Received: 2 December 2022 | Revised: 7 July 2023 | Accepted: 29 October 2023

DOI: 10.1002/eap.2937

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Thresholds and alternative states in a Neotropical dry forest in response to fire severity

H. Raúl Peinetti[1] | **Brandon T. Bestelmeyer**[2] | **Claudia C. Chirino**[1] | **Florencia L. Vivalda**[1] | **Alicia G. Kin**[1]

[1]Facultad de Agronomía, Universidad Nacional de La Pampa, Santa Rosa, Argentina

[2]USDA-ARS Jornada Experimental Range, New Mexico State University, Las Cruces, New Mexico, USA

Correspondence
H. Raúl Peinetti
Email: peinetti@agro.unlpam.edu.ar

Funding information
Agricultural Research Service, Grant/Award Number: agreement 3050-11210-009-51-N; Jornada Basin Long-Term Ecological Research Program, Grant/Award Number: DEB-1832194; Universidad Nacional de La Pampa, Grant/Award Number: POIRE 2016-18

Handling Editor: Elisabeth Huber-Sannwald

Abstract

Neotropical xerophytic forest ecosystems evolved with fires that shaped their resilience to disturbance events. However, it is unknown whether forest resilience to fires persists under a new fire regime influenced by anthropogenic disturbance and climate change. We asked whether there was evidence for a fire severity threshold causing an abrupt transition from a forest to an alternative shrub thicket state in the presence of typical postfire management. We studied a heterogeneous wildfire event to assess medium-term effects (11 years) of varying fire severity in a xerophytic Caldén forest in central Argentina. We conducted vegetation surveys in patches that were exposed to low (LFS), medium (MFS), and high (HFS) fire severities but had similar prefire woody canopy cover. Satellite images were used to quantify fire severity using a delta Normalized Burning Ratio (dNBR) and to map prefire canopy cover. Postfire total woody canopy cover was higher in low and medium than high severity patches, but the understory woody component was highest in HFS patches. The density of woody plants was over three times higher under HFS than MFS and LFS due to the contribution of small woody plants to the total density. Unlike LFS and MFS patches, the small plants in HFS patches were persistent, multistem shrubs that resulted from the resprouting of top-killed *Prosopis caldenia* trees and, more importantly, from young shrubs that probably established after the wildfire. Our results suggest that the Caldén forest is resilient to fires of low to moderate severities but not to high-severity fires. Fire severities with dNBR values > ~600 triggered an abrupt transition to a shrub thicket state. Postfire grazing and controlled-fire treatments likely contributed to shrub dominance after high-severity wildfire. Forest to shrub thicket transitions enable recurring high-severity fire events. We propose that repeated fires combined with grazing can trap the system in a shrub thicket state. Further studies are needed to determine whether the relationships between fire and vegetation structure examined in this case study represent general mechanisms of irreversible state changes across the Caldenal forest region and whether analogous threshold relationships exist in other fire-prone woodland ecosystems.

KEYWORDS
abrupt transition, fire regime, fire–vegetation feedbacks, forest resilience, normalized burn ratio index, resprouting, state change

INTRODUCTION

Abrupt transitions are becoming more common as a consequence of climate change and increasing human impacts in ecosystems (Bestelmeyer et al., 2011; Rocha et al., 2015; Turner et al., 2020). In particular, changes in the intensity, severity, and frequency of natural disturbance, such as fire, can cause abrupt and persistent vegetation state transitions (Beckage et al., 2009; Cesca et al., 2014; Suding et al., 2004). State transitions in terrestrial ecosystems typically involve large changes in vegetation characteristics occurring in the same environment, especially shifts in plant functional groups, dominant plant traits, and associated feedbacks between vegetation and ecological processes (Bestelmeyer et al., 2017). For example, spatially and temporally abrupt state transitions from savannas or open forests to shrub thickets or closed forest states, caused by changes in plant–fire feedbacks, are common global phenomena (Dantas et al., 2013; Pausas & Bond, 2020). "Thicketization" generally refers to increases in woody plant cover and density within savannas or open forests. Thicketization is a global concern because of its undesirable effects on ecosystem services including forage provision, carbon sequestration, hydrological regulation, and biodiversity maintenance (Archer et al., 2017). Thicketization is paralleled by a shift in fire regime, from predominantly low-severity surface fires associated with savanna/open forest states to high-severity crown fires characteristic of thicket states (Kitzberger et al., 2016; Peinetti et al., 2019).

Severe fire events can alter feedbacks between fire and vegetation and trigger thicketization (Blackhall et al., 2017; Knox & Clarke, 2012). The sign and strength of fire–vegetation feedbacks depends on fire characteristics, such as frequency, severity, and timing, which are linked to the ecological strategies of dominant plants (Knox & Clarke, 2012; Lawes et al., 2016). In savannas, an increase in flammability of postfire herbaceous vegetation generates a negative fire–vegetation feedback favoring savanna structure, whereas a positive feedback is produced when the flammability of pyrophytic woody plants increases after fire and favors dominance by woody plants (Tiribelli et al., 2018). Abrupt shifts in feedbacks between vegetation and flammability triggered by perturbations can precipitate transitions between savannas and closed forests (Pausas & Bond, 2020). Intense fires facilitated by exceptionally dry weather conditions can trigger a shift from fire-sensitive species to fire-tolerant species that successfully recover after fire. Weather-independent drivers, such as non-native species invasions or socioeconomic and policy changes affecting fire frequency, can also trigger vegetation state transitions (Pausas & Keeley, 2014). In open forests featuring low-severity fires, herbivory on grasses can decrease fire frequency, leading to the buildup of woody ladder fuels that lead to more intense fires. If the woody plants colonizing grazed areas are fire-tolerant resprouters, intense fire can cause the system to fall into a "fire trap" in which initial topkill leads to resprouting and repeated intense fires that prevent woody plants from reaching an adult size, forming persistent thicket states (Grady & Hoffmann, 2012; Grau & Veblen, 2000). To escape the fire trap, management actions should focus on maintaining long fire-free intervals required for saplings to grow into adult trees. In some cases, however, trees may remain trapped in a shrubby life form if multiple vigorous stems are maintained indefinitely, even in the long-term absence of fire (Grady & Hoffmann, 2012). In these cases, recovery of the open forest state requires major interventions (Peinetti et al., 2019).

Postfire management practices can inadvertently promote thicket states. For example, grazing can be used to reduce the risk of a severe fire by limiting accumulation of fuel biomass, but if grazing is maintained after the fire, it can prevent forest recovery and favor undesirable species (Blackhall et al., 2008). The nature of successful postfire interventions can also depend on fire effects (Pereira et al., 2018). Consequently, recognizing the spatial heterogeneity of ecosystem changes caused by fire is critical for postfire management (Carlson et al., 2011). For example, wildfires can create a mosaic of vegetation patches, and subsequent fires can propagate the effects of past disturbances when high-severity patches become dominated by flammable vegetation (Cansler & McKenzie, 2014). Overall, inadequate attention has been paid to postfire management of heterogeneously burned areas, in contrast to the focus on fire suppression and prevention (Moreira et al., 2012).

The open caldén forest of central Argentina is part of the Neotropical dry forest biome in which fire is known to govern ecosystem structure and function (Pennington et al., 2000). Forest dynamics reflect the life history characteristics of the dominant tree species, the endemic *Prosopis caldenia*. In the pre-European period, dispersal of *P. caldenia* was constrained by the abundance of wild herbivores that consume pods, scarify seeds, and spread the seeds through manure deposition. The introduction of large livestock herds following European colonization led to an increase in *P. caldenia* seed dispersal and recruitment, which caused a transition from an open to a closed forest state. This ecological transition was paralleled by a shift from predominantly surface fires to canopy fires of higher severity. Increasing tree density coupled to high-intensity fire has been postulated to result in a shift from open caldén forest to a shrub-dominated thicket state (Dussart et al., 2011; González-Roglich et al., 2015; Peinetti et al., 2019). Fire spread and intensity are determined by the amount and spatial distribution of fuel biomass (Whitlock et al., 2010). Thick-barked *P. caldenia* trees can survive fire events, as evidenced by records of multiple fire scars across years (Dussart et al., 2015; Medina, 2008). Burned *P. caldenia* trees can regenerate their biomass to levels similar to prefire conditions a few years after fires of moderate severity (H. R. Peinetti, July 10, 2013, personal observations). However, high-severity fires can top-kill young trees or even adults, resulting in the loss of apical dominance of the main stem and its permanent replacement by multiple stems that develop from basal buds. The resulting life form is similar to a shrub (Lacey & Johnston, 1990). Thus, fires of high severity can cause a transition from a closed forest to a shrub thicket state characterized by the dominance of the shrub life form of *P. caldenia* and other companion shrub species, with few or no trees. Thickets have been observed to persist for decades (Dussart et al., 2011; González-Roglich et al., 2015) because a dominant plant stem cannot gather enough resources to outcompete others and become trees and because shrub life forms fuel recurring high-intensity fires. Although very slow successional recovery might occur in the absence of repeated fire, successional trends have not been observed in thicket states, and existing evidence supports the interpretation of thickets as alternative stable states (Beisner et al., 2003; Bestelmeyer et al., 2017; Peinetti et al., 2019). Thicket states are associated with reduced forage quantity and quality and are locally regarded as a severe form of land degradation (Distel, 2016; Fernández et al., 2009).

In this study, we took advantage of a large-scale, unplanned fire event to examine the effects of naturally varying fire behavior on postfire vegetation. Observational studies of natural events (natural experiments) are able to represent real-world conditions and large spatial scales that can inform management and policy when carefully contextualized (Barley & Meeuwig, 2017; Catford et al., 2022). Natural experiments complement manipulative experiments by confirming the occurrence or applicability of hypothesized cause–effect relationships in natural settings (Sagarin & Pauchard, 2010). However, natural experiments are often poorly replicated or unreplicated, with low statistical power (Eberhardt & Thomas, 1991) and a lack of control of confounding effects (Catford et al., 2022). While a limited natural experiment such as the one described in our study may not provide sufficient evidence to test the generality of an ecological relationship, it can provide local evidence for or against the existence of a relationship that has been postulated in other studies (Barley & Meeuwig, 2017). Our study is intended to provide the latter function.

In our study, we evaluated the potential for threshold relationships in the effect of fire severity on caldén forest structure. We operationally define "fire severity" as the degree of changes in aboveground vegetation and soil surface caused by fire (Keeley, 2009) and "forest structure" as tree and shrub density and canopy cover as well as the cover of perennial grasses in the understory. We quantified the relationship between fire severity and forest structure 11 years after the fire and hypothesized the existence of a fire severity threshold at which open forest resilience is lost (Johnstone et al., 2016; Twidwell et al., 2013), leading to an abrupt transition to a persistent thicket state (Peinetti et al., 2019). The identification of a fire severity threshold is a first step toward reducing the likelihood of transitions to thicket ecological states.

MATERIALS AND METHODS

Study site

The study site covers 108 ha of a caldén forest within a fenced pasture of 800 ha in a private ranch, located 38 km north of Santa Rosa, La Pampa, Argentina (36°26′46″ S and 64°40′40″ W). The landscape features a smooth inclined surface with a slope <1.5%. The climate is temperate with mean annual precipitation of 740 mm and mean annual temperature of 13.6°C. Values correspond to means of the last 40 years of daily records from a weather station of the Universidad Nacional de La Pampa located 30 km away (36°33′2″ S and 64°17′49″ W). Soil is sandy loam, and a root-restrictive, calcium carbonate hardpan occurs at depths >150 cm.

Part of the existing forest had been cleared for cropland at some point, so current vegetation corresponds to a secondary, open forest of *P. caldenia* with a maximum height of ca. 8 m and a well-developed herbaceous understory. The forest started to recover ca. 60 years ago once cropland use was discontinued. Aerial photos (1:10.000) taken in the mid-1960s show scattered small woody plants but no trees in the study area.

The fenced pasture was used for livestock grazing after cropland was abandoned. There was only one reliable water source in the east part of the paddock at a distance of ca. 2.0 km from the study site. The stocking rate of the study pasture was <0.3 animal units per ha over the last 10 years. Grazing pressure in the study area, however, may have been higher considering that much of the pasture is occupied by a degraded closed forest and animals move freely within the pasture. A wildfire event in 2006 (see below), which affected the study site but not the rest of the pasture, may have accentuated uneven grazing distribution. Controlled fires are used in the Caldenal region to increase forage quality by eliminating accumulated senescent biomass and promote resprouting of bunchgrasses (Llorens, 1995). Controlled fires were applied at the study site every 3–4 years in the last 20 years, depending upon climatic and fuel conditions, but we could not detect controlled fire occurrence in the satellite images we inspected. Controlled fires are usually 100–300 ha and occasionally reach 600 ha. These fires typically have a negligible effect on taller trees but can cause significant damage to young plants (Holmes et al., 2011). According to the owners of the study site, there was only one significant wildfire in this part of the ranch, in September 2006. We corroborated this information by visually checking for evidence of fires in the complete available series of Landsat satellite images in the area of interest, starting from 1987. We found evidence of a single fire from a Landsat image taken in 22 October 2006.

Fire severity characterization

The 2006 wildfire severity (Keeley, 2009; Lentile et al., 2006) was described using a delta normalized burn ratio (dNBR) index (Escuin et al., 2008; Miller & Thode, 2007; Snyder et al., 2005). dNBR indices were calculated as a difference between pre- and postfire normalized burn ratio (NBR) indices multiplied by 10^3 (Key & Benson, 2006). Pre- and postfire NBRs were calculated based on Landsat images of 30-m pixel resolution, taken on 13 November 2005 and 15 October 2006, that were downloaded from the US Geological Survey (USGS) Earth Explorer data portal. Images were corrected by radiometry (Chander et al., 2009; Key & Benson, 2006) and geographic position via GPS ground points using ArcGIS 10 (ESRI, Redlands, CA, USA).

Three fire severity classes were characterized that included low, moderate, and high fire severity (LFS, MFS and HFS, respectively), defined by the following ranges of dNBR values: LFS: 270–440; MFS: 440–580; and HFS: 580–760. These ranges of dNBR were based on an existing scale of dNBR values (Key & Benson, 2006) and corresponded to different effects of fires on woody vegetation observed in the field (Table 1). Fire effects are similar to those reported by Key and Benson (2006).

Vegetation surveys

The structure and composition of woody and herbaceous vegetation was sampled during the 2017–2018 growing season (September to March) in areas affected by different severities of the 2006 wildfire. Sampling was performed by doing one replication per severity class at a time to account for variation in vegetation characteristics during a growing season. Sample locations were limited to areas of the forest that had an estimated canopy cover >50% the year prior to the fire event (which included 76 ha of the 108 ha we inspected). Prefire woody canopy cover was characterized from a high-resolution (<1 m) panchromatic Digital Globe image from September 2005. Woody canopy was delineated with a Feature Analyst TM (Overwatch Textron Systems, Providence, RI, USA) in ArcGIS 10 (ESRI, Redlands, CA, USA). We followed an iterative classification procedure using available tools to correct misclassified or nondigitized features and shapes. Percentage canopy cover was determined by superimposing a delineated canopy layer onto a 30-m-pixel resolution geographic raster frame of the dNBR map. The percentage of the pixel covered by woody canopies was computed using data management tools of ArcGIS 10 (ESRI, Redlands, CA, USA). The area that corresponded to the LFS class was much smaller than that of the other classes (9.2, 32.8, and 33.9 ha, for LFS, MFS, and HFS, respectively), but the LFS areas were arranged in several clusters that facilitated sampling and analysis (Figure 1). Four sampling sites per severity class

TABLE 1 Changes observed in woody vegetation in sites impacted by fires of different severity.

Fire severity class	Dominant trees: Killed	Dominant trees: Resprouted	Dominant trees: Burned canopy	Woody understory plants that are severely burned
Low	None	None	10%–30% lower fine branches	Few
Medium	None	Rare	30%–60% lower fine and coarse branches	>50%
High	>5%	>50%	>60% all canopy	All

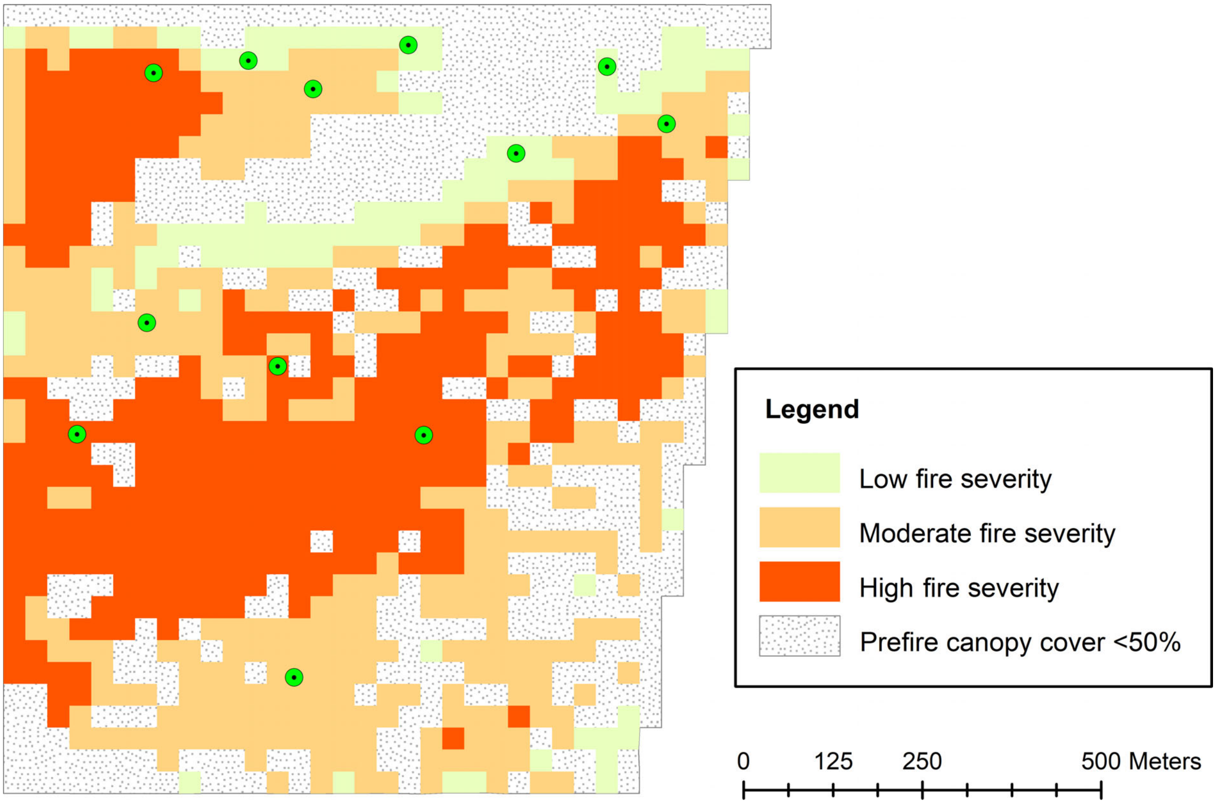

FIGURE 1 Fire severity classes and sampled points (circles) in the 108-ha study area.

were chosen from random points generated in areas assigned to each class, with a buffer zone of 100 m. At each survey site, a 30 × 20-m plot was established. The direction of a plot was set perpendicular to a slope or randomly in case of horizontal terrain.

We estimated canopy cover and density of woody plants for both postfire (2017/2018) and prefire (2005) conditions. Postfire canopy cover was estimated from the vertical projection of canopies in five 30-m transect lines placed inside each plot at regular spacing (5 m). Percentage canopy cover was measured as the ratio of the length of the summed projected canopy to the total length of the transect multiplied by 100. We differentiated tree (≥5 m) and understory woody canopies (≤3 m). Plants with a height from 3 to 5 m were considered trees if there was a spatial separation between woody and herbaceous canopy volume; if there was no separation, plants were considered understory canopy. Prefire canopy cover in each surveyed plot was estimated from the digitized woody cover area based on the 2005 satellite image. We were unable to differentiate trees from shrubs in prefire vegetation. To estimate the postfire woody density, we counted all woody plants inside each plot by species and life form, differentiating trees from shrubs. In addition, we measured the height and stem diameter of all *P. caldenia* plants. We measured the diameter of the main stem in the case of trees and the diameter of largest live or dead stem in the case of multistem plants. Estimates of prefire woody density was limited to dominant trees. Density estimates included living individuals in each plot with a diameter of basal trunk ≥30 cm and all dead or resprouted individuals with a diameter ≥25 cm, assuming a radial growth rate of 0.5 cm per year, following Dussart et al. (2015). We also measured the postfire foliar and basal cover of the herbaceous layer and litter and bare ground cover along one 30-m (middle) transect line using the line–point intercept method (Herrick et al., 2005). Canopy hits of each individual plants in the transect line were recorded by species. Canopy cover hits were grouped into four functional group categories (perennial or annual grasses or forbs).

Statistical analysis

Data used in analysis are available in Peinetti et al. (2021). The degree to which fire severity (dNBR) was spatially patchy was evaluated using Moran's *I* spatial autocorrelation (Anselin, 2003). Similarly, spatial cross-correlation was used to evaluate the association between prefire woody canopy cover and fire severity. Both variables were standardized to means equal to zero and variance equal to one. Moran's I was calculated using spatially lagged canopy cover values, which represent a weighted average of canopy cover for neighboring locations specified by a spatial weights matrix. All analyses were performed in GeoDa (Anselin, 2003) using a queen contiguity spatial matrix of order one. Next, we used orthogonal polynomial regression to test for linear, quadratic, cubic, and quartic trends in the relationship between dNBR and two responses: (1) changes in density of trees ≥25 cm and (2) density of woody plants ≤3 m after the fire. Given that these regressions produce a constant function of dNBR with no inflection points, we used piecewise regression following Ryan and Porth (2007) to estimate potential breakpoints that could be used in management decision-making. Breakpoints were estimated iteratively using the NLIN procedure (SAS Institute Inc., 2018) using code in Ryan and Porth (2007). Woody and herbaceous variables were compared between fire severity classes using one-way ANOVAs on transformed variables, which included lognormal for density and arcsin in the case of percentages. A Tukey test was used to compare means only when the ANOVA was significant at $p \leq 0.05$. Statistical analyses were conducted using Stats package in R version 4.0.2 (R Core Team, 2020).

RESULTS

Fire severity was highly heterogeneous, with clusters of low and high severity (Moran's $I = 0.82$, $p < 0.001$) (Figure 2a). Values of dNBR ranged from 200 to 760. Total woody canopy cover in 2005 was also highly heterogeneous, with pixel values ranging from 10% to 90% (Figure 2b). The spatial correspondence in patchiness between canopy cover and fire severity was significant but weak (Moran's $I = 0.363$, $p < 0.001$), which was largely driven by the low correspondence observed at medium to low dNBR values (Figure 2c).

Polynomial regressions to test for a decrease in density of trees ≥25 cm and an increase in density of woody plants ≤3 m after the fire as a function of dNBR indicated that, in both cases, the highest-order significant trends were quadratic (adjusted $R^2 = 0.69$; $F = 13.18$; df = 2.9; $p = 0.0139$ and adjusted $R^2 = 0.67$; $F = 12.17$; df = 2.9; $p = 0.0340$ respectively; Figure 3a,b). Given this result, we used piecewise regression to estimate breakpoint (threshold) values of dNBR where its relationship to tree and woody plant ≤3 m density changed. We note that, based on AIC_c, the quadratic models fit better than the piecewise regression models. For change in tree density, the AIC_c of the quadratic = 138.72 versus piecewise = 143.65. For woody plant ≤3 m density, the AIC_c of the quadratic = 205.45 versus piecewise = 208.90. In both cases, the quadratic models were more parsimonious than the piecewise models by one parameter (3 vs. 4). Nonetheless, we used the piecewise model results to provide quantitative estimates of breakpoints to inform operational thresholds for managers. For the decrease in density of trees ≥25 cm after the fire, the breakpoint model was significant and a good fit (adjusted $R^2 = 0.69$; $F = 9.07$; df = 3.8; $p = 0.0059$) with a breakpoint at dNBR = 598 ($p < 0.001$) (Figure 3a). Before the breakpoint, tree density did not vary with dNBR, but loss of trees ≥25 cm increased with dNBR after the breakpoint. We note that the extreme loss of large trees is supported by only a single plot observed at the highest dNBR measured. For the increase in postfire density of woody plants ≤3 m in height, the breakpoint model was also significant (adjusted $R^2 = 0.71$; $F = 9.84$; df = 3.8; $p = 0.046$), with dNBR = 529 (Figure 3b). Before the breakpoint, the density of smaller woody plants was insensitive to dNBR, but density increased rapidly after the breakpoint. Remarkably, both breakpoints broadly correspond to the shift from MFS to HFS classes (580) reported by Key and Benson (2006).

Prefire total woody canopy cover did not differ among fire severity classes ($F = 2.22$; df = 2.9; $p = 0.165$) (Table 2). Eleven years after the fire event, total woody canopy cover was similar in LFS and MFS and was significantly higher in both LFS and MFS than in HFS. The understory cover component of the woody canopy, however, was highest in HFS patches (Table 2 and Figure 3b). The understory canopy comprised almost half of the total canopy cover in HFS but was a minor component of MFS and LFS canopy cover. Total herbaceous foliar and basal cover did not differ among fire severity classes (Table 3). Canopy cover of annuals was similar between fire severity classes, with the exception of *Bromus catharticus*, which was markedly higher in LFS. Forbs (*Baccharis ulicina*, *Bowlesia incana*, *Gamochaeta calviceps*, *Parietaria debilis*) were well represented only in HFS. The percentage of litter was high (>70%) and bare ground cover was very low (<3%) in all fire severity classes.

The estimated prefire density of dominant trees was not statistically different between fire severity classes ($F = 1.28$; df = 2.9; $p = 0.364$) (Table 4). Eleven years after the fire event, total woody plant density of HFS sites was approximately six times higher than in both LFS and MFS, which did not differ from one another (Table 4). The high woody density in HFS was due to the relatively high contribution of understory plants (≤3 m) to the total woody plant density (93%). *Prosopis caldenia* was the dominant species in all fire severity classes (Table 4). *Condalia microphylla* density was highest in HFS. Other woody species were minor components in all fire severity classes.

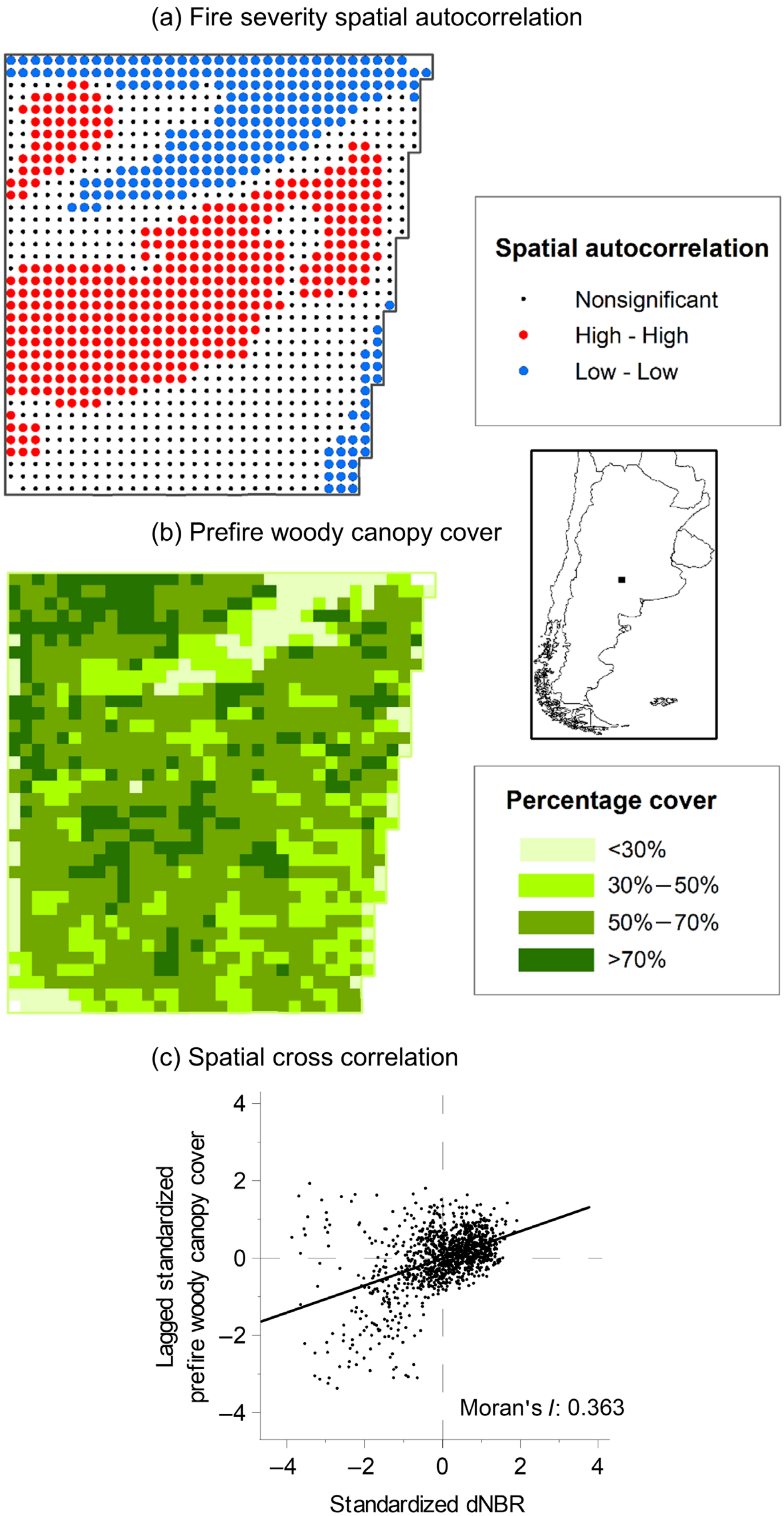

FIGURE 2 (a) Spatial autocorrelation of fire severity, (b) prefire woody canopy cover, and (c) spatial cross correlation of prefire woody canopy cover and fire severity on standardized variables in the 108-ha study site. Fire severity was described using a delta normalized burn ratio index (dNBR).

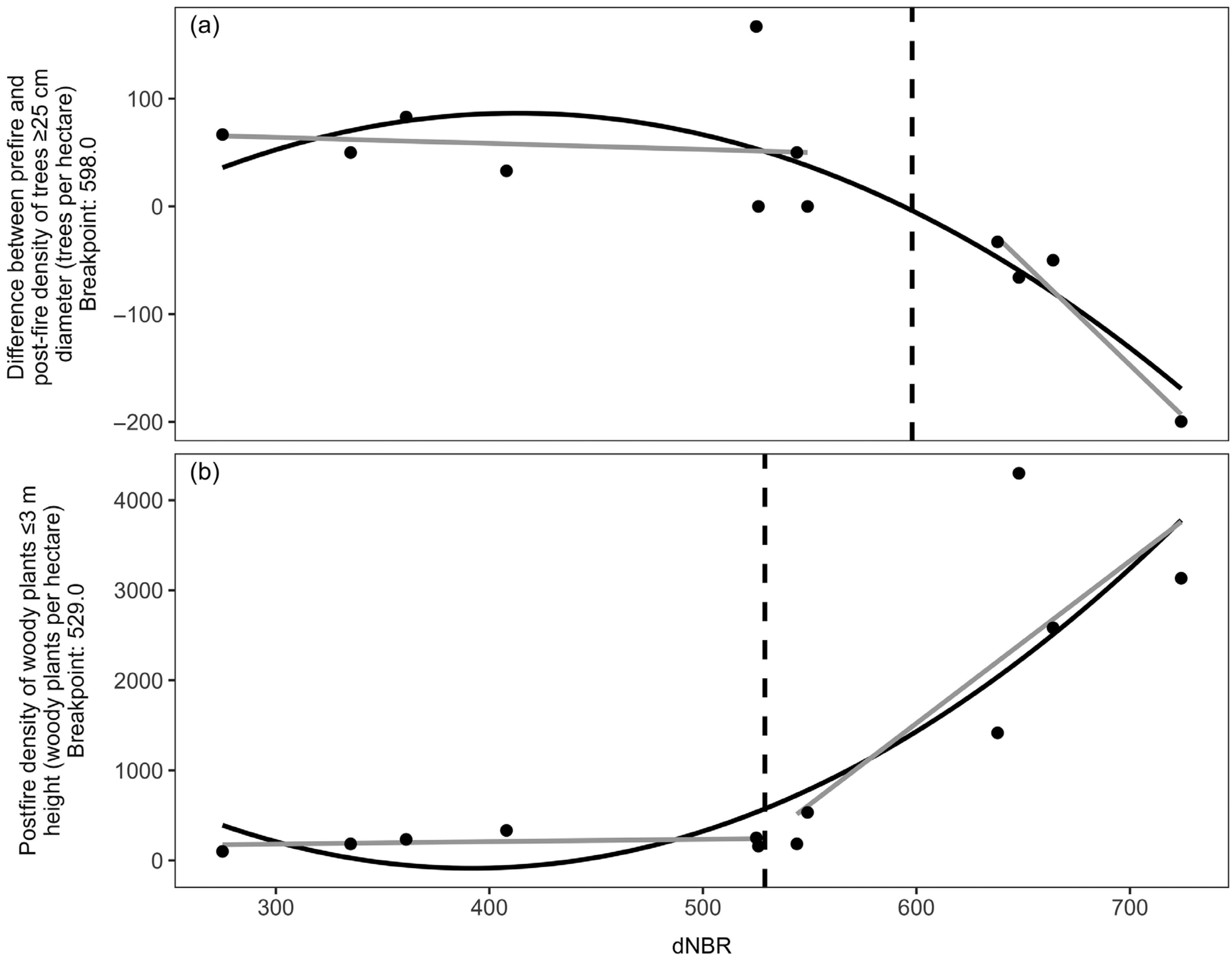

FIGURE 3 Relationship between fire severity (dNBR) and (a) changes in adult tree density (post- minus prefire) and (b) postfire density of shrubs using quadratic (dark line) and piecewise regression (gray line) models. Dashed line corresponds to breakpoint estimate of piecewise models.

TABLE 2 Prefire (1 year) and postfire (11 years) woody canopy cover (%) in different fire severity classes.

		Woody canopy cover (%)			
		Fire severity classes[c]			
Time		**LFS**	**MFS**	**HFS**	***p*-value**
Before fire	Total[a]	69 (3)[d] a[e]	69 (6)a	57 (4)a	0.165
After fire	Total[b]	90 (3)a	83 (4)a	59 (6)b	**0.0013**
	Understory	0 (0.2)a	4 (4)a	25 (5)b	**0.0026**

Note: Values correspond to means of four samples.
[a]Estimated from high-resolution (<1 m) panchromatic images.
[b]Estimated in the field.
[c]Low (LFS), medium (MFS), and high (HFS) fire severity.
[d]Values within parentheses are SEs.
[e]Different letters within row indicate significant differences at indicated *p*-value in bold.

Single-stem *P. caldenia* trees were the dominant life forms in LFS and MFS, whereas multistem shrubs were dominant in HFS (Figure 4). We were not able to detect differences in the density of large-diameter (≥30 cm) trees among fire severity classes ($F = 1.35$, $df = 2$, $p = 0.307$) due to the small sample size and high sample

TABLE 3 Foliar and basal cover (%) of key herbaceous species in different fire severity classes.

			Cover (%)			
			Fire severity classes[a]			
Cover type	Plant groups	Species	LFS	MFS	HFS	*p*-value
Foliar	Total	Total	119.7a[b]	109.5a	111.2a	0.89
	Perennial grass	*Hordeum stenostachys*	41.7a	40.5a	<0.1[c]	0.95
		Amelichloa brachychaeta	12.2a	22.9b	<0.1	**0.05**
		Jarava ichu	23.0a	20.0a	65.5b	**0.008**
		Nassella longiglumis	5.4a	8.4a	<0.1	0.65
	Annuals	*Parietaria debilis*	10.5a	7.5a	6.7a	0.69
		Gamochaeta calviceps	2.3a	4.5ab	10.7b	**0.02**
		Bowlesia incana	1.2a	3.3a	8.5a	0.15
		Bromus catharticus	23.4a	1.7b	1.9b	**0.02**
Basal	Total	Total	12.9a	14.2a	9.0a	0.61
	Perennial grass	*Hordeum stenostachys*	7.0a	5.5a	<0.1	0.64
		Amelichloa spp	2.2a	4.5a	0.4a	0.21
		Jarava ichu	3.0a	1.9a	8.7b	**0.01**
		Nassella longiglumis	0.7a	2.3a	<0.1	0.34

Note: Values correspond to means of four samples.
[a]Low (LFS), medium (MFS) and high (HFS) fire severity.
[b]Different letters within row indicates significant differences at indicated *p*-value in bold.
[c]<0.1 indicates that this species was present at very low cover in only one replication. The corresponding fire severity class was not included in the statistical analysis.

TABLE 4 Prefire (1 year) and postfire (11 years) woody plant density (no. ha^{-1}) in different fire severity classes.

		Woody density (no. ha^{-1})			
		Fire severity classes[c]			
Time	Plants groups	LFS	MFS	HFS	*p*-value
Before fire	Dominant plants[a]	183 (26)[d] a[e]	227 (10)a	237 (40)a	0.364
After fire	Total plants[b]	575 (63)a	677 (87)a	3083 (587)b	**<0.001**
	Plants ≤3 m tall	212 (49)a	281 (86)a	2858 (599)b	**<0.001**
	Prosopis caldenia	563 (66)a	630 (78)a	2483 (521)b	**0.00018**
	Condalia microphylla	9 (5)a	35 (11)a	558 (211)b	**0.0017**

Note: Values correspond to means of four samples.
[a]Live trees with diameter ≥30 cm and dead or resprouted trees with diameter ≥25 cm.
[b]Live woody plants.
[c]Low (LFS), medium (MFS) and high (HFS) fire severity.
[d]Values within parenthesis are standard errors.
[e]Different letters within the row indicates significant differences at the indicated *p*-value in bold.

variability, although tree densities were low in some HFS patches (Figure 4a). Trees with a medium-size diameter (<30 to ≤10 cm) tended to be lower in HFS, but differences were marginally significant ($F = 3.41$, df $= 2$, $p = 0.079$) (Figure 4b). The density of young trees (diameter <10 cm) was highest in HFS ($F = 6.71$, df $= 2$, $p = 0.016$) (Figure 4c). Shrubs originating from the resprouting of top-killed large and medium-size trees were observed only in HFS (Figure 4d,e). We found that all top-killed trees were able to resprout from the base of the main trunk. However, most of the *P. caldenia* shrubs corresponded to young individuals (diameter <10 cm). This category was nearly absent in LFS (which is why LFS was not included in the model). MFS had much

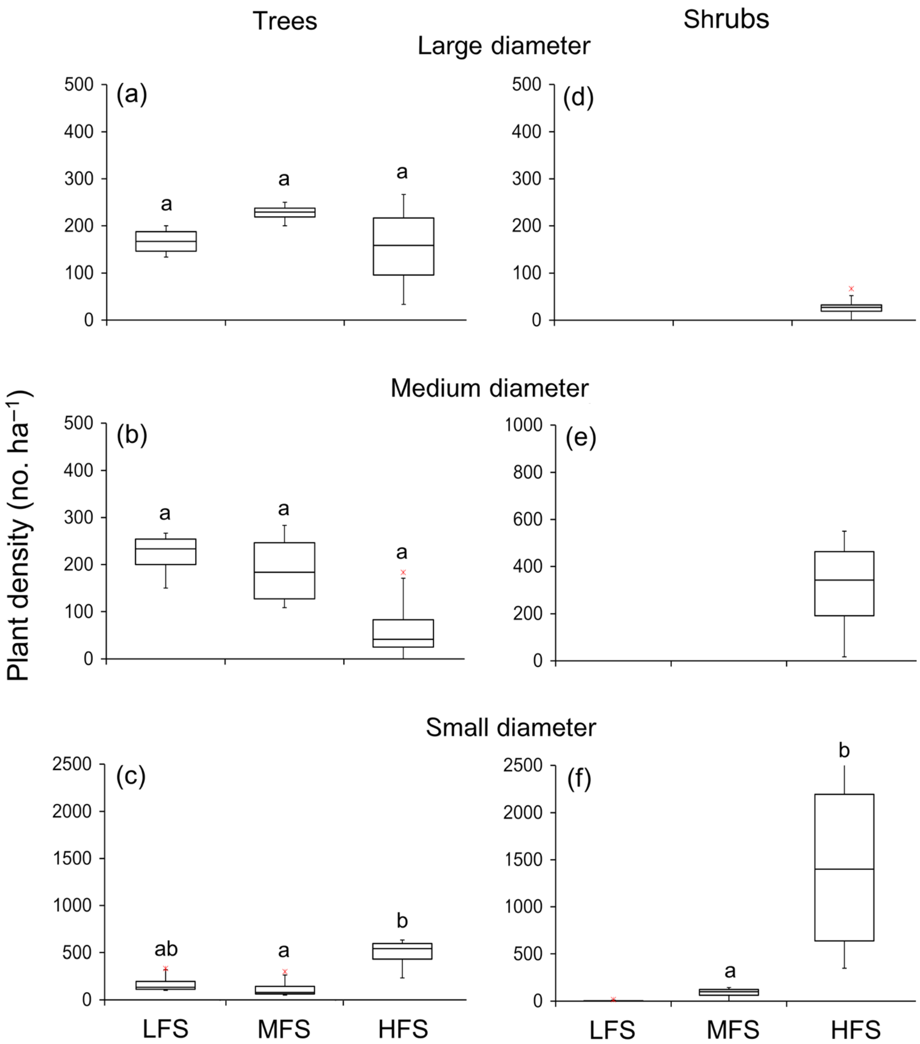

FIGURE 4 Relationship between fire severity and density of live *Prosopis caldenia* trees and shrubs differentiated by the diameter of the main stem in the case of trees or the largest live or dead basal stem in the case of shrubs. Plants were classified considering the following stem diameter categories (in centimeters): large (≥30), medium (30; ≤10) and small (<10). Different letters within a plot indicate significant difference at $p < 0.05$.

lower density of small shrubs than HFS ($F = 11.45$, df $= 1$, $p = 0.015$) (Figure 4f).

DISCUSSION

Our results suggest that caldén forest ecosystems can be resilient to fires of low to medium severity, but not to those of high severity. Despite the small sample sizes available in this study, which could have led to nonsignificant differences in some measured variables, we found strong evidence for a threshold response of vegetation to fire intensity in several metrics. Patches burned at high severity reduced tree dominance and promoted the shrub life form of *P. caldenia*. Considering evidence that shrub life forms promote repeated fire and persist as shrubs for decades or longer (Fernández-García et al., 2020; Minor et al., 2017), the structural change from tree to shrub dominance likely constitutes a persistent state transition. We propose that repeated high-severity fire followed by controlled fires can prevent apical dominance and trap the system in a shrub thicket state. The transition to a shrub thicket state also strongly affects herbaceous plant composition, favoring plants that have low forage value (*Jarava ichu*), consistent with earlier observations (Distel, 2016). We suggest that an operational threshold of dNBR ~600 corresponds to a forest-shrub thicket transition in this study site.

Resprouting is an important trait that confers resilience to fire in Neotropical forests (Cury et al., 2020; Kammesheidt, 1999), but in some tree species it leads to the conversion to a shrub life form (Lacey & Johnston, 1990). However, trees that were top-killed in HFS patches represented a small fraction of total shrubs found in the shrub thicket state (Figure 4d,e). We found that most shrubs (~80%) were young individuals, as indicated by the basal diameter of the largest stem and the lack of evidence of large trunks at the ground level that would indicate resprouted of top-killed young trees (Figure 4f). Even though some shrubs might have been present prior to the fire, a significant proportion of them likely established after the 2006 wildfire event. Based on patterns observed in this study and the previously documented mechanisms described below, we propose that shrub recruitment, which ultimately constitutes the shrub thicket state, depends on the interplay between a high-severity fire and postfire management practices. High shrub recruitment was likely due to the combination of seed dispersal by livestock in the context of reduced tree canopy cover and open ground after the fire. Fires and grazing are known to enhance synergistically woody plant establishment through the removal of grasses (Grellier et al., 2012; Wakeling et al., 2015), the dispersal of woody plant seeds (Lerner & Peinetti, 1996), and seed scarification (De Villalobos et al., 2007; Peinetti et al., 1993). Furthermore, there is evidence from dendrochronological studies carried out within the study region that *P. caldenia* recruitment occurred following severe fire events (Bogino et al., 2015; Dussart et al., 1998). Prescribed fires that were regularly applied after the 2006 wildfire event would likely have been severe enough to cause most young *P. caldenia* plants to adopt a shrub life form (Figure 4f). Thus, we propose that the trigger for a transition to a shrub thicket state requires a severe wildfire event that is reinforced by typical postfire management practices that combine grazing with repeated controlled fires.

We found that open areas of forest in the northeast corner of the study site with pre-2006 canopy cover in the range of 10%–30% burned at low severity (Figures 1 and 2). In contrast, fire severity was highly heterogeneous in areas with higher canopy cover (>30% to 90%). Heterogeneity in canopy cover or arrangement can alter fire–atmosphere interactions, causing differences in the duration and magnitude of crown fires (Parsons et al., 2011 and references therein). Consequently, wildfires can produce a mosaic of patches of high and low fire severity at local scales (<100 m) (Carlson et al., 2011). If fire severity exceeds the resilience of forest trees in a patch, the change in vegetation structure can lead to a new fire regime in that patch (Calder et al., 2019; McLauchlan et al., 2020; Pulla et al., 2015). Our results suggest that spatial variations in fire severity lead to patchy state transitions (Chia et al., 2015; Lentile et al., 2006; Turner et al., 1994). Once patches of vegetation prone to high-severity fires have taken hold in part of the landscape, such patches might expand over time, requiring landscape-level strategies for managing forest resilience. For example, thinning treatments to reduce fire risk could be targeted to patches of high woody plant density in closed forest states (González-Olabarria & Pukkala, 2011).

The shrub thicket state of the caldén forest may favor a fire regime characterized by a lower frequency of fire events due to reduced fine fuel in the herbaceous stratum, but also a higher fire severity due to a greater amount of woody fuel accumulation imparted by a uniform shrub canopy layer. High-severity fires reinforce shrub dominance because top-killed plants will resprout stems that maintain the shrub life form (Coop et al., 2020; Paritsis et al., 2015). Our site-based results suggest that in patches with dNBR values >600 (which can be evaluated using satellite data), livestock grazing could be deferred in order to reduce caldén seed dispersal and seedling establishment. This management strategy could reduce the risk of forest thicketization. However, shrubs originating from resprouted top-killed trees will only revert to the previous tree life form through restoration pruning on sprouts to stimulate the growth of a single stem. Extreme weather conditions, combined with anthropogenic ignitions, can generate fires of high severity even in well-managed forest ecosystems (Lydersen et al., 2014; Pausas & Bond, 2020). Given that severe wildfires are likely to become more frequent in warmer climates of the future, managers should develop strategies to monitor fire severity and to reconsider management goals in recent disturbed forests as well as altered forest states (McKenzie et al., 2004; McLauchlan et al., 2020). Our study of this unplanned fire event points to the need for additional research on the causes of spatial heterogeneity in fire severity and the role of grazing–fire interactions in postfire vegetation trajectories.

CONCLUSION

Wildfires have played a critical role in shaping the caldén forest. However, fire characteristics are changing rapidly as a consequence of increased intensity of human activity coupled to warmer climate conditions (Abatzoglou et al., 2019; Keeley et al., 2021). The caldén forest likely evolved with fires of low severity. We expect that an increasing rate of ignitions and more severe wildfires in the future will compromise the persistence of the forest state. Methods to quantify spatial variations in resilience (Cumming et al., 2017) and detect patchy thresholds such that management interventions can mitigate undesirable changes and disasters (Krishnamurthy et al., 2020) are critical needs in modern applied ecology. Our relatively simple example provides hope that operational approaches to threshold detection, based on the monitoring of critical disturbances that interact with management, can be used in spatially explicit management strategies that control state transitions. Future research should examine whether the threshold response observed in our study site can be generalized throughout the caldén forest region and whether analogous thresholds can be identified in other fire-prone forests at risk of thicketization. Observations of additional fires will be needed to test our ability to use satellite-based threshold detection to promote open forest recovery.

ACKNOWLEDGMENTS

We thank ranch owners for providing us with access to their property and information on management practices. This work was supported by POIRE 2016-18 UNLPam and Facultad de Agronomía, UNLPam, Argentina, US Department of Agriculture Agricultural Research Service (USDA-ARS) Agreement 3050-11210-009-51-N, and the Jornada Basin Long-Term Ecological Research Program (DEB-1832194). Darren James from the USDA-ARS provided help with the breakpoint analysis. We thank two anonymous reviewers for their efforts to improve this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Peinetti et al., 2021) are available in the EDI Data Portal at https://doi.org/10.6073/pasta/e1978467bd09fc4f6e0cd8509b06f28d. Landsat images were downloaded from the USGS Earth Explorer data portal (https://earthexplorer.usgs.gov/) by using the following search criteria: Path = "228," Row = "085," Data Sets = "Landsat 4-5 TM C2 L 2," Dates = "2005/11/13" and "2006/10/15".

ORCID

H. Raúl Peinetti https://orcid.org/0000-0003-4527-4673
Brandon T. Bestelmeyer https://orcid.org/0000-0001-5060-9955
Alicia G. Kin https://orcid.org/0000-0002-1928-5777

REFERENCES

Abatzoglou, J. T., A. P. Williams, and R. Barbero. 2019. "Global Emergence of Anthropogenic Climate Change in Fire Weather Indices." *Geophysical Research Letters* 46: 326–336. https://doi.org/10.1029/2018GL080959.

Anselin, L. 2003. "GeoDa 0.9 User's Guide." Spatial Analysis Laboratory (SAL). Department of Agricultural and Consumer Economics, University of Illinois, Urbana-Champaign, Il. http://www.csiss.org/.

Archer, S., E. Andersen, K. Predick, S. Schwinning, R. Steidl, and S. Woods. 2017. "Woody Plant Encroachment: Causes and Consequences." In *Rangeland Systems: Processes, Management and Challenges*, edited by D. Briske, 25–84. Springer Series on Environmental Management. Cham: Springer. https://doi.org/10.1007/978-3-319-46709-2_2.

Barley, S. C., and J. J. Meeuwig. 2017. "The Power and the Pitfalls of Large-Scale, Unreplicated Natural Experiments." *Ecosystems* 20: 331–39. https://doi.org/10.1007/s10021-016-0028-5.

Beckage, B., W. J. Platt, and L. J. Gross. 2009. "Vegetation, Fire, and Feedbacks: A Disturbance-Mediated Model of Savannas." *American Naturalist* 174: 805–818. https://doi.org/10.1086/648458.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. "Alternative Stable States in Ecology." *Frontiers in Ecology and the Environment* 1: 376–382. https://doi.org/10.2307/3868190.

Bestelmeyer, B. T., A. Ash, J. R. Brown, B. Densambuu, M. Fernández-Giménez, J. Johanson, M. Levi, et al. 2017. "State and Transition Models: Theory, Applications, and Challenges." In *Rangeland Systems: Processes, Management and Challenges*, edited by D. Briske, 303–345. Springer Series on Environmental Management. Cham: Springer. https://doi.org/10.1007/978-3-319-46709-2_9.

Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, K. B. Gorman, S. J. Holbrook, C. M. Laney, M. D. Ohman, et al. 2011. "Analysis of Abrupt Transitions in Ecological Systems." *Ecosphere* 2: art 26. https://doi.org/10.1890/es11-00216.1.

Blackhall, M., E. Raffaele, J. Paritsis, F. Tiribelli, J. M. Morales, T. Kitzberger, J. H. Gowda, and T. T. Veblen. 2017. "Effects of Biological Legacies and Herbivory on Fuels and Flammability Traits: A Long-Term Experimental Study of Alternative Stable States." *Journal of Ecology* 105: 1309–22. https://doi.org/10.1111/1365-2745.12796.

Blackhall, M., E. Raffaele, and T. T. Veblen. 2008. "Cattle Affect Early Post-Fire Regeneration in a *Nothofagus dombeyi-Austrocedrus chilensis* Mixed Forest in Northern Patagonia, Argentina." *Biological Conservation* 141: 2251–61. https://doi.org/10.1016/j.biocon.2008.06.016.

Bogino, S., S. C. Roa-Giménez, A. T. Velasco-Sastre, M. L. Cangiano, L. Risio-Allione, and V. Rozas. 2015. "Synergetic Effects of Fire, Climate, and Management History on *Prosopis caldenia* Recruitment in the Argentinean Pampas." *Journal of Arid Environments* 117: 59–66. https://doi.org/10.1016/j.jaridenv.2015.02.014.

Calder, W. J., I. Stefanova, and B. Shuman. 2019. "Climate–Fire–Vegetation Interactions and the Rise of Novel Landscape Patterns in Subalpine Ecosystems, Colorado." *Journal of Ecology* 107: 1689–1703. https://doi.org/10.1111/1365-2745.13138.

Cansler, C. A., and D. McKenzie. 2014. "Climate, Fire Size, and Biophysical Setting Control Fire Severity and Spatial Pattern in the Northern Cascade Range, USA." *Ecological Applications* 24: 1037–56. https://doi.org/10.1890/13-1077.1.

Carlson, D. J., P. B. Reich, and L. E. Frelich. 2011. "Fine-Scale Heterogeneity in Overstory Composition Contributes to Heterogeneity of Wildfire Severity in Southern Boreal Forest." *Journal of Forest Research* 16: 203–214. https://doi.org/10.1007/s10310-011-0251-z.

Catford, J. A., J. R. U. Wilson, P. Pyšek, P. E. Hulme, and R. P. Duncan. 2022. "Addressing Context Dependence in Ecology."

Trends in Ecology & Evolution 37: 158–170. https://doi.org/10.1016/j.tree.2021.09.007.

Cesca, E. M., P. E. Villagra, and J. A. Alvarez. 2014. "From Forest to Shrubland: Structural Responses to Different Fire Histories in Prosopis Flexuosa Woodland from the Central Monte (Argentina)." *Journal of Arid Environments* 110: 1–7. https://doi.org/10.1016/j.jaridenv.2014.05.025.

Chander, G., B. L. Markham, and D. L. Helder. 2009. "Summary of Current Radiometric Calibration Coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI Sensors." *Remote Sensing of Environment* 113: 893–903. https://doi.org/10.1016/j.rse.2009.01.007.

Chia, E. K., M. Bassett, D. G. Nimmo, S. W. J. Leonard, E. G. Ritchie, M. F. Clarke, A. F. Bennett, and D. P. C. Peters. 2015. "Fire Severity and Fire-Induced Landscape Heterogeneity Affect Arboreal Mammals in Fire-Prone Forests." *Ecosphere* 6: 1–14. https://doi.org/10.1890/ES15-00327.1.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *Bioscience* 70: 659–673. https://doi.org/10.1093/biosci/biaa061.

Cumming, G., T. Morrison, and T. Hughes. 2017. "New Directions for Understanding the Spatial Resilience of Social–Ecological Systems." *Ecosystems* 20: 649–664. https://doi.org/10.1007/s10021-016-0089-5.

Cury, R. T. D. S., J. K. Balch, P. M. Brando, R. B. Andrade, R. P. Scervino, and J. M. D. Torezan. 2020. "Higher Fire Frequency Impaired Woody Species Regeneration in a South-Eastern Amazonian Forest." *Journal of Tropical Ecology* 36: 1–9. https://doi.org/10.1017/S0266467420000176.

Dantas, V., M. A. Batalha, and J. G. Pausas. 2013. "Fire Drives Functional Thresholds on the Savanna–Forest Transition." *Ecology* 94: 2454–63. https://doi.org/10.1890/12-1629.1.

De Villalobos, A. E., D. V. Peláez, R. M. Bóo, M. D. Mayor, and O. R. Elia. 2007. "Effect of a Postfire Environment on the Establishment of *Prosopis caldenia* Seedlings in Central Semiarid Argentina." *Austral Ecology* 32: 581–591. https://doi.org/10.1111/j.1442-9993.2007.01731.x.

Distel, R. A. 2016. "Grazing ecology and the conservation of the Caldenal rangelands, Argentina." *Journal of Arid Environments* 134: 49–55. https://doi.org/10.1016/j.jaridenv.2016.06.019.

Dussart, E., A. Medina, and S. Bogino. 2015. "Dendroecología en la pampa Argentina: investigaciones actuales, pasadas y futuros desafíos." *Ecosistemas: Revista Cietifica y Tecnica de Ecologia y Medio Ambiente* 24: 51–59. https://doi.org/10.7818/ECOS.2015.24-2.08.

Dussart, E. G., C. C. Chirino, E. A. Morici, and H. R. Peinetti. 2011. "Reconstrucción del paisaje del Caldenal pampeano en los últimos 250 años." *Quebracho—Revista de Ciencias Forestales* 19: 54–65.

Dussart, E. G., P. D. Lerner, and H. R. Peinetti. 1998. "Long Term Dynamics of 2 Populations of *Prosopis caldenia* Burkart." *Journal of Range Management* 51: 685–691. https://doi.org/10.2307/4003613.

Eberhardt, L. L., and J. M. Thomas. 1991. "Designing Environmental Field Studies." *Ecological Monographs* 61: 53–73. https://doi.org/10.2307/1942999.

Escuin, S., R. Navarro, and P. Fernández. 2008. "Fire Severity Assessment by Using NBR (Normalized Burn Ratio) and NDVI (Normalized Difference Vegetation Index) Derived from LANDSAT TM/ETM Images." *International Journal of Remote Sensing* 29: 1053–73. https://doi.org/10.1080/01431160701281072.

Fernández, O. A., M. E. Gil, and R. A. Distel. 2009. "The Challenge of Rangeland Degradation in a Temperate Semiarid Region of Argentina: The Caldenal." *Land Degradation & Development* 20: 431–440.

Fernández-García, V., E. Marcos, P. Z. Fulé, O. Reyes, V. M. Santana, and L. Calvo. 2020. "Fire Regimes Shape Diversity and Traits of Vegetation under Different Climatic Conditions." *Science of the Total Environment* 716: 137137. https://doi.org/10.1016/j.scitotenv.2020.137137.

González-Olabarria, J. R., and T. Pukkala. 2011. "Integrating Fire Risk Considerations in Landscape-Level Forest Planning." *Forest Ecology and Management* 261: 278–287. https://doi.org/10.1016/j.foreco.2010.10.017.

González-Roglich, M., J. J. Swenson, D. Villarreal, E. G. Jobbágy, and R. B. Jackson. 2015. "Woody Plant-Cover Dynamics in Argentine Savannas from the 1880s to 2000s: The Interplay of Encroachment and Agriculture Conversion at Varying Scales." *Ecosystems* 18: 481–492. https://doi.org/10.1007/s10021-015-9841-5.

Grady, J. M., and W. A. Hoffmann. 2012. "Caught in a Fire Trap: Recurring Fire Creates Stable Size Equilibria in Woody Resprouters." *Ecology* 93: 2052–60. https://doi.org/10.1890/12-0354.1.

Grau, H. R., and T. T. Veblen. 2000. "Rainfall Variability, Fire and Vegetation Dynamics in Neotropical Montane Ecosystems in North-Western Argentina." *Journal of Biogeography* 27: 1107–21. https://doi.org/10.1046/j.1365-2699.2000.00488.x.

Grellier, S., S. Barot, J.-L. Janeau, and D. Ward. 2012. "Grass Competition Is more Important than Seed Ingestion by Livestock for Acacia Recruitment in South Africa." *Plant Ecology* 213: 899–908. https://doi.org/10.1007/s11258-012-0051-3.

Herrick, J. E., J. W. Van Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford. 2005. *Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems*. USDA-ARS Jornada Experimental Range. Tucson: The University of Arizona Press.

Holmes, K. A., K. E. Veblen, A. M. Berry, and T. P. Young. 2011. "Effects of Prescribed Fires on Young Valley Oak Trees at a Research Restoration Site in the Central Valley of California." *Restoration Ecology* 19: 118–125. https://doi.org/10.1111/j.1526-100X.2009.00529.x.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, et al. 2016. "Changing Disturbance Regimes, Ecological Memory, and Forest Resilience." *Frontiers in Ecology and the Environment* 14: 369–378. https://doi.org/10.1002/fee.1311.

Kammesheidt, L. 1999. "Forest Recovery by Root Suckers and above-Ground Sprouts after Slash-and-Burn Agriculture, Fire and Logging in Paraguay and Venezuela." *Journal of Tropical Ecology* 15: 143–157. https://doi.org/10.1017/S0266467499000723.

Keeley, J. E. 2009. "Fire Intensity, Fire Severity and Burn Severity: A Brief Review and Suggested Usage." *International Journal of Wildland Fire* 18: 116–126. https://doi.org/10.1071/WF07049.

Keeley, J. E., J. Guzman-Morales, A. Gershunov, A. D. Syphard, D. Cayan, D. W. Pierce, M. Flannigan, and T. J. Brown. 2021. "Ignitions Explain More than Temperature or Precipitation in Driving Santa Ana Wind Fires." *Science Advances* 7: eabh2262. https://doi.org/10.1126/sciadv.abh2262.

Key, C. H., and N. C. Benson. 2006. "Landscape Assessment: Ground Measure of Severity, the Composite Burn Index; and Remote Sensing of Severity, the Normalized Burn Ratio." In *FIREMON: Fire Effects Monitoring and Inventory System*, edited by D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi, 1–15. Ogden: USDA Forest Service, Rocky Mountain Research Station.

Kitzberger, T., G. L. W. Perry, J. Paritsis, J. H. Gowda, A. J. Tepley, A. Holz, and T. T. Veblen. 2016. "Fire–Vegetation Feedbacks and Alternative States: Common Mechanisms of Temperate Forest Vulnerability to Fire in Southern South America and New Zealand." *New Zealand Journal of Botany* 54: 247–272. https://doi.org/10.1080/0028825X.2016.1151903.

Knox, K. J. E., and P. J. Clarke. 2012. "Fire Severity, Feedback Effects and Resilience to Alternative Community States in Forest Assemblages." *Forest Ecology and Management* 265: 47–54. https://doi.org/10.1016/j.foreco.2011.10.025.

Krishnamurthy, R. P. K., J. B. Fisher, D. S. Schimel, and P. M. Kareiva. 2020. "Applying Tipping Point Theory to Remote Sensing Science to Improve Early Warning Drought Signals for Food Security." *Earth's Future* 8: 1–14. https://doi.org/10.1029/2019EF001456.

Lacey, C. J., and R. D. Johnston. 1990. "Woody Clumps and Clumpwoods." *Australian Journal of Botany* 38: 299–334. https://doi.org/10.1071/BT9900299.

Lawes, M. J., D. A. Keith, and R. A. Bradstock. 2016. "Advances in Understanding the Influence of Fire on the Ecology and Evolution of Plants: A Tribute to Peter J. Clarke." *Plant Ecology* 217: 597–605. https://doi.org/10.1007/s11258-016-0625-6.

Lentile, L. B., Z. A. Holden, A. M. S. Smith, M. J. Falkowski, A. T. Hudak, P. Morgan, S. A. Lewis, P. E. Gessler, and N. C. Benson. 2006. "Remote Sensing Techniques to Assess Active Fire Characteristics and Post-Fire Effects." *International Journal of Wildland Fire* 15: 319–345. https://doi.org/10.1071/WF05097.

Lerner, P. D., and H. R. Peinetti. 1996. "Importance of Predation and Germination on Losses from the Seed Bank of Calden (*Prosopis caldenia*)." *Journal of Range Management* 49: 147–150. https://doi.org/10.2307/4002685.

Llorens, E. M. 1995. "Viewpoint: The State and Transition Model Applied to the Herbaceous Layer of Argentina's Calden Forest." *Journal of Range Management* 48: 442–47. https://doi.org/10.2307/4002249.

Lydersen, J. M., M. P. North, and B. M. Collins. 2014. "Severity of an Uncharacteristically Large Wildfire, the Rim Fire, in Forests with Relatively Restored Frequent Fire Regimes." *Forest Ecology and Management* 328: 326–334. https://doi.org/10.1016/j.foreco.2014.06.005.

McKenzie, D., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. "Climatic Change, Wildfire, and Conservation." *Conservation Biology* 18: 890–902. https://doi.org/10.1111/j.1523-1739.2004.00492.x.

McLauchlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, et al. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers." *Journal of Ecology* 108: 2047–69. https://doi.org/10.1111/1365-2745.13403.

Medina, A. A. 2008. "Cicatrices de fuego en el leño de *Prosopis caldenia* en Luán Toro, provincia de La Pampa, Argentina." *Bosque* 29: 115–19.

Miller, J. D., and A. E. Thode. 2007. "Quantifying Burn Severity in a Heterogeneous Landscape with a Relative Version of the Delta Normalized Burn Ratio (dNBR)." *Remote Sensing of Environment* 109: 66–80. https://doi.org/10.1016/j.rse.2006.12.006.

Minor, J., D. A. Falk, and G. A. Barron-Gafford. 2017. "Fire Severity and Regeneration Strategy Influence Shrub Patch Size and Structure Following Disturbance." *Forests* 8: 221. https://doi.org/10.3390/f8070221.

Moreira, F., M. Arianoutsou, V. R. Vallejo, J. d. l. Heras, P. Corona, G. Xanthopoulos, P. Fernandes, and K. Papageorgiou. 2012. "Setting the Scene for Post-Fire Management." In *Post-Fire Forest Management in Southern Europe: A COST Action for Gathering and Disseminating Scientific Knowledge*, edited by M. A. Moreira, P. Corona, and J. d. l. Heras, 1–19. Dordrecht: Springer. https://doi.org/10.1007/978-94-007-2208-8.

Paritsis, J., T. T. Veblen, and A. Holz. 2015. "Positive Fire Feedbacks Contribute to Shifts from *Nothofagus pumilio* Forests to Fire-Prone Shrublands in Patagonia." *Journal of Vegetation Science* 26: 89–101. https://doi.org/10.1111/jvs.12225.

Parsons, R. A., W. E. Mell, and P. McCauley. 2011. "Linking 3D Spatial Models of Fuels and Fire: Effects of Spatial Heterogeneity on Fire Behavior." *Ecological Modelling* 222: 679–691. https://doi.org/10.1016/j.ecolmodel.2010.10.023.

Pausas, J. G., and W. J. Bond. 2020. "Alternative Biome States in Terrestrial Ecosystems." *Trends in Plant Science* 25: 250–263. https://doi.org/10.1016/j.tplants.2019.11.003.

Pausas, J. G., and J. E. Keeley. 2014. "Abrupt climate-independent fire regime changes." *Ecosystems* 17: 1109–20. https://doi.org/10.1007/s10021-014-9773-5.

Peinetti, H. R., B. T. Bestelmeyer, C. C. Chirino, A. G. Kin, and M. E. Frank. 2019. "Generalized and Specific State-and-Transition Models to Guide Management and Restoration of Caldenal Forests." *Rangeland Ecology & Management* 72: 230–36. https://doi.org/10.1016/j.rama.2018.11.002.

Peinetti, H. R., B. T. Bestelmeyer, C. C. Chirino, F. L. Vivalda, and A. G. Kin. 2021. "Thresholds and Alternative States in a Neotropical Dry Forest in Response to Fire Severity." 2005–2018 ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/e1978467bd09fc4f6e0cd8509b06f28d.

Peinetti, H. R., M. Pereyra, A. G. Kin, and A. A. Sosa. 1993. "Effects of Cattle Ingestion on Viability and Germination Rate of Calden (*Prosopis caldenia*) Seeds." *Journal of Range Management* 46: 483–86. https://doi.org/10.2307/4002856.

Pennington, R. T., D. E. Prado, and C. A. Pendry. 2000. "Neotropical Seasonally Dry Forests and Quaternary Vegetation Changes." *Journal of Biogeography* 27: 261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x.

Pereira, P., M. Francos, E. C. Brevik, X. Ubeda, and I. Bogunovic. 2018. "Post-fire soil management." *Current Opinion in Environmental Science & Health* 5: 26–32. https://doi.org/10.1016/j.coesh.2018.04.002.

Pulla, S., G. Ramaswami, N. Mondal, R. Chitra-Tarak, H. S. Suresh, H. S. Dattaraja, P. Vivek, N. Parthasarathy, B. R. Ramesh, and R. Sukumar. 2015. "Assessing the Resilience of Global Seasonally Dry Tropical Forests." *International Forestry Review* 17: 91–113. https://doi.org/10.1505/146554815815834796.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing https://www.R-project.org/.

Rocha, J. C., G. D. Peterson, and R. Biggs. 2015. "Regime Shifts in the Anthropocene: Drivers, Risks, and Resilience." *PLoS One* 10: e0134639. https://doi.org/10.1371/journal.pone.0134639.

Ryan, S. E., and L. S. Porth. 2007. *A Tutorial on the Piecewise Regression Approach Applied to Bedload Transport Data*. General Technical Reports RMRS-GTR-189. Fort Collins: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sagarin, R., and A. Pauchard. 2010. "Observational Approaches in Ecology Open New Ground in a Changing World." *Frontiers in Ecology and the Environment* 8: 379–386. https://doi.org/10.1890/090001.

SAS Institute Inc. 2018. *SAS/STAT® 15.1 User's Guide*. Cary: SAS Institute Inc.

Snyder, A., P. Fulé, and J. Crouse. 2005. "Comparison of Burn Severity Assessment Using Differenced Normalized Burn Ratio and Ground Data." *International Journal of Wildland Fire* 14: 189–198. https://doi.org/10.1071/WF04010.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. "Alternative States and Positive Feedbacks in Restoration Ecology." *Trends in Ecology and Evolution* 19: 46–53. https://doi.org/10.1016/j.tree.2003.10.005.

Tiribelli, F., T. Kitzberger, and J. M. Morales. 2018. "Changes in Vegetation Structure and Fuel Characteristics along Post-Fire Succession Promote Alternative Stable States and Positive Fire–Vegetation Feedbacks." *Journal of Vegetation Science* 29: 147–156. https://doi.org/10.1111/jvs.12620.

Turner, M. G., W. J. Calder, G. S. Cumming, T. P. Hughes, A. Jentsch, S. L. LaDeau, T. M. Lenton, et al. 2020. "Climate Change, Ecosystems and Abrupt Change: Science Priorities." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375: 20190105. https://doi.org/10.1098/rstb.2019.0105.

Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. "Effects of Fire on Landscape Heterogeneity in Yellowstone National Park, Wyoming." *Journal of Vegetation Science* 5: 731–742. https://doi.org/10.2307/3235886.

Twidwell, D., S. D. Fuhlendorf, C. A. Taylor, and W. E. Rogers. 2013. "Refining Thresholds in Coupled Fire-Vegetation Models to Improve Management of Encroaching Woody Plants in Grasslands." *Journal of Applied Ecology* 50: 603–613. https://doi.org/10.1111/1365-2664.12063.

Wakeling, J. L., W. J. Bond, M. Ghaui, and E. C. February. 2015. "Grass Competition and the Savanna-Grassland "Treeline": A Question of Root Gaps?" *South African Journal of Botany* 101: 91–97. https://doi.org/10.1016/j.sajb.2014.09.007.

Whitlock, C., P. E. Higuera, D. B. McWethy, and C. E. Briles. 2010. "Paleoecological Perspectives on Fire Regime Concept." *The Open Ecology Journal* 3: 6–23. https://doi.org/10.2174/1874213001003020006.

How to cite this article: Peinetti, H. Raúl, Brandon T. Bestelmeyer, Claudia C. Chirino, Florencia L. Vivalda, and Alicia G. Kin. 2024. "Thresholds and Alternative States in a Neotropical Dry Forest in Response to Fire Severity." *Ecological Applications* 34(2): e2937. https://doi.org/10.1002/eap.2937