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Fire-driven alternative vegetation states across the temperate Andes

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The theory of alternative stable states, as applied to terrestrial ecosystems, suggests that under common environmental conditions, different vegetation types may remain stable by contrasting feedback processes. In the temperate Andes, forests and shrublands of *Nothofagus* species have been proposed as fire-driven alternative vegetation states (AVS): while high fire frequency would promote the stability of pyrophilic shrublands, the absence of fires would stabilize pyrophobic forests. However, to confirm this hypothesis, it must be demonstrated that fire-vegetation feedbacks occur under the same environmental conditions. We aimed to (i) identify to what extent *Nothofagus* forests and shrublands occur in the same environmental conditions across the temperate Andes and (ii) to understand how the fire regime explains the distribution patterns of these states. We used global environmental databases and local fire data to (i) estimate the environmental niche overlap of forests and shrublands and (ii) to obtain an indicator of the fire activity at micro-basin scale (percentage of the cumulative burned area (PBA); the higher the PBA the higher the fire activity). The environmental niches of forests and shrublands overlapped by more than 70%. Shrublands become more frequent as PBA increases, suggesting that stabilizing fire-vegetation feedbacks promote their persistence. Our results provide broad-scale evidence of fire-driven AVS beyond the tropics.

This article is part of the theme issue 'Novel fire regimes under climate changes and human influences: impacts, ecosystem responses and feedbacks'.

1. Introduction

The theory of alternative stable states proposes that a system can maintain different stable equilibrium states under the same external condition(s) [1]. In those systems, a complex suite of stabilizing (or negative) feedbacks promote stability of a given state. Stochastic events (disturbances; cf. [2]) may destabilize the system, inducing amplifying (positive) feedbacks that reinforce the effects of the disturbance and may produce a shift to an alternative state [3,4]. The alternative stable states theory has been applied to terrestrial ecosystems as a plausible explanation for the occurrence of strikingly different vegetation types (i.e. alternative vegetation states (AVS)) under the same environmental conditions [5,6]. Different processes have been proposed as drivers of change from one vegetation type to another (e.g. freezing, drought and hurricanes), with fire being the most widely studied, as changes in fire regime may switch between amplifying and stabilizing feedbacks [6].

The pioneering work on what we currently call fire-driven AVS was framed in California and Tasmania [7,8]. Since then, most research on AVS has been performed in tropical ecosystems and tropical forest–savanna mosaics have become the paradigm of fire-driven AVS [6]. These vegetation types can develop in the same environment yet are characterized by functionally distinctive community assemblages [9–12]. Contrasting fire regimes confer stability to both states through different feedback processes [6,13]: in savannas, shade-intolerant, flammable grasses promote frequent fires, thereby favouring the dominance and persistence of these fire-adapted species; in forests, the closed canopy of fire-sensitive trees provide shade that inhibits flammable grasses and maintains conditions that preclude fires (high moisture and low wind). Under extreme weather conditions, severe fires percolate into forests, inducing a shift to an open state [14,15]; conversely, long fire-free intervals permit the establishment of trees in the savanna and ultimately the development of a closed forest [16]. In the last decades, the evidence supporting fire-driven AVS beyond the tropics is growing [6], with some examples in temperate ecosystems of Australia, New Zealand [17–19] and South America [20,21]. Temperate ecosystems are typically characterized by a drought-limited fire regime, with high fuel loads that remain wet for much of the year due to high annual rainfall and low evaporative demand [22,23]. However, a rare dry period can potentially drive the forest to a different stable state. Because these processes occur at slower rates than in tropical ecosystems [24], they are more difficult to depict.

The temperate forests of southern South America represent the most extensive regions of temperate forests in the southern hemisphere [25,26], with widespread mosaics of vegetation dominated by tree species of the genus *Nothofagus* [27,28]. In this region, subalpine *Nothofagus pumilio* forests and *Nothofagus antarctica* shrublands are two of the most common vegetation types along 18° of latitude in Chile and Argentina. The established idea is that *N. antarctica* shrublands develop under the most harsh conditions, like xeric sites, poor soils and depressions subjected to cold air drainage or waterlogging [28]. In contrast, *N. pumilio* forests have been associated with more mesic sites, with fertile, well-drained and developed soils [28,29]. However, the differences in the environmental requirements of both formations have not been systematically addressed. On the eastern side of the Andean Patagonia, remarkable field studies have led to the proposal of fire regime as another modulator of the distribution patterns of both vegetation types. *Nothofagus pumilio* forest are fire-sensitive due to the lack fire-persistence traits of the dominant species, such as resprouting ability, thick bark or fire-resistant seed banks [24]. These pyrophobic forests rarely burn, because the moist, cool and shaded conditions generate a low flammable environment [20,30]. In addition, both the scarcity of dead fine fuels and the vertical discontinuity between the understory and the canopy limit fire propagation [20,21,31]. Under extreme climatic events, high-severity fires can burn the forests, promoting the transition to shrublands [32–34]. Shrublands of the resprouter *N. antarctica* are fire-resilient, due to the high post-fire resprouting capacity of this species. These pyrophilic shrublands burn readily because the open canopy promotes dry micro-environmental conditions, and there is vertical continuity of highly flammable fine fuels [20,21,33,35]. Taken together, all of this background suggests that different fire-vegetation feedbacks would confer stability to *N. pumilio* forests and *N. antarctica* shrublands.

The existence of vegetation-fire feedbacks alone cannot be considered unequivocal evidence of AVS [36]. By definition, alternative states must be able to develop and remain stable in a site under given environmental conditions [1]. Given the difficulty of demonstrating state switches in a given site in long-lived woody plants, spatial analyses emerge as a valuable tool to detect AVS [6,10,37]. Local evidence suggests that *N. pumilio* forests and *N. antarctica* shrublands coexist in the same environment, at least in the eastern side of the Southern Andes, which is dry and, thus, fire-prone [27,38]. Here, we ask about the generality of this process across a wide range of environmental conditions, from meso-Mediterranean to subantarctic environments, spanning a broad latitudinal range (18°, which is about the distance between Barcelona and Oslo). Specifically, we aimed to evaluate the hypothesis that *N. pumilio* forests and *N. antarctica* shrublands are AVS maintained by different fire regimes and that this occurs over a wide geographical and environmental range across the temperate Andes. We predict that, across the study area, different fire regimes explain the distribution patterns of both states under the same environment, with low flammable forests being more common in areas with less fires, while flammable shrublands dominate sites with high fire activity. Finding evidence for this hypothesis would support the idea that fire and AVS are key mechanisms in understanding vegetation patterns across large areas of South America.

2. Methods

(a) Study area

The study was conducted in the western Andes (36°–54° S), covering most of the distribution of *N. pumilio* forests and *N. antarctica* shrublands in Chile (figure 1). Only the western (Chilean) distribution of these species was considered because it is where detailed vegetation and wildfire information are available. In this area, it is possible to find mosaics of coexisting *N. pumilio* forests and *N. antarctica* shrublands under similar environmental conditions and separated by abrupt boundaries (figure 2). The climate is predominantly temperate, with Mediterranean influence in the northernmost end, which becomes increasingly rainy and colder towards the south, giving way to a subantarctic climate south of 43° S [39,40]. Soils originate from volcanic ashes, are deficient in elemental nutrients like phosphorus and have high levels of toxic aluminium [41].

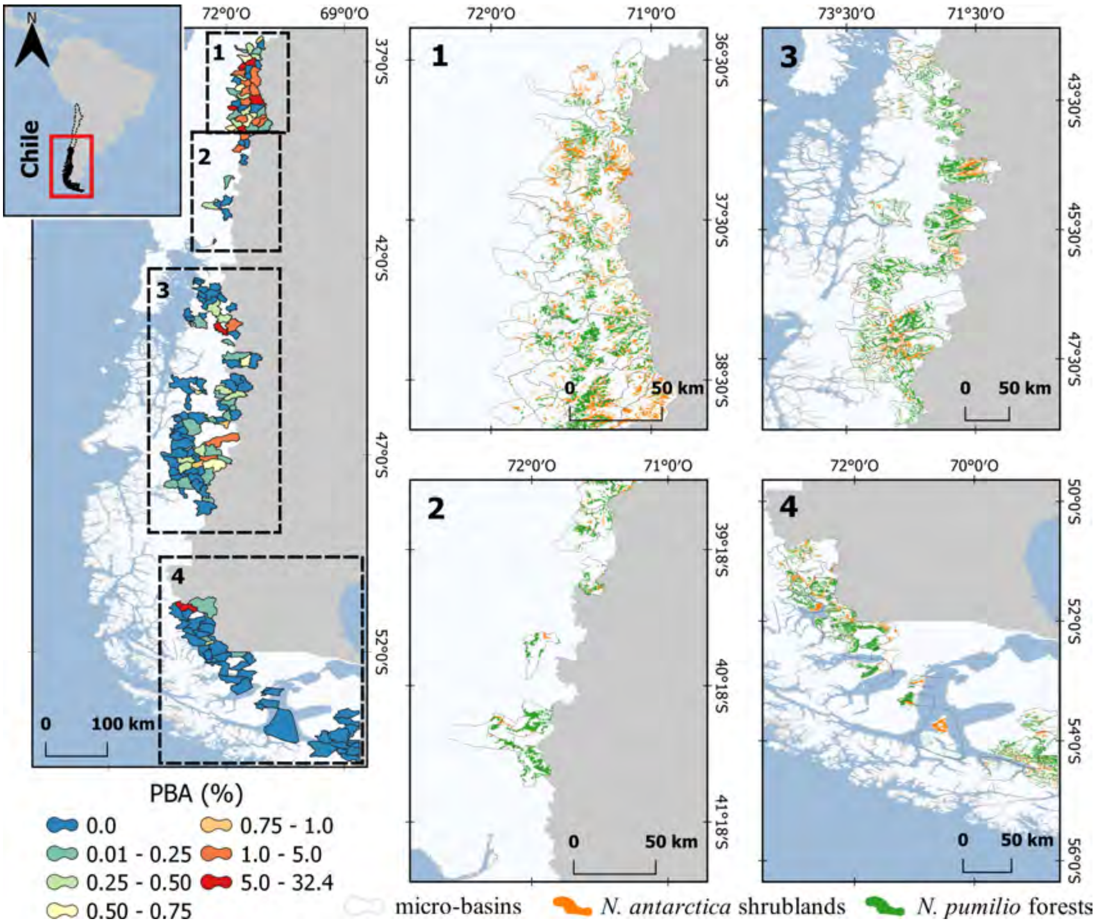

Figure 1. Map of the study area. The left panel shows the micro-basins, classified according to the percentage of the cumulative burned area (PBA) during the study period (1985–2018). The four panels on the right show the *N. pumilio* forests (green) and *N. antarctica* shrublands (orange) within the micro-basins (grey contours). The number of each of these four panels corresponds to those of the left panel. The scale of each panel varies to enhance visualization.

(b) Study sites

To identify patches of *N. pumilio* forest and *N. antarctica* shrubland, we used the national vegetation survey maps of the Chilean National Forest Service (CONAF; minimum mapping unit of 0.5 ha) [42]. We define *N. pumilio* forest and *N. antarctica* shrubland as any homogeneous patch with at least 25% vegetation cover dominated by the corresponding *Nothofagus* species.

We characterized the fire activity at the micro-basin level using the micro-basins map from the Chilean Water General Directorate [43]. We selected those micro-basins where both *N. pumilio* forests and *N. antarctica* shrublands were present (i.e. both covering at least 1% of the micro-basin's area). These micro-basins range between 2926 and 351 103 ha (48 197 ha on average). To obtain an indicator of the fire activity for each micro-basin, we used the wildfire database provided by the CONAF. This database records the ignition location and burned area, considering different land covers (e.g. forest, shrublands, forest plantations and others) for all fires larger than 0.01 ha during the 1985–2018 period. Note that the database does not specify the dominant species for each land cover polygon, except in the case of forest plantations. Satellite burned area products (e.g. MODIS Burned Area) were not considered because of the short time window of data available limits their use in our system, with relatively long fire return intervals [44,45]. The fire activity of each micro-basin was defined as the percentage of the cumulative burned area (PBA) of the micro-basin relative to its burnable area (hereafter PBA; figure 1). The cumulative burned area of each micro-basin was obtained as the sum of the burned area in forests and shrublands (regardless of the species), considering those fires starting in the micro-basin. We excluded fires burning less than 10 ha, as they are often confounded with agricultural burning [46], representing only 2% of the cumulative burned area in our study area. The burnable area of each micro-basin was measured as the total surface area of forests and shrublands in the micro-basin (also regardless of the dominant species), obtained from the national vegetation survey maps.

We used global gridded databases to characterize the climatic, edaphic and topographic conditions in which *N. pumilio* forests and *N. antarctica* shrublands develop. To achieve this, a stratified random sampling was carried out. First, micro-basins were categorized as 'NoFire' (PBA = 0%), 'LowFire' ($0 < \text{PBA} \leq \text{mean}$) and 'HighFire' ($\text{PBA} > \text{mean}$), where the mean refers to the average of PBA for the micro-basin with fire occurrence. Then, 10 000 random points (hereafter, observations) were distributed proportionally across the area occupied by forests and shrublands in each fire category, with a minimum distance of 1 km between each point (electronic supplementary material, table S1). For each point, we extracted a set of environmental variables that characterize *N. pumilio* and *N. antarctica* auto-ecology (table 1; see §1 for details), avoiding redundant variables to prevent multicollinearity problems [51]. We obtained the minimum monthly climate moisture index (MImin; table 1) and the number of growing degree days above 5°C (NGD5), with a spatial resolution of 1 km from the CHELSA dataset [47]. Edaphic variables

Figure 2. Abrupt boundary between *N. antarctica* shrubland (left) and *N. pumilio* forest (right) in Villarrica National Park (39°35′ S–71°31′ W). Photo: Diego P. Ramírez.

Table 1. Description and data source of the variables used to define the environmental niche of forests and shrublands.

variable	code	description
minimum monthly climate moisture index (kg m^{-2} $month^{-1}$)[a]	MImin	difference between precipitation and monthly potential evapotranspiration of the month with the highest precipitation deficit
number of growing degree days[a]	NGD5	number of days per year at which the main daily air temperature was >5°C
soil pH[b]	pH	edaphic pH in H_20 (100–200 cm depth)
soil cation exchange capacity ($mmol^+$ kg^{-1})[b]	CEC	cation exchange capacity of the fine soil fraction (100–200 cm depth)
soil organic carbon (dg kg^{-1})[b]	Corg	edaphic organic carbon concentration (100–200 cm depth)
soil volumetric water content at −33 kPa (%)[c]	SWC	percentage of the volume of water retained by a volume of soil at field capacity (138–229 cm depth)
elevation (m a.s.l.)[d]	elev	elevation above sea level according to the ALOS-PALSAR satellite DEM
terrain ruggedness index (m)[d]	TRI	sum change in elevation between a grid cell and its eight neighbour cells. The higher the index, the higher the heterogeneity

[a] CHELSA [47].

[b] SoilGrids250 [48].

[c] Global Soil Dataset for Earth System Modelling [49].

[d] IDE [50].

were obtained from SoilGrids [48] and Global Soil Dataset [49], at resolution of 0.25 and 1 km, respectively. Specifically, we obtained the soil pH (in H_2O), soil cation exchange capacity (at pH 7; CEC) and the soil organic carbon (Corg) from SoilGrids, as well as the soil volumetric water content at −33 kPa (SWC) from Global Soil Dataset. Edaphic layers were obtained at the greatest available depth, in order to characterize soil properties that depend on bedrock rather than vegetation (table 1). Finally, we obtained the elevation using the digital elevation model (DEM) ALOS-PALSAR (Advanced Land Observing Satellite Phased Array L-band Synthetic Aperture Radar; spatial resolution of 12.5 m) generated by the Japan Aerospace Exploration Agency and available on the Centre of Information of Natural Resources of the Chilean Ministry of Agriculture [50]. Using the DEM, we obtained the terrain ruggedness index (TRI) [52]. The correlation between the predictor variables did not exceed an $|r| > 0.72$ (electronic supplementary material, figure S1), which is very close to the recommended threshold for this type of analysis [51]. The spatial data processing was performed in QGIS 3.28 [53]. Notice that, to avoid the loss of fine-grained resolution and to obtain a more reliable geographical projection of the ecological niches, we discarded the upscaling of the finer data.

(c) Environmental overlap between forests and shrublands

To estimate the overlap between the environmental conditions of *N. pumilio* forests and *N. antarctica* shrublands, we first model the ecological niche for each vegetation type. With this aim, we summarized the environmental variables into three orthogonal axes of variation using a principal component analysis (PCA). Variables were centred and scaled prior to the analysis. The ecological niches were computed using an ellipsoid envelope model based on the *minimum volume ellipsoid* method. The ellipsoids were delimited to include the 95% of the observations of each vegetation type, thus excluding marginal environmental conditions that could overestimate the ecological niche [54]. Then, to quantify the niche overlap, we first defined the three-dimensional space enclosing all the observations used to create the ellipsoids. Within this volume, 1 000 000 random points were generated, and the points within each ellipsoid and in the overlap zone were recorded. Iterating this process 100 times, we assessed whether the niche overlap was significantly greater than zero using a one-tailed Student's *t*-test. Additionally, the principal components (PCs) scores of the PCA (PC1, PC2 and PC3) of the observations used for the niche modelling were compared between non-overlapping *N. pumilio* forests, non-overlapping *N. antarctica* shrublands and the overlap zone using a one-way ANOVA based on trimmed means (with a 20% trimming level), followed by a corresponding *post hoc* test to compare between groups. This approach was chosen because the data were non-normal and heteroscedastic.

(d) Distribution patterns of forests and shrublands along the fire gradient

To infer whether fire regimes promote the stability of *N. pumilio* forests and *N. antarctica* shrublands growing under equivalent environmental conditions, we compared their occurrence along the gradient of PBA (see above) considering exclusively those areas where the niche overlapping conditions are present. For this, we first projected the niche overlap zone onto the geographical space of the study area by creating a raster layer for each of the three PCs of the PCA used to delimit the ellipsoids. Using the three PCA layers, we generated a suitability map for each vegetation type. The two suitability maps were intersected to identify where the niche overlapping conditions are present and thus the areas where *N. pumilio* forests and *N. antarctica* shrublands are AVS. Inside this geographical area, we recorded the vegetation type and micro-basin PBA of 10 000 random points. Then, the non-parametric Kolmogorov–Smirnov test was conducted to assess whether the frequency distribution of PBA differs between forests and shrublands. To identify where parts of the PBA gradient differ between the two vegetation types, we compared the percentiles of the two frequency distributions using 95% confidence intervals estimated by bootstrap and controlling the type I error with the Hochberg's method.

All analyses were performed in R, using packages *ellipsenm*, *SIBER* and *WRS2* [55–58].

3. Results

(a) Spatial extension of the study area

We selected 177 micro-basins covering 1 475 919 ha of *N. pumilio* forests and 513 416 ha of *N. antarctica* shrublands, between the 36° and 55° S (figure 1 and electronic supplementary material, table S1). Overall, the fire activity in the study area was low, with PBA values ranging from 0 to 32.4% (figure 1). Most micro-basins (102) were categorized as 'NoFire' (0% PBA). The average PBA of the 75 micro-basins with PBA > 0 was 2.3%, which was the threshold used to categorize them as 'LowFire' (63) or 'HighFire' (12; electronic supplementary material, figure S2).

(b) Environmental overlap between forests and shrublands

The PCA was performed with a total of 9787 observations after discarding those with no or unreliable environmental data. The three PCs of the PCA explained 69% of the total variance. PC1 explained 34% of the variance, was negatively correlated to the moisture index and soil organic carbon and positively to the number of degree days and pH (electronic supplementary material, figure S3). PC2 and PC3 explained 22 and 13% of the variance, respectively; the former was negatively correlated to the soil water content, elevation and terrain ruggedness, whereas the latter was negatively correlated to CEC and number of degree days and positively to pH (electronic supplementary material, figure S3).

The ellipsoids of *N. pumilio* forest and *N. antarctica* shrubland were modelled with 7280 and 2507 observations, respectively (figure 3). In terms of the overlap of the niches, the ellipsoid of *N. pumilio* forest has a 77% shared volume with *N. antarctica* (t-value = 5188.9; p-value < 0.001), while the ellipsoid of *N. antarctica* shrubland shares 72% of its volume with that of *N. pumilio* (t-value = 5514.5; p-value < 0.001). PC scores of overlap and non-overlapping zones were significantly different, with differences observed in all comparisons (figure 3 and electronic supplementary material, figure S4).

(c) Distribution pattern of forests and shrublands along the fire gradient

Niche overlapping conditions are present in 173 of the 177 micro-basins. The area with such conditions extends over 1 669 320 ha, covering 84% of the study area (electronic supplementary material, figure S5). From this, 73% is currently covered by *N. pumilio* forests (1 226 860 ha) and the remaining (442 460 ha) by *N. antarctica* shrublands.

Considering only the overlapping niche areas, the PBA frequency distributions differed between forests and shrublands (D = 0.07; p-value < 0.001). Due the predominance of 'NoFire' micro-basins, the difference emerged above the 0.4 percentile and

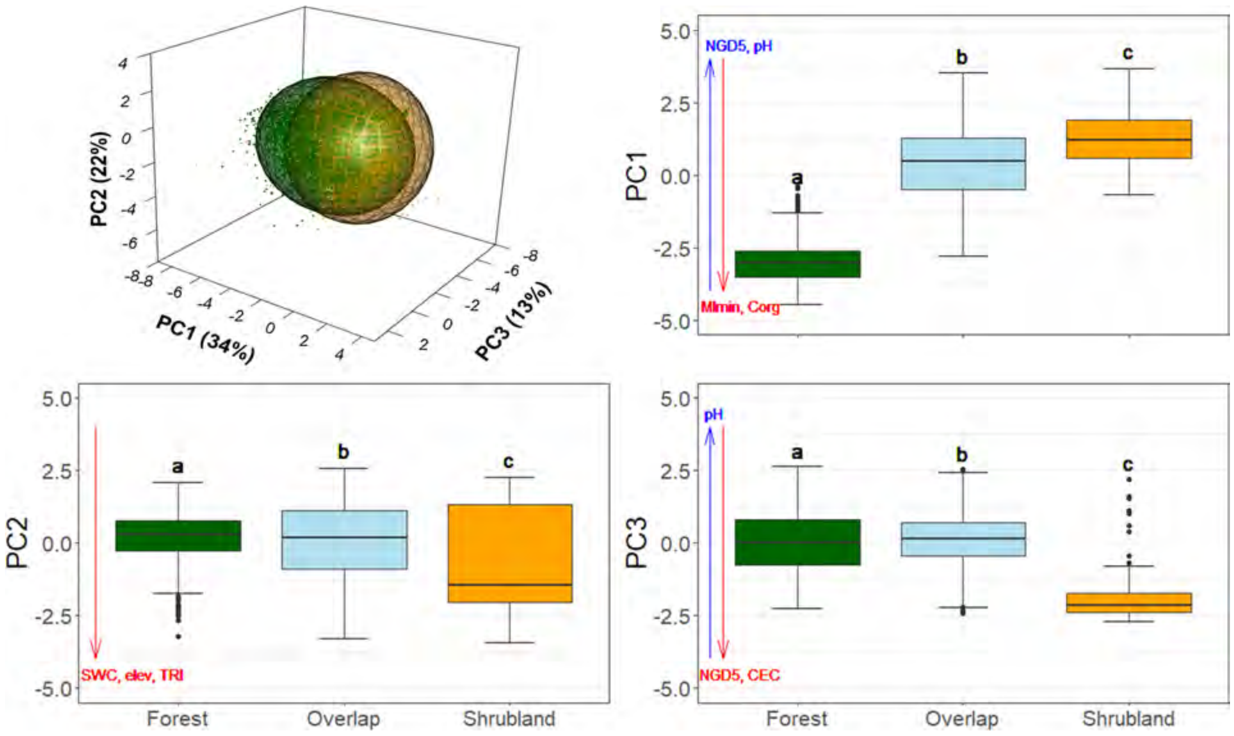

Figure 3. The top left panel represents the environmental niches of *N. pumilio* forest (green) and *N. antarctica* shrubland (orange) through ellipsoid envelopes. The environmental space corresponds to the first three PCs used for niche modelling. The bottom left and right panels show box plots of the PC scores exclusive for *N. pumilio* forests, exclusive for *N. antarctica* shrublands and for the overlapping zone of the ecological niches. The environmental variables more strongly correlated to each PC is shown in blue (positively correlated) and red (negatively correlated). Different letters between box plots indicate significant differences between the PC scores, obtained from the one-way ANOVA analysis based on trimmed means (see §2). The results of the analysis are shown in electronic supplementary material, figure S4. MImin: minimum monthly climate moisture index; NDG5: number of growing degree days >5°C; pH: soil pH; Corg: soil organic carbon; CEC: soil cation exchange capacity; SWC: soil volumetric water content; elev: elevation; TRI: terrain ruggedness index.

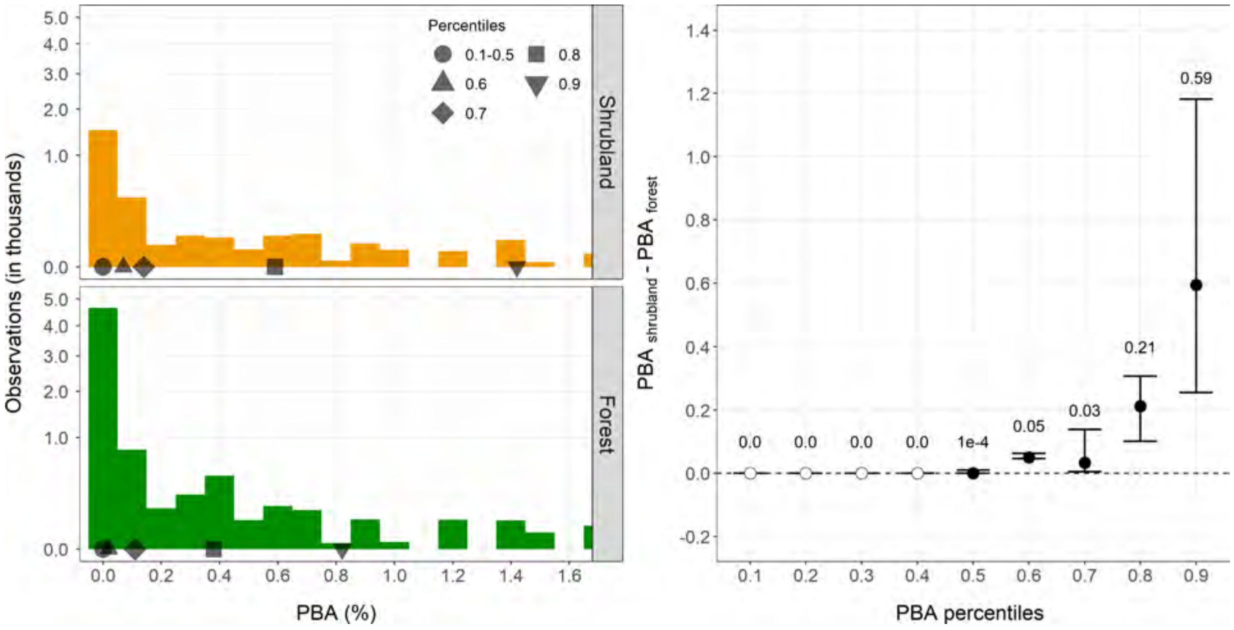

Figure 4. Left panel: frequency distribution of the PBA for the *N. pumilio* forests and the *N. antarctica* shrublands. Different symbols in the *x*-axis show the percentiles of each frequency distribution. For visualization purposes, a square root transformation was applied on the *y*-axes, and extreme values on the *x*-axis were excluded. Right panel: PBA percentile differences (± 95% bootstrapping confidence interval) between shrublands and forests. Black symbols represent significant differences (i.e. bootstrapping confidence interval does not include zero); white symbols were used otherwise. The difference between the percentiles is indicated above each point.

suggest that shrublands become more frequent than forests as the PBA increases, with more pronounced differences in the highest percentile (figure 4).

4. Discussion

Our results support the hypothesis that *N. pumilio* forests and *N. antarctica* shrublands represent fire-driven AVS across a wide geographical and environmental range. Firstly, the extensive niche overlapping of *N. pumilio* forests and *N. antarctica* shrublands provides strong evidence that shrublands occur in conditions suitable for forests and *vice versa* (figure 3), thus supporting the AVS hypothesis [1]. Secondly, in micro-basins with higher PBA, the niche overlapping areas are preferably occupied by *N. antarctica* shrublands, supporting the hypothesis that those shrublands are maintained by fire (figure 4) [20].

Our results challenge the traditional notion that the *N. antarctica* shrublands can only thrive in conditions too harsh for the establishment of *N. pumilio* forests [28]. In fact, the ecological niche of forests and shrublands overlaps across diverse climatic, edaphic and topographic variables (figure 3 and electronic supplementary material, figure S6) that occur over a wide latitudinal range, from meso-Mediterranean (36° S) to subantarctic (54° S) ecosystems (electronic supplementary material, figure S5). Although the three PCA axes used for the reconstruction of ecological niches captured an important part of the environmental variability of the study area, there is a part of this variability that was not considered (31%). Therefore, we cannot rule out a possible overestimation of the niche overlap. However, it is worth mentioning that the environmental conditions of the non-overlapping *N. antarctica* shrublands (i.e. the part of the niche that does not overlap with that of *N. pumilio* forests) are consistent with the restrictive conditions traditionally associated with this vegetation type, that is, on flat terrains with soils that are poor in organic carbon and relatively high pH in warmer and drier sites (higher PC1 values), or on undulating terrain at altitude with waterlogged soils (lower PC2 values; figure 3 and electronic supplementary material, figures S4 and S6) [28]. Thus, our modelled ecological niches reflect both the shared conditions between *Nothofagus* forests and shrublands, but also the conditions exclusive to *N. pumilio* and *N. antarctica*.

The higher frequency of *N. antarctica* shrublands compared to *N. pumilio* forests in micro-basins with high PBA is consistent with the hypothesis that fire-vegetation feedbacks promote their stability in areas where forests and shrublands represent AVS [38]. These dynamics may have been occurring for a long period as they are dominated by two contrasting woody life forms: a non-resprouting tree and a resprouting shrubby tree. It is also interesting that they are congeneric, and thus it is tempting to suggest that the AVS may have been the appropriate framework for those evolutionary divergences [59].

However, the two states were equally probable in micro-basins without fires during the studied period (percentiles 0.1–0.4 in figure 4). We argue that this is due to the long history of human-ignited fires in the region and the slow dynamics of this vegetation type. The *N. antarctica* shrublands expanded in the past due to the use of fire by native settlements and during the Euro-Chilean colonization [32,60], being a common practice until the middle of the twentieth century for agricultural purposes [61]. Therefore, fires prior to the period assessed (i.e. 1985–2018) could have promoted the establishment of shrublands in the current ‘NoFire’ micro-basins, most of them located in the southernmost areas of the study area (figure 1 and electronic supplementary material, figure S2). Both the scarcity of climatic conditions conducive to fires in these areas and the fire-suppression policies established in the country since 1980 would have prevented them from burning during the period evaluated. However, the time elapsed was not enough for the establishment of *N. pumilio*, which requires between 40 and 80 years to form forests after fires [62], explaining why this state is not dominant in micro-basins without recent fires. Field studies are needed to evaluate the presence of *N. pumilio* saplings in shrublands of ‘NoFire’ micro-basins. In any case, the fact that *N. pumilio* forests predominate throughout the study area, being a region with low fire activity (figure 1) evidences the stability of these forests in the absence of fire.

5. Conclusion

Previous studies used field approaches to demonstrate the existence of fire-vegetation feedbacks that stabilize forests and shrublands in the dry and fire-prone region of northeastern Patagonia [20,21,31,34]. Here, we have provided evidence for the existence of fire-driven AVS across the temperate Andes. Using an ecological niche modelling approach, we demonstrated that *N. pumilio* forests and *N. antarctica* shrublands can develop under the same set of environmental conditions. Additionally, our results give support for the role of fire in explaining the vegetation distribution patterns over a wide geographical and environmental range, from meso-Mediterranean to subantarctic environments spanning 18° of latitude. Therefore, we provide evidence of the importance of fire in the vegetation dynamics even under cold-wet conditions typically considered non-fire prone. Our study contributes to the understanding of the importance of fire in the vegetation dynamics of the temperate Andes and generates new evidence for the existence of fire-driven AVS beyond the tropics in South America [10,37]. Altogether, this evidence supports the key role of fire-driven AVS as a mechanism for shaping vegetation patterns at the continental scale.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data were obtained from published sources as indicated in §2. Our aggregated data are openly available from the Dryad Digital Repository [63].

Electronic supplementary material is available online [64].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors’ contributions. D.P.R.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; S.A.E.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; A.M.: data curation, investigation, methodology, writing—review and editing; J.G.P.: conceptualization, investigation, writing—review and editing; S.P.: conceptualization, formal analysis, funding acquisition, investigation, methodology, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests declaration. We declare we have no competing interests.

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References

1. Scheffer M. 2009 Alternative stable states and regime shifts in ecosystems. In *The Princeton guide to ecology*, pp. 395–406. Princeton, NJ: Princeton University Press. (doi:10.1515/9781400833023.395)
2. Rykiel EJ JR. 1985 Towards a definition of ecological disturbance. *Aust. J. Ecol*. **10**, 361–365. (doi:10.1111/j.1442-9993.1985.tb00897.x)
3. DeAngelis D, Post WM, Travis CC. 1986 *Positive feedback in natural systems*. Heidelberg, Germany: Springer Berlin. (doi:10.1007/978-3-642-82625-2)
4. Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001 Catastrophic shifts in ecosystems. *Nature* **413**, 591–596. (doi:10.1038/35098000)
5. Wilson JB, Agnew AD. 1992 Positive-feedback switches in plant communities. In *Advances in ecological research advances in ecological research volume 23* (eds M Begon, AH Fitter), pp. 263–336. London, UK: Academic Press. (doi:10.1016/s0065-2504(08)60149-x)
6. Pausas JG, Bond WJ. 2020 Alternative biome states in terrestrial ecosystems. *Trends Plant Sci*. **25**, 250–263. (doi:10.1016/j.tplants.2019.11.003)
7. Wells PV. 1962 Vegetation in relation to geological substratum and fire in the San Luis Obispo Quadrangle, California. *Ecol. Monogr*. **32**, 79–103. (doi:10.2307/1942361)
8. Jackson WD. 1968 Fire, air, water and earth—an elemental ecology of Tasmania. In *Proceedings of the Ecological Society of Australia*, vol. **3**, pp. 9–16, Canberra, Australia: Ecological Society of Australia.
9. Hirota M, Holmgren M, Van Nes EH, Scheffer M. 2011 Global resilience of tropical forest and savanna to critical transitions. *Science* **334**, 232–235. (doi:10.1126/science.1210657)
10. Staver AC, Archibald S, Levin SA. 2011 The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**, 230–232. (doi:10.1126/science.1210465)
11. Dantas VL, Batalha MA, Pausas JG. 2013 Fire drives functional thresholds on the savanna–forest transition. *Ecology* **94**, 2454–2463. (doi:10.1890/12-1629.1)
12. Charles-Dominique T, Staver AC, Midgley GF, Bond WJ. 2015 Functional differentiation of biomes in an African savanna/forest mosaic. *South Afr. J. Bot*. **101**, 82–90. (doi:10.1016/j.sajb.2015.05.005)
13. Murphy BP, Bowman DMJS. 2012 What controls the distribution of tropical forest and savanna? *Ecol. Lett*. **15**, 748–758. (doi:10.1111/j.1461-0248.2012.01771.x)
14. Beckett H, Staver AC, Charles-Dominique T, Bond WJ. 2022 Pathways of savannization in a mesic African savanna–forest mosaic following an extreme fire. *J. Ecol*. **110**, 902–915. (doi:10.1111/1365-2745.13851)
15. Bowd EJ, McBurney L, Lindenmayer DB. 2023 The characteristics of regeneration failure and their potential to shift wet temperate forests into alternate stable states. *For. Ecol. Manag*. **529**, 120673. (doi:10.1016/j.foreco.2022.120673)
16. Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC. 2012 Ecological thresholds at the savanna–forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett*. **15**, 759–768. (doi:10.1111/j.1461-0248.2012.01789.x)
17. Fletcher MS, Wood SW, Haberle SG. 2014 A fire-driven shift from forest to non-forest: evidence for alternative stable states? *Ecology* **95**, 2504–2513. (doi:10.1890/12-1766.1)
18. Bowman DMJS, Perry GLW. 2017 Soil or fire: what causes treeless sedgelands in Tasmanian wet forests? *Plant Soil* **420**, 1–18. (doi:10.1007/s11104-017-3386-7)
19. Fairman TA, Nitschke CR, Bennett LT. 2015 Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *Int. J. Wildland Fire* **25**, 831–848. (doi:10.1071/wf15010)
20. Paritsis J, Veblen TT, Holz A. 2015 Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. *J. Veg. Sci*. **26**, 89–101. (doi:10.1111/jvs.12225)
21. Tiribelli F, Kitzberger T, Morales JM. 2018 Changes in vegetation structure and fuel characteristics along post-fire succession promote alternative stable states and positive fire–vegetation feedbacks. *J. Veg. Sci*. **29**, 147–156. (doi:10.1111/jvs.12620)
22. Holz A, Kitzberger T, Paritsis J, Veblen TT. 2012 Ecological and climatic controls of modern wildfire activity patterns across southwestern South America. *Ecosphere* **3**, 1–25. (doi:10.1890/es12-00234.1)
23. Pausas JG, Ribeiro E. 2013 The global fire–productivity relationship. *Glob. Ecol. Biogeogr*. **22**, 728–736. (doi:10.1111/geb.12043)
24. Pausas JG. 2015 Alternative fire-driven vegetation states. *J. Veg. Sci*. **26**, 4–6. (doi:10.1111/jvs.12237)
25. Olson DM *et al*. 2001 Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* **51**, 933. (doi:10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2)
26. Veblen TT. 2007 Temperate forests of the southern Andean region. In *The physical geography of South America* (eds TT Veblen, KR Young, AR Orme), pp. 217–231. Oxford, UK: Oxford University Press. (doi:10.1093/oso/9780195313413.003.0021)
27. Veblen TT, Kitzberger T, Lara A. 1992 Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *J. Veg. Sci*. **3**, 507–520. (doi:10.2307/3235807)
28. Veblen TT, Donoso C, Kitzberger T, Rebertus AJ. 1996 Ecology of southern Chilean and Argentinean Nothofagus forests. In *The ecology and biogeography of Nothofagus forests* (eds TT Veblen, RS Hill, J Read), pp. 293–353. Yale, CT: Yale University Press.
29. Veblen TT, Schlegel FM. 1982 Reseña ecologica de los bosques del sur de Chile. *Bosque* **4**, 73–115. (doi:10.4206/bosque.1982.v4n2-03)
30. Mermoz M, Kitzberger T, Veblen TT. 2005 Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. *Ecology* **86**, 2705–2715. (doi:10.1890/04-1850)
31. Blackhall M, Raffaele E, Paritsis J, Tiribelli F, Morales JM, Kitzberger T, Gowda JH, Veblen TT. 2017 Effects of biological legacies and herbivory on fuels and flammability traits: a long-term experimental study of alternative stable states. *J. Ecol*. **105**, 1309–1322. (doi:10.1111/1365-2745.12796)
32. Veblen TT, Lorenz DC. 1988 Recent vegetation changes along the forest/steppe ecotone of northern Patagonia. *Ann. Assoc. Am. Geogr*. **78**, 93–111. (doi:10.1111/j.1467-8306.1988.tb00193.x)
33. Veblen TT, Kitzberger T, Raffaele E, Mermoz M, González ME, Sibold JS, Holz A. 2008 The historical range of variability of fires in the Andean–Patagonian *Nothofagus* forest region. *Int. J. Wildland Fire* **17**, 724. (doi:10.1071/wf07152)
34. Landesmann JB, Tiribelli F, Paritsis J, Veblen TT, Kitzberger T. 2021 Increased fire severity triggers positive feedbacks of greater vegetation flammability and favors plant community-type conversions. *J. Veg. Sci*. **32**, e12936. (doi:10.1111/jvs.12936)

35. Blackhall M, Raffaele E. 2019 Flammability of Patagonian invaders and natives: when exotic plant species affect live fine fuel ignitability in wildland–urban interfaces. *Landsc. Urban Plan*. **189**, 1–10. (doi:10.1016/j.landurbplan.2019.04.002)

36. Kéfi S, Holmgren M, Scheffer M. 2016 When can positive interactions cause alternative stable states in ecosystems? *Funct. Ecol*. **30**, 88–97. (doi:10.1111/1365-2435.12601)

37. Dantas V de L, Hirota M, Oliveira RS, Pausas JG. 2016 Disturbance maintains alternative biome states. *Ecol. Lett*. **19**, 12–19. (doi:10.1111/ele.12537)

38. Kitzberger T, Perry G, Paritsis J, Gowda J, Tepley A, Holz A, Veblen T. 2016 Fire–vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in Southern South America and New Zealand. *N. Z. J. Bot*. **54**, 247–272. (doi:10.1080/0028825x.2016.1151903)

39. Di Castri F, Hajek E. 1976 *Bioclimatología de chile*. Santiago, Chile: Vicerrectoría Académica Universidad Católica de Chile.

40. Sarricolea P, Herrera-Ossandon M, Meseguer-Ruiz Ó. 2017 Climatic regionalisation of continental Chile. *J. Maps* **13**, 66–73. (doi:10.1080/17445647.2016.1259592)

41. Casanova M, Salazar O, Seguel O, Luzio W. 2013 *The soils of chile*. Dordrecht, The Netherlands: Springer Dordrecht. (doi:10.1007/978-94-007-5949-7)

42. Corporación Nacional Forestal (CONAF). 2021 Catastro de los Recursos Vegetacionales Nativos de Chile al año. See https://sit.conaf.cl/varios/Catastros_Recursos_Vegetacionales_Nativos_de_Chile_Nov2021.pdf.

43. Dirección General de Aguas (DGA). 2014 Inventario de Cuencas, Subcuencas, y Subsubcuencas de Chile. See https://snia.mop.gob.cl/sad/CUH5690.pdf.

44. González ME, Veblen TT, Sibold JS. 2005 Fire history of *Araucaria–Nothofagus* forests in Villarrica National Park, Chile. *J. Biogeogr*. **32**, 1187–1202. (doi:10.1111/j.1365-2699.2005.01262.x)

45. González ME, Muñoz AA, González-Reyes Á, Christie DA, Sibold J. 2020 Fire history in Andean *Araucaria–Nothofagus* forests: coupled influences of past human land-use and climate on fire regimes in north-west Patagonia. *Int. J. Wildland Fire* **29**, 649. (doi:10.1071/wf19174)

46. Miranda A *et al*. 2022 The landscape fire scars database: mapping historical burned area and fire severity in Chile. *Earth Syst. Sci. Data* **14**, 3599–3613. (doi:10.5194/essd-14-3599-2022)

47. Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M. 2017 Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4** 1-20. . (doi:10.1038/sdata.2017.122)

48. Hengl T *et al*. 2017 SoilGrids250m: global gridded soil information based on machine learning. *PLoS One* **12**, e0169748. (doi:10.1371/journal.pone.0169748)

49. Shangguan W, Dai Y, Duan Q, Liu B, Yuan H. 2014 A global soil data set for earth system modeling. *J. Adv. Model. Earth Syst*. **6**, 249–263. (doi:10.1002/2013ms000293)

50. IDE. 2016 Catalogo Nacional de Información Geoespacial. Geoportal de Chile. See https://www.geoportal.cl/geoportal/catalog.

51. Dormann CF *et al*. 2013 Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46. (doi:10.1111/j.1600-0587.2012.07348.x)

52. Riley SJ, DeGloria SD, Elliot R. 1999 Index that quantifies topographic heterogeneity. *Intermt. J. Sci*. **5**, 23–27.

53. QGIS.org. 2024 *QGIS Geographic Information System*. QGIS Association. See http://www.qgis.org.

54. Soley-Guardia M, Radosavljevic A, Rivera JL, Anderson RP. 2014 The effect of spatially marginal localities in modelling species niches and distributions. *J. Biogeogr*. **41**, 1390–1401. (doi:10.1111/jbi.12297)

55. R Core Team. 2023 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.

56. Cobos M, Osorio-Olvera L, Soberon J, Peterson A, Barve V, Barve N. 2022 ellipsenm: ecological Niche's characterizations using ellipsoids. R package version 0.3.4. See https://github.com/marlonecobos/ellipsenm.

57. Jackson A, Parnell A. 2015 SIBER: stable isotope bayesian ellipses in R. R package version 2.1.7. See https://cran.r-project.org/web/packages/SIBER/index.html.

58. Mair P, Wilcox R. 2020 Robust statistical methods in R using the WRS2 package. *Behav. Res. Methods* **52**, 464–488. (doi:10.3758/s13428-019-01246-w)

59. Pausas JG, Bond WJ. 2022 Feedbacks in ecology and evolution. *Trends Ecol. Evol*. **37**, 637–644. (doi:10.1016/j.tree.2022.03.008)

60. Heusser CJ. 1994 Paleoindians and fire during the late Quaternary in southern South America. *Rev. Chil. De Hist. Nat*. **67**, 435–443.

61. Martinic M. 2005 *De la Trapananda al Aysén: una mirada reflexiva sobre el acontecer de la Región de Aysén desde la prehistoria hasta nuestros días*. Santiago, Chile: Pehuén Editores.

62. González ME, Veblen TT, Sibold JS. 2010 Influence of fire severity on stand development of *Araucaria araucana–Nothofagus pumilio* stands in the Andean cordillera of south-central Chile. *Austral Ecol*. **35**, 597–615. (doi:10.1111/j.1442-9993.2009.02064.x)

63. Ramírez DP, Paula S, Estay S, Pausas G, Miranda A. Fire-driven alternative vegetation states across the temperate Andes. Dryad Digital Repository. ()

64. Ramírez DP, Estay S, Miranda A, Pausas J, Paula S. 2025 Supplementary material from: Fire-driven alternative vegetation states across the temperate Andes. Fighsare. (doi:10.6084/m9.figshare.c.7736481)