 3–4 |
| | Vertical connectivity | VC | 1–3 |
| Fire event scale (645 points) | | | |
| Topographic position | Topographic position index | TPI | −3.3 |
| Slope | Slope | SLP | 0–41 |
| Elevation | Elevation | ELV | 1051–1734 |
| Ruggedness | Topographic Ruggedness Index | TRI | 0.3–28.5 |
| Heat Load | Folded aspect for heat load | FAhl | 0–180 |
| | Heat Load Index | HLI | 0.04–1.49 |
| Radiation | Folded aspect for radiation | FArad | 0–180 |
| | Potential Direct Incident Radiation | PDIR | 0.04–1.51 |
| Vegetation | Vegetation type | VT | Shrubby Broadleaved (sB)/tall Broadleaved (tB)/tall Conifer (tC)/mixed tC and sB (tCsB)/mixed tC and tB (tCB) |

random effects. Model fit was assessed through LR tests and $R^2$ coefficients (marginal and conditional $R^2$ for binomial models with random effects, based on fixed and fixed plus random effects, respectively, and McFadden $R^2$ for multinomial models); AUC (area under the receiver-operator characteristic curve—ROC; Hosmer et al. 2013) values were obtained by applying the leave-one-out cross-validation method. This method was selected because it maximizes the sample size for modeling when the number of observations is low, as is the case for plot-scale models in this study. The AUC is a measure of overall performance that synthesizes the discrimination capacity of a classifier; a value of 0.5 indicates no discrimination, while poor, acceptable, excellent, and outstanding discriminations are indicated by values up to 0.7, 0.8, 0.9, and 1, respectively (Hosmer et al. 2013). Model assumptions were tested for factor collinearity, independence, distribution and homoscedasticity of residuals, and independence of irrelevant alternatives. All analyses were performed in R (R Core Team 2019), using glmmTMB (Brooks et al. 2017) and mlogit (Croissant 2020) packages for binomial models and multinomial models, respectively. Finally, predicted probabilities of the most accurate models in terms of AUC were plotted for each scale.

At the tree scale, we examined the relation between tree mortality and tree size, species and crown features (Table 1), and their interactions with plot burn severity; fire year and site were included as random effects to account for top–down controls (i.e., seasonal to annual climate and fire weather) and

**Table 2** Outline of models for tree-, plot- and fire event-scale: general components of the models (dependent variable and factors, in italics) and selected variables with the associated predictions

| | Variable | Prediction |
|---|---|---|
| *Tree scale** | | *logit D/L ~ Size + Crown + Species + Severity + + \|fire year\| + \|site\|* |
| Size | DBH/BA/CD | Lower mortality of bigger/dominant trees |
| Crown | CC | Higher mortality of trees with more connected crowns |
| Species | SP | Higher mortality of fire-sensitive *N. pumilio* trees |
| Severity | SEV | |
| Interactions | Size*Severity | Milder effect of size as plot severity increases |
| | Species*Severity | Milder effect of species as plot severity increases |
| | Crown*Severity | Stronger effect of crown connectivity as plot severity increases (crown fires) |
| | Size*Species | Stronger effect of size on fire-sensitive *N. pumilio* |
| *Plot scale*** | *logit M/L* | *~ Stocking + Composition + Canopy connectivity* |
| | *logit M/H* | |
| Stocking | D / BA | Higher severity in denser/more heavily stocked stands |
| Composition | Daa / BAaa | Higher severity in plots with lower dominance of fire-resistant *A. Araucana* |
| Canopy connectivity | CC / mCC / MCC / VC | Higher severity in plots with higher canopy connectivity |
| Interactions | Stocking*Canopy connectivity | Milder effect of connectivity in less dense/stocked plots |
| | Composition*Canopy connectivity | Stronger effect of connectivity as dominance of fire-resistant *A. araucana* increases |
| | Composition*Stocking | Stronger effect of stocking as dominance of fire-resistant *A. araucana* increases |
| *Fire event scale**** | *logit H/L ~ Topographic position + Slope + Elevation + Ruggedness + Heat Load + Radiation + Vegetation + \|fire year\|* | |
| Topographic position | TPI | Higher severity on valleys, lower severity in hillsides |
| Slope | SLP | Higher severity in steeper slopes |
| Elevation | ELV | Higher severity in higher elevations |
| Ruggedness | TRI | Higher severity in less rugged areas |
| Heat Load | FAhl/HLI | Higher severity in areas with higher heat load |
| Radiation | Farad/PDIR | Higher severity in areas with higher radiation |
| Vegetation | VT | Higher severity in areas dominated by broadleaved species |
| Interactions | Ruggedness*Heat Load | Milder effect of heat load as ruggedness increases |
| | Ruggedness*Radiation | Milder effect of radiation as ruggedness increases |

Dependent variables are logit functions of probability of death caused by fire vs. survival (tree scale), probability of moderate vs. low/high burn severity (plot scale) and probability of high vs. low burn severity (fire event sale)

*Tree scale: D/L, probability of Dead/probability of Live

**Plot scale: M/L, probability of Moderate severity/probability of Low severity; M/H, probability of Moderate severity/probability of High severity

***Fire event scale: H/L, probability of High severity/probability of Low severity

bottom–up controls (i.e., differences in vegetation within fire perimeters). Trees that were dead before each fire were not included. At the plot level, we tested the influences of stocking, composition, and canopy connectivity on burn severity. Models testing the influence of canopy connectivity did not include data from 1987 fire because those variables could not be confidently reconstructed. Due to the small sample size (27–36 observations) and lack of any significant effect of fire year and site, we excluded random effects from the plot-scale models. At the fire event level, we assessed topographic influences on occurrence of high- and low-burn severity, excluding moderate severity because it was the least accurately identified class in the burn severity maps (Franco et al. 2020). Fire year was included as a random effect to control for differing climatic/weather influences on the events. To interpret possible climatic influences on the vegetation and terrain-related drivers of burn severity, Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010) data were downloaded from the Global SPEI database (http://sac.csic.es/spei/database.html) for each of the 3 fire years. SPEI is a drought index that combines precipitation and potential evapotranspiration, based on the accumulated values over the preceding months. The 3-month period index (SPEI3) corresponding to the year of each event (autumn to summer of the fire) was selected for analyses.

## Results

### Tree scale

At the individual tree level, crown connectivity and size were the relevant variables that predict tree mortality, the latter one in interaction with species (Table 3). As expected, top–down and bottom–up controls were important. Both severity at the plot level and site conditions combined with fire year and site were statistically significant, but severity showed no significant interaction with the other variables. The probability of death was lower for larger *A. araucana* trees in striking contrast to *N. pumilio* which exhibited a higher probability of death as tree size increased probability (Fig. 3b). Regardless of the species, trees were less likely to die as their crowns were more connected (Fig. 3a), but plot burn severity highly determined the probability of death (Fig. 3c). All models were statistically significant and the discrimination capacity ranged from acceptable to excellent (0.78–0.88).

### Plot scale

At the plot level, most models were not statistically significant ($P < 0.05$), and all of them resulted in poor discrimination (never above 0.70). However, canopy connectivity seemed to have a combined effect with stocking on burn severity, whereas the effect of composition was not significant (Table 3). Plots with more horizontally connected canopies increased the probability of being in the low severity fire class, whereas moderate or high severity was more likely in stands with low horizontal connectivity (Fig. 3d). Plots with low vertical connectivity tended to burn at moderate severity (Fig. 3e). Additionally, stands with isolated trees (mCC of 0) tended to burn more severely as stocking increased, but the opposite occurred as crowns tended to overlap more (Fig. 3f–h).

### Fire event scale

At the scale of fire events, topographic position and vegetation appeared to drive burn severity across the wildfire event, along with heat load and radiation, but the effect of ruggedness was only significant in interaction with either heat load or radiation (Table 3). All these models were statistically significant and produced acceptable discriminations (0.79–0.81). High burn severity was more likely in valleys (i.e., TPI < 1), in areas where radiation was higher and in more rugged areas with high heat load (NW aspect) and less rugged ones with low heat load (SE aspect) (Fig. 3i–l). Conifer-shrub stands, followed by shrublands, were the most prone to high severity; mixed tall forest was associated with the lowest probability (Fig. 3c). Climate and weather also exerted a significant control (fire year represented 10% of $R^2$) (Table 3) which, to some extent, might be explained by the different water balances of the fire years; the 1987 fire followed a slightly above average SPEI3, the 2009 fire burned at the end of a 5-month drought, and the 2014 fires started in a very dry December (Fig. 4).

## Discussion

Our study of the drivers of burn severity in four large fire events in vegetation dominated by *Araucaria araucana* revealed significant influences across the full range of scales from the tree- to the plot- to the fire-event scale. Burn severity measured as tree mortality is strongly influenced by tree size and crown connectivity at the scale of individual trees. At the plot scale, crown connectivity and stand stocking parameters had relatively modest influences on burn severity. At the landscape scale, terrain-related factors and vegetation type were strong controls of burn severity.

At a tree scale, we found that smaller and less connected trees are more likely to be killed by fire than grouped ones. However, large *N. pumilio* trees seem to be more susceptible to fire-caused death than small individuals of this species in the mixed stands. At the

**Table 3** Logit models for tree-, plot-, and fire event-scale: significance of random and fixed factors (*p-values*) and general performance (LR test, $R^2$ and AUC); bold lettering indicates statistical significance ($p < 0.05$)

| **Tree scale*** | | Model | | | | | | | LR test | $R^2$ | AUC |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *logit D/L ~ Size + Crown + Species + Severity + \|fire year\| + \|site\|* | | | | | | | | | |
| Additive effects models | M1 | **DBH** + **CC** + SP + **SEV** + **\|FY\|** + **\|SITE\|** | | | | | | | ***<0.001*** | 0.44/0.61 | 0.87 |
| | | ***<0.001*** | ***<0.001*** | 0.12 | ***<0.001*** | ***<0.001*** | 0.018 | | | | |
| | M2 | **CD** + **CC** + SP + **SEV** + **\|FY\|** + **\|SITE** | | | | | | | ***<0.001*** | 0.41/0.650 | 0.88 |
| | | ***<0.001*** | ***<0.001*** | 0.12 | ***<0.001*** | ***<0.001*** | ***<0.001*** | | | | |
| Interactive effects models | M3 | DBH*SEV + **DBH** + **CC** + SP + **SEV** + **\|FY\|** + **\|SITE\|** | | | | | | | ***<0.001*** | 0.42/0.60 | 0.87 |
| | | *0.59* | ***<0.001*** | ***<0.001*** | 0.13 | ***<0.001*** | ***<0.001*** | 0.12 | | | |
| | M4 | SP*SEV + **DBH** + **CC** + SP + **SEV** + **\|FY\|** + **\|SITE\|** | | | | | | | | 0.81/0.87 | 0.87 |
| | | 0.79 | ***<0.001*** | ***<0.001*** | 0.44 | ***<0.001*** | ***<0.001*** | 0.13 | | | |
| | M5 | CC*SEV + **DBH** + **CC** + SP + **SEV** + **\|FY\|** + **\|SITE\|** | | | | | | | ***<0.001*** | 0.45/0.62 | 0.87 |
| | | 0.53 | ***<0.001*** | ***<0.001*** | 0.13 | ***<0.001*** | ***<0.001*** | 0.014 | | | |
| | M6 | **DBH*SP** +**DBH** + **CC** + SP + **SEV** + **\|FY\|** + **\|SITE\|** | | | | | | | ***<0.001*** | 0.52/0.65 | 0.88 |
| | | ***<0.001*** | ***<0.001*** | ***<0.001*** | 0.27 | ***<0.001*** | ***<0.001*** | 0.18 | | | |
| ***Plot scale**** | | *logit M/H* | | | | | | *~ Stocking + Composition + Canopy connectivity* | | | |
| | | *logit M/H* | | | | | | | | | |
| Additive effects models | M1 | D + Daa + **CC** + mCC + **VC** | | | | | | | 0.018 | 0.35 | 0.60 |
| | | *0.76* | *0.35* | ***0.02*** | *0.16* | ***0.03*** | | | | | |
| | M2 | D + Daa + CC + MCC + **VC** | | | | | | | 0.030 | 0.32 | 0.54 |
| | | *0.98* | *0.26* | *0.30* | *0.37* | ***0.04*** | | | | | |
| | M3 | D + BAaa + **CC** + mCC + **VC** | | | | | | | 0.019 | 0.35 | 0.61 |
| | | *0.85* | *0.38* | ***0.02*** | *0.14* | ***0.04*** | | | | | |
| Interactive effects models | M4 | BA + BAaa + **CC** + MCC + **VC** | | | | | | | 0.019 | 0.35 | 0.61 |
| | | *0.69* | *0.31* | ***0.03*** | *0.13* | ***0.03*** | | | | | |
| | M5 | **BA*mCC** + **BA** + Daa + **CC** + **mCC** + VC | | | | | | | 0.016 | 0.35 | 0.61 |
| | | ***0.01*** | ***0.02*** | *0.09* | ***0.05*** | ***0.01*** | *0.05* | | | | |
| | M6 | Daa*CC + BA + **Daa** + CC + mCC + **VC** | | | | | | | 0.029 | 0.39 | 0.55 |
| | | *0.52* | *0.64* | ***0.04*** | *0.27* | *0.26* | ***0.02*** | | | | |

**Table 3** (continued)

| ***Plot scale**** | | *logit M/H* | | | | | | *~ Stocking + Composition + Canopy connectivity* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *logit M/H* | | | | | | | | | | |
| | M7 | BA*Daa + BA + Daa + CC + mCC + **VC** | | | | | | | | 0.042 | 0.37 | 0.52 |
| | | *0.94* | *0.97* | *0.93* | *0.13* | *0.23* | ***0.02*** | | | | | |
| | M8 | **BA*mCC** + Daa*CC + **BA** + **Daa** + CC + **mCC** + **VC** | | | | | | | | | | |
| | | ***0.01*** | *0.08* | ***0.01*** | ***0.04*** | *0.05* | ***<0.001*** | ***0.01*** | | | | |
| ***Fire event scale**** | | *logit H/L ~ Topographic position + Slope + Elevation + Ruggedness + Heat Load + Radiation + Vegetation + \|fire year\|* | | | | | | | | | | |
| Additive effects models | M1 | **TPI** + TRI + FAhl + PDIR + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.50/0.64 | 0.79 |
| | | ***<0.001*** | *0.17* | *0.14* | *0.91* | ***<0.001*** | ***<0.001*** | | | | | |
| | M2 | **TPI** + **TRI** + HLI + FArad + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.50/0.64 | 0.79 |
| | | ***<0.001*** | ***0.05*** | *0.17* | *0.24* | ***<0.001*** | ***<0.001*** | | | | | |
| | M3 | **TPI** + TRI + **FAhl** + **FArad** + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.49/0.65 | 0.80 |
| | | ***<0.001*** | *0.11* | ***0.02*** | ***0.01*** | ***<0.001*** | ***<0.001*** | | | | | |
| | M4 | **TPI** + **SLP** + **FAhl** + **FArad** + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.50/0.65 | 0.81 |
| | | ***<0.001*** | ***0.03*** | ***0.01*** | ***0.01*** | ***6e-5*** | ***<0.001*** | | | | | |
| | M5 | **TPI** + **ELV** + **FAhl** + **FArad** + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.49/0.65 | 0.81 |
| | | ***<0.001*** | ***0.01*** | ***<0.001*** | ***<0.001*** | ***<0.001*** | ***<0.001*** | | | | | |
| Interactive effects models | M6 | **TRI*FAhl** + **TPI** + **ELV** +TRI + **FAhl** + **FArad** + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.49/0.65 | 0.81 |
| | | ***0.01*** | ***<0.001*** | ***0.01*** | *0.08* | ***<0.001*** | ***<0.001*** | ***<0.001*** | ***<0.001*** | | | |
| | M7 | **TRI*FArad** + **TPI** + **ELV** +TRI + **FAhl** + **FArad** + **VT** + **\|FY\|** | | | | | | | | ***<0.001*** | 0.49/0.65 | 0.81 |
| | | ***0.02*** | ***<0.001*** | ***0.02*** | *0.83* | ***0.01*** | ***0.01*** | ***<0.001*** | ***<0.001*** | | | |

*p*- values of random and fixed factors are presented in italics and bold lettering indicates statistical significance($p<0.05$)

*Tree scale: D/L, probability of Dead/probability of Live

**Plot scale: M/L, probability of Moderate severity/probability of Low severity; M/H, probability of Moderate severity/probability of High severity

***Fire event scale: H/L, probability of High severity/probability of Low severity

$R^2$ values: marginal $R^2$/conditional $R^2$ for binomial models with random effects and McFadden $R^2$ for multinomial models

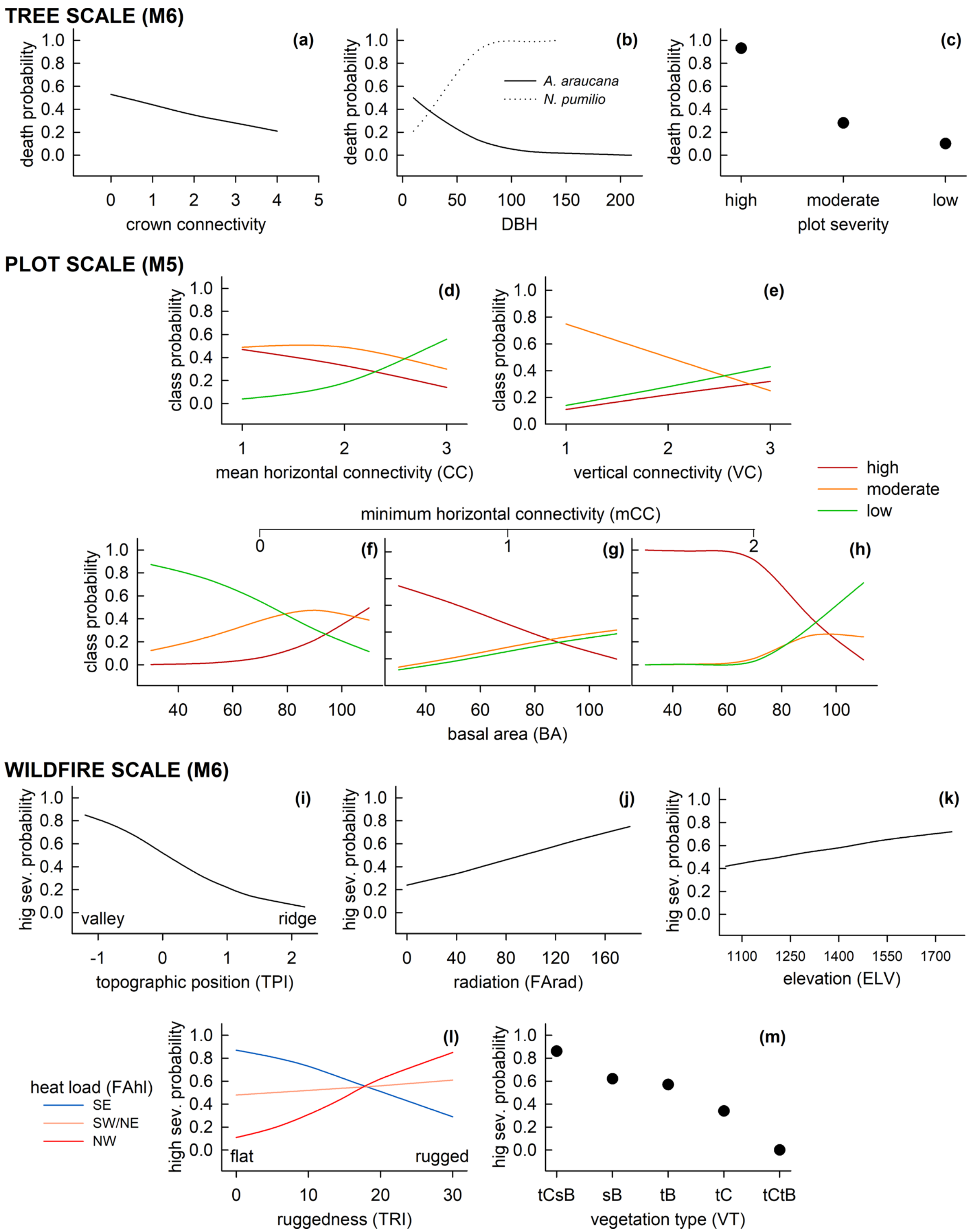


**Fig. 3** Predicted probabilities by the significant variables of the most accurate model at tree- (**a**), plot- (**b**) and fire event- (**c**) scales. The model presented at each level is indicated in brackets. At a wildfire-event scale, vegetation types are shrubby Broadleaved (sB), tall Broadleaved (tB), tall Conifer (tC), mixed tC and sB (tCsB), and mixed tC and tB (tCB)

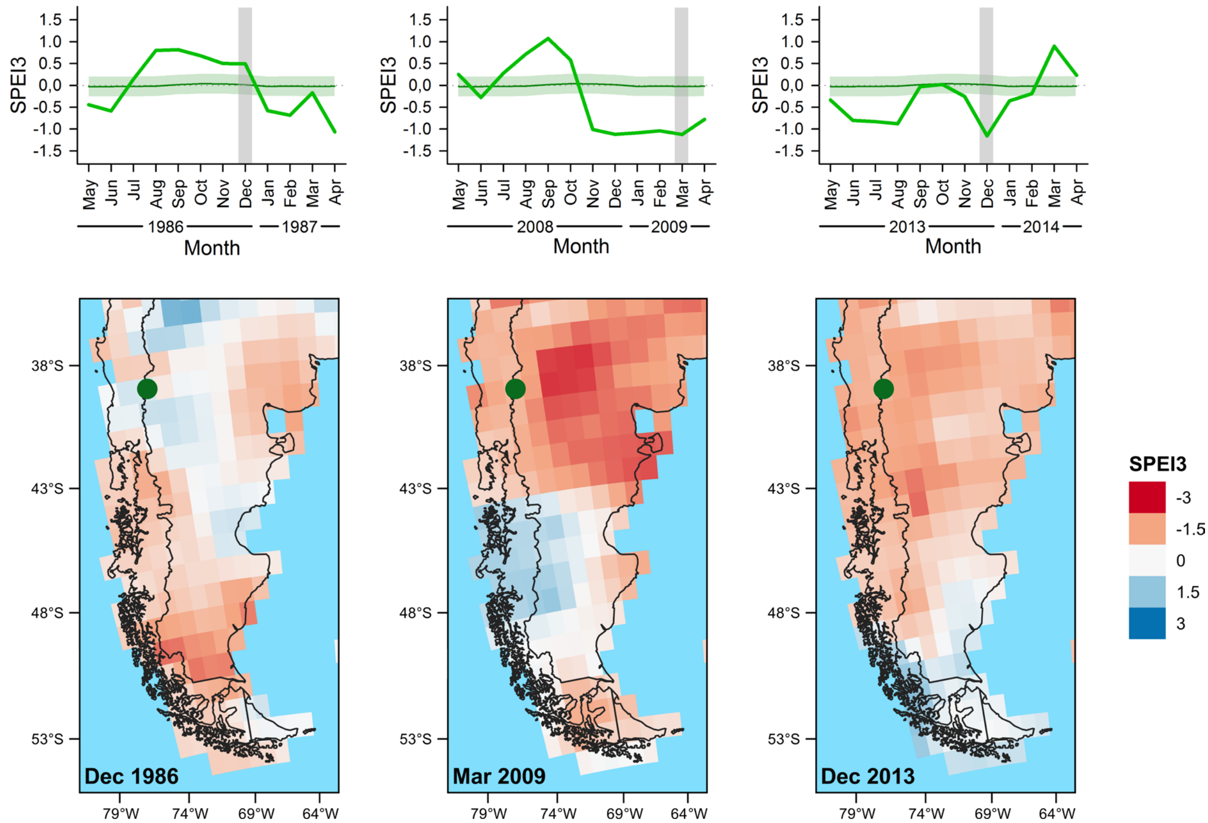


**Fig. 4** SPEI3 temporal evolution (May–April) for each fire season (1987, 2009, 2014 from left to right in upper panels). In the bottom panels, SPEI3 gridded spatial pattern corresponding to month when each fire ignited (December 1986, March 2009, December 2013 from left to right). Red and blue colors represent droughts and humid periods, respectively. Gray bars indicate the month of the fire event in the upper panels

plot level, higher tree death probability was strongly associated with higher burn severity which integrates all fire impacts, including average tree-damage and biomass consumption. A tree size influence on tree mortality previously has been reported for trees growing in temperate and tropical forests (Brando et al. 2012; Belote et al. 2015). The higher susceptibility of smaller trees has been related to lower crowns that can be more easily reached by fire and to thinner stems that are more easily ignited or damaged by heat due to thinner bark. Furthermore, Belote et al. (2015) reported tree survival being controlled by the combined effect of species, tree size, and burn severity. In the case of *A. araucana,* results are consistent with its fire-resistant characterization. Its thick corky bark gradually increases in thickness as the tree ages protecting the cambium from high temperatures during a wildfire. Furthermore, trees self-prune lower branches as they age, thus elevating the base of the crown over time. In contrast, our finding suggesting higher susceptibility of larger *N. pumilio* trees was not anticipated. Other studies have reported a decline in the risk of fire reaching the canopy of *N. pumilio* as they grow tall enough to reduce fine fuel continuity with understory vegetation (Paritsis et al. 2015). Our results may be influenced by the fact that we did not sample pure stands of this species so that unaccounted factors such as species, size, or distribution of neighboring trees could explain this counter-intuitive result. However, it is possible that larger *N. pumilio* trees were more vulnerable to fire-caused death due to the predisposing effects of episodic severe droughts that have been driving tree mortality and partial crown dieback in the region, particularly in dry-mesic sites (Rodríguez-Catón et al. 2016; Tarabini et al. 2021). Considering that connected fuels are known to facilitate fire spread, we were expecting trees with less horizontally connected crowns to be less susceptible to death caused by crown fires. However, our results suggest that grouped trees are more fire-resistant in these forests possibly reflecting shorter and sparser understory fuels and a cooler and wetter microclimate that reduces fuel aridity beneath patches of trees with inter-connected crowns (Paritsis et al. 2015). The significant effect of fire year on probability of tree death suggests a top-down control on tree mortality exerted by seasonal climate and fire weather. The site effect reflects possible influences of climate, topography, and vegetation.

Crown connectivity scales up to drive burn severity at the plot scale, along with total basal area, but with weak explanatory power. No statistically significant effect of species composition (proportion of *A. araucana* in terms of density or basal area) on burn severity was detected. The lower mortality of grouped trees translates to higher probability of low burn severity in plots with more connected canopies and high severity prevalence in areas with sparse trees. Fuel connectivity is known to influence fire behavior, partially mediating the occurrence and transition between surface and crown fires, along with structure, topography, and weather (Van Wagner 1977; Alvarez et al. 2013). Our results suggest that the presence of isolated trees determines different severities when stocking is considered; less stocked stands with grouped trees burn more severely than those with isolated trees and the opposite happens in stands with higher stocking. The likelihood of an inverse relationship between tree crown cover and height and abundance of understory shrub fuels may explain these counter-intuitive results; based on our plot descriptions, a key understorey fuel in these forests would be the bamboo *Chusquea culeou* which is more abundant where the tree canopy is less dense (Veblen et al. 1996). Other authors have reported tree density being either uncorrelated or positively associated with lower mortality (Belote et al. 2015). In our study, low vertical connectivity (i.e., shallow and elevated canopy) determines a higher probability of moderate severity fires; when vertical connectivity is high, there was no prevalent severity class. These results differ from reports of higher vertical fuel continuity being associated with higher severity fires (Lecina-Diaz et al. 2014; Fernández-Guisuraga et al. 2021). Contrary to our predictions, species composition (proportion of *A. araucana*) was not statistically significant in determining plot-level burn severity. However, it is possible that the low sample size or some spatial autocorrelation restricted the capacity of the models to capture significant influences of these variables. Moreover, the loss of physical evidence in reburned plots could also obscure the effect pre-fire structure on burn severity, particularly in terms of stem density (including understory bamboos and subcanopy *N. antarctica*). Nevertheless, difficulties in identifying the importance of predictor variables are not rare, especially if they change depending on burn severity or climatic context (Povak et al. 2020).

Similar to our findings, most studies point to topography and vegetation as the main drivers of burn severity, with differences in the ranking of the relative importance of each (Bradstock et al. 2010; Harris and Taylor 2015; Parks et al. 2018). Our results indicate that topography and vegetation control on burn severity largely determine the heterogeneity of fire impact across the burnt area, in combination with the influences of the top-down controls of burning conditions of each event. Higher burn severity is more likely to occur in areas that are more exposed to greater solar radiation, located at higher elevation (also correlated with steeper slopes), north-facing (i.e., equatorward facing) rugged slopes (on aspects with higher heat load), on less rugged slopes (on south-facing of lower heat load) or in valleys. Topographic influences on burn severity have been widely studied and there is general consensus about the influence of some features such as aspect and heat load, whereas others are known to be system-dependent (e.g., topographic position, elevation, slope; Carlson et al. 2011; Cansler and Mckenzie 2014; Clarke et al. 2014; Holsinger et al. 2016) as found in our study. Vegetation type also determines burn severity: mixed *N. antarctica-A. araucana* stands are the most prone to high-severity fires, followed by *N. antarctica* shrublands; mixed *A. araucana-N. pumilio* forests tend to burn with lower severity, followed by pure stands of *A. araucana.* These results are consistent with the findings for similar vegetation in the Andean-Patagonian region lacking the fire-resistant *A. araucana* that have demonstrated that fire is less likely to spread in tall forests than in the tall shrublands typically characterized by *N. antarctica* (Mermoz et al. 2005; Kitzberger et al. 2012; Tiribelli et al. 2018). The high susceptibility of *A. araucana-N.*

*antarctica* shrublands to high-severity fires reinforces the idea that, once the forest is burned initially and a tall shrubland is established, increased flammability increases the likelihood that the area remains a shrubland (Tiribelli et al. 2018; Landesmann et al. 2021). Our findings are also consistent with emerging literature stressing the strong fire-to-fire influence, in some ecosystems negative but in others positive, as well as the influence of species' fire-resistance traits on burn severity in other temperate forests (e.g., Harvey et al. 2016; Tepley et al. 2018; Furlaud et al. 2021; Cansler et al. 2022).

Top–down control, indirectly assessed through the inclusion of fire year and fire event as random variables in our models, included climatic conditions of the year of the event as measured by water balance. Among the four studied events, the one with more heterogeneous severity (1987) occurred at the beginning of the summer of a year with somewhat above moisture availability. In contrast, the two most severe events burned in 2014 during January in association with severe drought. The two overlapping fires that burned the area near Ñorquinco Lake had contrasting patterns of severity; the area burned at high severity in association with greater drought in 2014 was much greater than the area burned in 1987 under less extreme fire weather (Fig. 1). This is consistent with many reports that extreme weather conditions (i.e., drought) diminish the influence of local drivers of burn severity (Bradstock et al. 2010; Dillon et al. 2011; Birch et al. 2015; Fang et al. 2015; Povak et al. 2020). However, it is also possible that the higher severity in 2014 was a consequence of a fire-vegetation feedback induced by a previous event analogous to positive feedbacks of antecedent fires in resprouting *Eucalyptus* forests in southeast Australia (Collins et al. 2021). The presence of highly flammable *N. antarctica* shrublands within the fire perimeter is consistent with that interpretation (Mermoz et al. 2005).

In synthesis, our results suggest that burn severity in *A. araucana*-dominated vegetation is driven by individual tree features that influence tree mortality at a fine-scale and also is strongly driven by vegetation type and terrain-related factors at a landscape scale. Canopy connectivity, tree size, and species are strong predictors of the probability of death of individual trees. As tree size of the fire-resistant *A. araucana* increases, probability of fire-induced death declines. Tree-level attributes scale up to influence fire severity at the plot scale but were only weakly predictive possibly due to the absence of quantitative data on understory fuel loads. These individual tree and plot-scale drivers in combination with terrain-related drivers shape fire severity across a landscape scale. Climatic and weather conditions associated with the four fire events were strong drivers of fire severity at the landscape scale. Overall, our study highlights the importance of considering bottom–up drivers of fire severity operating across a range of spatial scales from the individual tree- to plot-level to the landscape scale, although their effects are contingent on top-down climatic and weather conditions. Moreover, our findings are consistent with the expectation for Andean-Patagonia forests under continued climate warming that pyrophobic forests are becoming increasingly susceptible to burning and are being replaced by more pyrophytic vegetation dominated by tall shrubs. These changes in vegetation cover would reduce the extent of this forest type and increase overall landscape flammability, leading to a prevalence of more severe fires in the future (Veblen et al. 2008; Kitzberger et al. 2016; Landesmann et al. 2021). While the focus of the current study has been on burn severity, further studies should examine the links between fire legacies and post-fire recovery to better assess the resilience of these forests under an altered fire regime.

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**Data availability** The datasets generated and analyzed during the current study are available from the corresponding author based on appropriate request.

**Code availability** Not applicable.

**Declarations**

**Conflict of interest** The authors have no conflicts of interest to declare in this work.

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