Ecología Austral 30:268-281 Agosto 2020
Asociación Argentina de Ecología
https://doi.org/10.25260/EA.20.30.2.0.1054

Fire incidence along an elevation gradient in the mountains of central Argentina

Juan P. Argañaraz[1,✉]; Ana M. Cingolani[2]; Laura M. Bellis[1,3] & Melisa A. Giorgis[2]

[1] Instituto de Altos Estudios Espaciales "Mario Gulich" (CONAE-UNC), CONICET. Falda del Cañete, Argentina. [2] Instituto Multidisciplinario de Biodiversidad Vegetal, CONICET-Universidad Nacional de Córdoba. Córdoba, Argentina. [3] Cátedra de Ecología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Córdoba, Argentina.

Abstract. In mountain ecosystems, vegetation distribution along elevation has been traditionally interpreted in terms of the decreasing temperature from base to top, but wildfires may co-vary with the elevation gradient, also playing an important role. In the mountains of central Argentina (500-2800 m a. s. l.) wildfires are one of the main disturbances, which may have an important role in shaping vegetation dynamics along elevation. However, to date, no study described the fire pattern along the elevation gradient. We compared fire incidence among five elevation intervals using an 18-year spatially explicit fire database derived from remote sensing. For each interval, we discarded unburnable areas and calculated fire incidence per year as the percentage of burned area. Fire incidence showed a hump-shaped pattern along the elevation gradient. The highest fire incidence occurred at intermediate elevations, in the 1301-1700 m and 901-1300 m intervals, with averages of 3.2 and 2.7% of the area being burned annually, respectively. The lowest fire incidence occurred at the lowest interval (500-900 m), with 1.3% being burned annually on average. The greater fire incidence observed at intermediate elevations is consistent with a sharp increase in the cover of grasslands above 900 m a. s. l., with an associated reduction in forest occupation. Towards higher elevations, the lower fire incidence is consistent with the presence of topographic breaks, greater proportion of unburnable surfaces that work as firebreaks and moister conditions. The greater fire incidence observed at intermediate elevations may be limiting forest expansion in those areas. At higher elevations the low forest cover may be explained by a combination of fire and livestock pressure. Our study is the first to show how fire incidence varies along the complete elevation gradient, bringing an important tool to understand vegetation distribution and plan future conservation and restoration strategies.

[Keywords: fire-vegetation patterns, fire frequency, forest, grassland, landscape ecology, remote sensing, sierras de Córdoba, spatial analyses, treeline]

Resumen. Incidencia del fuego en un gradiente altitudinal de las sierras del centro de la Argentina. En los ecosistemas de montaña, la distribución de la vegetación a lo largo del gradiente altitudinal fue tradicionalmente interpretada en términos de la temperatura decreciente desde la base hacia arriba; pero los fuegos pueden co-variar con el gradiente de altitud, también cumpliendo un papel importante. En las montañas del centro de la Argentina (500-2800 m s. n. m.), los fuegos son uno de los disturbios principales y pueden cumplir una función importante en modular la dinámica de la vegetación a lo largo de la altitud. Sin embargo, hasta ahora ningún estudio describió la incidencia del fuego a lo largo del gradiente altitudinal. Nosotros comparamos la incidencia del fuego entre cinco intervalos altitudinales usando una base de datos de fuegos espacialmente explícita, de 18 años, derivada de sensores remotos. Para cada intervalo, descartamos las áreas no combustibles y calculamos para cada año la incidencia del fuego como el porcentaje de área quemada. La incidencia de fuego mostró un patrón unimodal a lo largo del gradiente de altitud. Las incidencias más altas se registraron a altitudes intermedias, en los intervalos de 1301-1700 m y 901-1300 m, con 3.2% y 2.7% de incidencia anual, respectivamente. La incidencia de fuego más baja se registró en el intervalo inferior (500-900 m), con 1.3% quemado anualmente, en promedio. La mayor incidencia del fuego observada a altitudes intermedias es consistente con un aumento importante de la cobertura de pastizales por encima de los 900 m s. n. m., con una simultánea reducción en la extensión de bosques. Hacia mayores altitudes, la menor incidencia del fuego es consistente con la presencia de barreras impuestas por la topografía y por las áreas rocosas no combustibles, y con las condiciones más húmedas. La mayor incidencia de fuegos observada a altitudes intermedias puede estar limitando la expansión de bosques en dichas áreas. A mayores altitudes, la baja cobertura arbórea podría estar explicada por una combinación de fuegos y presión ganadera. Nuestro estudio es el primero que muestra cómo varía la incidencia del fuego a lo largo del gradiente completo de altitud, brindando una herramienta importante para entender la distribución de la vegetación y planificar estrategias de conservación y restauración.

[Palabras clave: patrones fuego-vegetación, frecuencia de incendios, bosque, pastizal, ecología de paisajes, teledetección, sierras de Córdoba, análisis espacial, límite altitudinal de los bosques]

Editora asociada: Roxana Aragón
✉ argajuan@gmail.com
Recibido: 29 de Octubre de 2019
Aceptado: 24 de Abril de 2020

INTRODUCTION

Wildfires are a major disturbance in many ecosystems around the world (Bowman et al. 2009; Staver et al. 2011; Archibald et al. 2018). They play a key role in landscapes by causing strong impacts on vegetation structure and distribution (Whelan 1995; McKenzie et al. 2011; Pausas and Ribeiro 2017). Because of this reason, the description of fire spatial patterns and their association with environmental gradients is important to understand vegetation distribution in systems prone to wildfires.

In mountain ecosystems, vegetation distribution along the elevation gradient has been traditionally interpreted in terms of the decreasing temperature from base to top (Holdridge 1947; Whittaker 1956; Körner 2003), but wildfires may co-vary with the elevation gradient, and also play an important role. The climatic variation along elevation affects vegetation type and productivity, as well as soil and fuel moisture, thus influencing fire incidence (Mermoz et al. 2005; Hemp 2005; Nogués-Bravo et al. 2008; Haugo et al. 2010; Metlen et al. 2018). Additionally, other natural and human-related drivers of fire ignitions and propagation, such as local geomorphology or population density, may co-vary with elevation, further affecting fire patterns (Mermoz et al. 2005; Syphard et al. 2007, 2008; Nogués-Bravo et al. 2008). Due to these multiple drivers, the emergent response of fire to elevation in a particular mountain system may be difficult to predict. Either positive, negative, or hump-shaped relationships between elevation and fire have been described in different studies around the world (Caprio and Swetnam 1995; Mermoz et al. 2005; Brooks and Matchett 2006; Syphard et al. 2008). The relationship between fire and vegetation is particularly complex, because vegetation is not only a driver of fire, but it may be also a consequence of the fire regime. Wildfires affect vegetation by eliminating biomass and slowing ecological succession (Paritsis et al. 2015; Syphard et al. 2018). As a consequence of these relationships, positive or negative feedbacks between fire and vegetation often arise (Mermoz et al. 2005; Kitzberger et al. 2012; Tepley et al. 2018). Thus, the description of fire patterns along elevation gradients is important to aid in the interpretation of vegetation response to elevation, bearing in mind that fire is both a cause and a consequence of vegetation characteristics.

As in other mountains in the world, in central Argentina the vegetation distribution is not homogeneous along the elevation gradient (500-2800 m a. s. l.). As elevation increases, forest and successional shrublands are progressively scarcer and grasslands occupy larger areas (Kurtz 1904; Luti et al. 1979; Giorgis et al. 2013, 2017; Cabido et al. 2018) (Table 1). This pattern has been often explicitly or implicitly interpreted as a consequence of the climatic variation along the elevation gradient (e.g., Luti et al. 1979; Cabido and Acosta 1988; Acosta et al. 1992), but more recently some authors have drawn attention about the role of fire in shaping mountain vegetation (e.g., Giorgis et al. 2013). Wildfires are one of the main disturbances in the mountains of central Argentina. In an intensively studied part of these mountains, nearly 456864 ha (19% of total study area) were burned between 1999 and 2011, with some of those areas being burned three or more times over this short period (Argañaraz et al. 2015a). According to different

Table 1. Proportion (%) of forests, shrublands and grasslands, defined according to the dominant stratum, in relation to total area covered with natural vegetation (i.e., excluding crops, water bodies and urban and rocky areas) in the Córdoba mountains. We report range of values for five elevation intervals, obtained from different sources[1], involving —in some cases— only a sector of the total mountain area included in the present study.

Tabla 1. Proporción (%) de bosques, arbustales y pastizales, definidos según el estrato dominante, en relación con el área total ocupada por vegetación natural (i.e., excluyendo cultivos, cuerpos de agua y áreas urbanas y rocosas) en las Sierras de Córdoba. Reportamos rangos de valores para cinco intervalos altitudinales, obtenidos a partir de diferentes fuentes[1], comprendiendo, —en algunos casos— sólo un sector del área montañosa incluida en este trabajo.

Mountain belt	Elevation interval (m a. s. l.)	% Forest	% Shrubland	% Grassland
Chaco	500-900	15-40	50-70	10-20
	901-1300	10-25	25-50	30-55
Transition	1301-1700	2-15	5-40	30-93
Andes	1701-2100	1-20	0-30	50-100
	>2100	0-5	0-15	80-100

[1] Cingolani et al. (2004); Zak (2008); Giorgis et al. (2017); Cingolani et al. (unpublished map).

studies, ecosystems in these mountains experience a positive feedback between vegetation and fire. Early successional stages dominated by grasses and/or shrubs facilitate fire spread, which in turn contribute to the persistence of these early successional grasslands and shrublands (Giorgis et al. 2013, 2017; Argañaraz et al. 2015a; Alinari et al. 2019; Kowaljow et al. 2019). This has been repeatedly discussed as one of the causes of the persistently low forest cover in the Córdoba mountains along the whole gradient, but particularly at the medium and highest elevations (Renison et al. 2006; Cingolani et al. 2008; Giorgis et al. 2013, 2017; Alinari et al. 2015, 2019; Argibay and Renison 2018). Nevertheless, to date the pattern of fire incidence along the elevation gradient is not clear, blurring any interpretation about the role of fire on vegetation response to elevation. A previous study found the highest fire incidence at intermediate elevations (Mari 2005), but it was not conclusive, since it involved only a small area, a restricted elevation range (650-2350 m a. s. l.) and a short period (3 years). Thus, it is necessary to better explore the relationship between elevation and fire incidence across a larger area, including the complete elevation gradient over a longer period.

In this context, our objective was to describe fire incidence along an extensive elevation gradient in the mountains of Córdoba, in central Argentina. We compared fire incidence at different elevations using a spatially explicit 18-year fire database derived from remote sensing. Our description will contribute to improve our understanding of the multiple co-occurring factors which condition the vegetation response to elevation, and to better focus our conservation and restoration projects.

Materials and Methods

Study area

The study was conducted in the Córdoba mountains in central Argentina (ca. 19000 km^2) (Figure 1, Annex 1 and 2). They consist in three main ranges that run 110 km from east to west (63°19′ W - 65°27′ W) and 430 km from north to south (29°33′ S - 33°18′ S). Their elevation varies from *ca*. 500 to 2790 m a. s. l., with Mt. Champaquí being the highest peak (Figure 1). We analyzed fire incidence in non-cultivated lands included in the eastern and central mountain ranges, comprising four

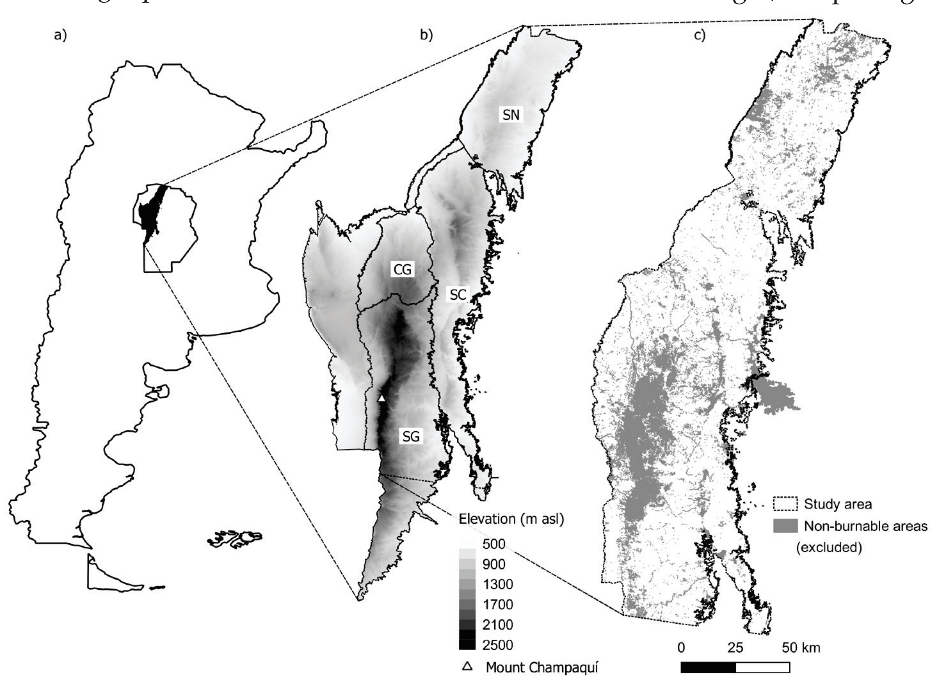

Figure 1. a) Córdoba mountains in central Argentina (areas with elevation above 500 m a. s. l.). b) Elevation gradient in Córdoba mountains and the four studied mountain systems (SN: Sierras del Norte; SC: Sierras Chicas; CG: Cumbres de Gaspar; SG: Sierras Grandes). c) Study area showing excluded non-burnable areas (water bodies, rocky and urban areas).

Figura 1. a) Sierras de Córdoba en el centro de Argentina (áreas con altitud mayor a 500 m s. n. m.). b) Gradiente altitudinal de las Sierras de Córdoba y los cuatro sistemas serranos estudiados (SN: Sierras del Norte; SC: Sierras Chicas; CG: Cumbres de Gaspar; SG: Sierras Grandes). c) Área de estudio indicando las áreas no combustibles excluidas (cuerpos de agua, áreas rocosas y urbanizadas).

mountain systems (Figure 1, Annex 1 and 2). The western mountain range was not included in the study area due to the lack of spatially explicit fire databases at medium-high spatial resolution.

As in any typical mountain system, the climate in the Córdoba mountains is largely associated with the elevation gradient, with a minor influence of geographic gradients or other topographic features (Marcora et al. 2008; Giorgis et al. 2015; Sparacino et al. 2019). In the study area, mean annual temperature vary from an average of 16.5 °C below 900 m a. s. l. to 7.5 °C at the highest elevation in Mt Champaquí, with potential evapotranspiration following a similar decreasing trend (Table 2) (Marcora et al. 2008; Fick and Hijmans 2017). In the upper portion of the study area, mean annual precipitation reaches more than 900 mm, whereas at low elevations there is a regional rainfall gradient from east (annual rainfall 700-800 mm) to west (annual rainfall 500-600 mm), with most rainfall being concentrated in the warmest months (Colladon and Pazos 2014; Giorgis et al. 2015; Colladon 2018) (Table 2). Relatively high temperatures occur in August and September, after some months of very low rainfall, favoring seasonal fires in late winter and early spring. In the 1999-2011 period, large fires (>1000 ha) accounted for 74% of the burned area, although they only represented 3.5% of fire events (Argañaraz et al. 2015a). According to the Ministry of Environment and Sustainable Development of Argentina (2001-2014), 91% of wildfires in Córdoba are accidentally or intentionally ignited by humans. Part of these fires are set by farmers to promote forage re-growth during the dry season and to clear forest areas for cattle breeding. Under appropriate weather and fuel moisture conditions, these fires often escape from control, affecting large areas (Argañaraz et al. 2018). The fire return interval in non-cultivated lands is on average about 50 years (calculated from Argañaraz et al. 2015a), with high spatial variability according to different factors, such as rainfall, potential evapotranspiration, land cover type, and proximity to human settlements among others (Argañaraz et al. 2015b).

The elevation gradient in central Argentina can be divided into two distinct belts with different phytogeographic affinities, potentially covered by different forest types, with a transition belt between them (Kurtz 1904; Prado 1993; Cabido et al. 1998; Martínez et al. 2017). The flora in the lowest belt, up to 1300 m a. s. l., is related to the Chaco Phytogeographic Province, with forests characterized by the trees *Lithraea molleoides* (Vell.) Engl., *Celtis ehrenbergiana* (Klotzch) Liebm. and/or *Schinopsis marginata* Engl. (Kurtz

Table 2. Mean annual temperature, annual potential evapotranspiration and annual precipitation for different elevation intervals in the Córdoba mountains. Averages, along with maximum and minimum values, are provided for each interval[1,2,3].

Tabla 2. Temperatura media anual, evapotranspiración potencial anual y precipitación anual para diferentes intervalos altitudinales en las Sierras de Córdoba. Se indican los promedios, junto con los valores máximos y mínimos de cada intervalo[1,2,3].

Mountain belt	Elevation interval (m a. s. l.)	Temperature[1] (°C)	Potential ET[2] (mm/year)	Precipitation[3] (mm/year)
Chaco	500-900	16.5 (14.3-18.8)	811 (724-924)	711 (641-781)
	901-1300	14.7 (13.0-16.4)	740 (688-810)	779 (752-823)
Transition	1301-1700	13.0 (11.5-14.5)	688 (647-748)	868 (825-911)
Andes	1701-2100	11.1 (9.8-12.7)	635 (589-690)	924 (924-924)
	>2100	9.5 (7.5-10.4)	595 (537-634)	953 (921-993)

[1] Data obtained from WorldClim averages for the period 1970-2000 (Fick and Hijmans 2017). [2] Calculated from WorldClim monthly temperature averages and light hours using the Thornthwaite index (1948). [3] Data obtained from 10 meteorological stations (1992-2017) plus one rain gauge (1994-2018) in the San Antonio watershed, located in the Sierras Grandes eastern range (Colladon and Pazos 2014; Colladon 2018; R. Renison, personal communication).

[1] Datos obtenidos a partir de promedios del período 1970-2000 de WorldClim (Fick and Hijmans 2017). [2] Calculado a partir de los promedios de temperatura mensual de WorldClim y horas de luz utilizando el índice de Thornthwaite (1948). [3] Datos obtenidos a partir de 10 estaciones meteorológicas (1992-2017) y un pluviómetro (1994-2018) ubicados en la cuenca del Río San Antonio, en la vertiente este de las Sierras Grandes (Colladon and Pazos 2014; Colladon 2018; R. Renison, comunicación personal).

1904; Luti et al. 1979; Giorgis et al. 2017). The flora in the upper belt, above 1700 m a. s. l., is related to the Andes, with forests characterized by *Polylepis australis* and *Maytenus boaria* (Kurtz 1904; Luti et al. 1979; Cabido et al. 2018). The transition belt, between 1300 and 1700 m a. s. l., has a Chaco flora in the lowest part, that is progressively replaced with the Andes flora of the upper belt.

The current landscape is a complex mosaic of native and alien forests, shrublands, grasslands, outcrops and rock pavements. These different patches occur along the entire elevation gradient, but their relative cover changes with elevation (Table 1). The lowest part of the Chaco belt up to 900 m a. s. l. is dominated by native and alien forests and shrublands, whereas grasslands become more abundant above 900 m a. s. l. The transition belt between 1300 and 1700 m a. s. l. is dominated by grasslands and shrublands, with small forest patches (Giorgis et al. 2017). The Andes belt is dominated by grasslands, rocky outcrops and pavements, with little woody vegetation (Tables 1 and 3); although some relatively large forest patches can be found (Cingolani et al. 2004). Fire eliminates a large proportion of aerial tissues, but underground tissues of most native perennial species survive (Lipoma et al. 2016). Herbaceous plants rapidly recover their biomass and are very abundant a few years after fire (Giorgis et al. 2013; Alinari 2017; Jaacks 2019). Woody species have high survival rates, usually more than 80%, except in cases of extremely severe fires (Gurvich et al. 2005; Torres et al. 2014; Herrero et al. 2016; Argibay and Renison 2018; Alinari et al. 2019). They generally resprout from basal meristems, and only small individuals recover their pre-fire size two or three years after the fire. Large individuals have more probability of partially escape the fire, but often lose all their aerial biomass. In those cases, despite their initially high resprouting vigor, they need longer periods to recover their large pre-fire size (Renison et al. 2002; Gurvich et al. 2005; Alinari et al. 2015, 2019; Herrero et al. 2016).

Fire data

To analyze fire incidence along the elevation gradient, we obtained a database of fires that occurred between 1999 and 2017. The database was derived from Landsat TM/ETM+/OLI imagery (Path/rows: 229/81, 229/82; 30 m pixel) acquired between 1999 and 2017, with the exception of 2012, when Landsat 5 was no longer operational. We used the same fire database as in Argañaraz et al. (2015a), in which fire perimeters from 1999 to 2011 were extracted using the two-phase algorithm proposed by Bastarrika et al. (2011). During the first phase, pixels with high chances of being burnt are identified (seeds) and serve as the starting point for the second phase, when a region growing algorithm is applied to delineate the burned patch and its unburned islands within fire perimeters. We added the 2013-2017 period with an updated version of the Burned Area Mapping Software (BAMS, Bastarrika et al. 2014) implemented in Google Earth Engine (GEE). BAMS is based on a supervised classification strategy, in which the user provides samples of burned areas by visual interpretation and then this information is used to extract burned perimeters. The minimum mapping unit of the fire database was 5 ha, because smaller areas had higher error rates and accounted only for a small proportion of the total burned area. The producer's accuracy of the fire database ranged from 88 to 97% and the user's accuracy ranged from 71 to 96% (Argañaraz et al. 2015a).

Sampling design and data analyses

We divided our elevation gradient into five intervals, two of them corresponding to the Chaco belt (500-900, 901-1300 m a. s. l.), one corresponding to the transition belt (1301-1700 m a. s. l.), and two corresponding to the Andes belt (1701-2100 and >2100 m a. s. l.). For this purpose, we used the Advanced Spaceborne Thermal Emission and Reflection Radiometer Global Digital Elevation Model (ASTER GDEM) version 2 (30-m spatial resolution (Tachikawa et al. 2011). To limit our analysis to burnable areas, we excluded rocky and urban patches, as well as water bodies (Table 3). The rock mask was derived from Landsat TM images acquired in 2009, through a supervised classification based in training areas (A.M. Cingolani, unpublished map). The urban mask was obtained by visual interpretation of Google Earth images and the mask for water bodies was derived from a vector layer provided by the Administration of Water Resources of Córdoba Province. For each study year, we assessed fire incidence as the total burned proportion (%) at each elevation interval for the whole study area, and for each mountain system separately (Sierras Grandes, Sierras Chicas, Cumbres de Gaspar and Sierras del Norte) (Figure 1, Annex 1 and 2).

Table 3. Unburnable proportion (%) for each elevation interval in the four studied mountain systems in Córdoba (Argentina).

Tabla 3. Proporción de área no combustible (%) por intervalo altitudinal en los cuatro sistemas serranos estudiados en Córdoba (Argentina).

Mountain belt	Elevation interval (m a. s. l.)	Sierras Chicas	Sierras Grandes	Cumbres de Gaspar	Sierras del Norte	Total[1]
Chaco	500-900	7.63	3.86	2.49	1.50	4.13
	901-1300	2.29	1.05	0.77	0.80	1.45
Transition	1301-1700	0.28	4.57	3.90	-	3.60
Andes	1701-2100	0.18	17.16	15.21	-	16.35
	> 2100	-	19.36	-	-	19.36
	Total[1]	5.47	7.15	2.68	1.45	4.69

[1] The last column and row indicate the total unburnable proportions (%) for each elevation interval and mountain system, respectively. The unburnable proportion includes areas occupied by rock, urban areas and water bodies, and was discarded from the comparisons of fire incidence among elevation intervals.

[1] La última columna y fila indican las proporciones no combustibles totales (%) de cada intervalo altitudinal y sistema serrano, respectivamente. La proporción de área no combustible incluye áreas ocupadas por roca, urbanizaciones y cuerpos de agua, y fue descartada de la comparación de incidencia del fuego entre intervalos altitudinales.

To analyze if fire incidence differed among elevation intervals, we used a general mixed linear model with the elevation interval included as a fixed factor and year (n=18) as a random factor, followed by Fisher LSD post-hoc comparisons (P<0.05). We performed this analysis for the whole study area, and for each mountain system separately. Statistical analyses were performed with Infostat (Di Rienzo et al. 2017) using an R interface (version 3.4.0, 2017). Finally, for each elevation interval, we calculated the average fire return interval as the time required to burn an area equivalent to the total burnable area.

Results

All elevation intervals evidenced fire activity almost every year, reaching burned proportions close to 10% in some extreme years. Fire incidence showed a hump-shaped pattern along the elevation gradient (Figure 2). The highest fire incidence occurred at intermediate elevations, in the 1301-1700 m interval, with an average of 3.2% of the area burned annually (ranging from 0.1-10.0%). It was significantly different from incidence in the lowermost and uppermost intervals (500-900 m and >2100 m, respectively), and tended to be different than in the 1701-2100 m interval (P=0.06). The 901-1300 m interval ranked second, with 2.7% burned annually on average (ranging from 0.1 to 11.4%), and showed no significant differences from the 1301-1700 m interval. In the third and fourth place, 1.9 and 1.7% of the area in the upper intervals was burned annually on average (ranging from 0.2 to 9.0% and 0.0 to 13.2%, for the 1701-2100 and >2100 m intervals, respectively), with no differences between them (Figure 2). The lowermost interval (500-900 m) showed the lowest fire incidence, with 1.3% being burned annually (ranging from <0.1-4.0%), and the differences from the two intervals following in elevation were significant (Figure 2). Based on our results, we calculated an average fire return interval of 80 years for the lowest interval (500-900 m), of 37 and 32 years for the following intervals (901-1300 m and 1301-1700 m, respectively), and of 53 and 59 years for both upper intervals (1701-2100 m and >2100 m, respectively). For further details, the fire frequency map and proportion of each elevation interval burned with different fire frequencies are provided in Annex 1.

The analyses of each mountain system separately showed similar patterns (Figure 3), but without significant differences due to the high variability in the data, except in Sierras Grandes, where the differences between the lowest and the upward intervals were significant. For two of the four mountain systems, the highest fire incidence occurred in the 1301-1700 m interval, and for the remaining two, in the 901-1300 m interval, but one of them, Sierras del Norte, does not reach elevations higher than 1300 m a. s. l. (Annex 2).

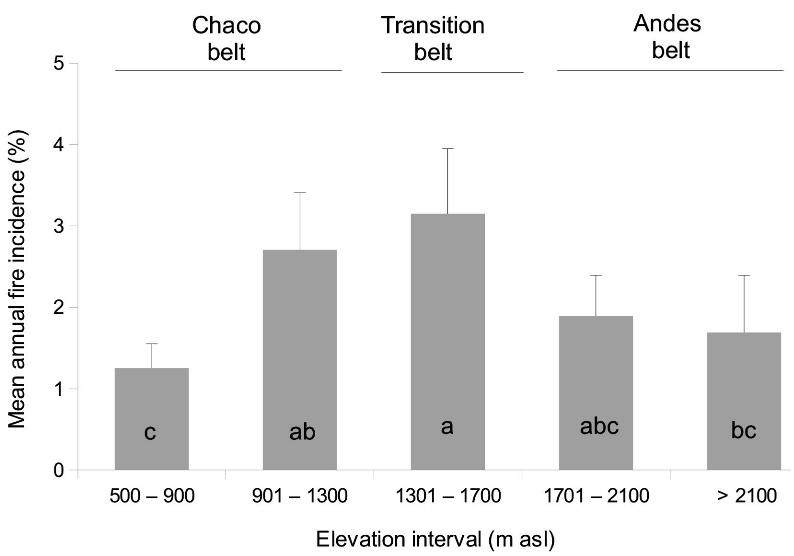

Figure 2. Mean annual fire incidence (%) and standard error for each elevation interval in the mountains of Córdoba (Argentina) between 1999 and 2017. Different letters indicate significant differences among intervals (P<0.05, n=18 years). P-value was close to significance (P=0.06) between the 1301-1700 and 1701-2100 m intervals.

Figura 2. Incidencia media anual del fuego (%) y error estándar para cada intervalo altitudinal en las Sierras de Córdoba (Argentina) entre 1999 y 2017. Letras diferentes indican diferencias significativas entre intervalos (P<0.05, n=18 años). El valor de P se aproximó a la significancia (P=0.06) entre los intervalos 1301-1700 y 1701-2100 m.

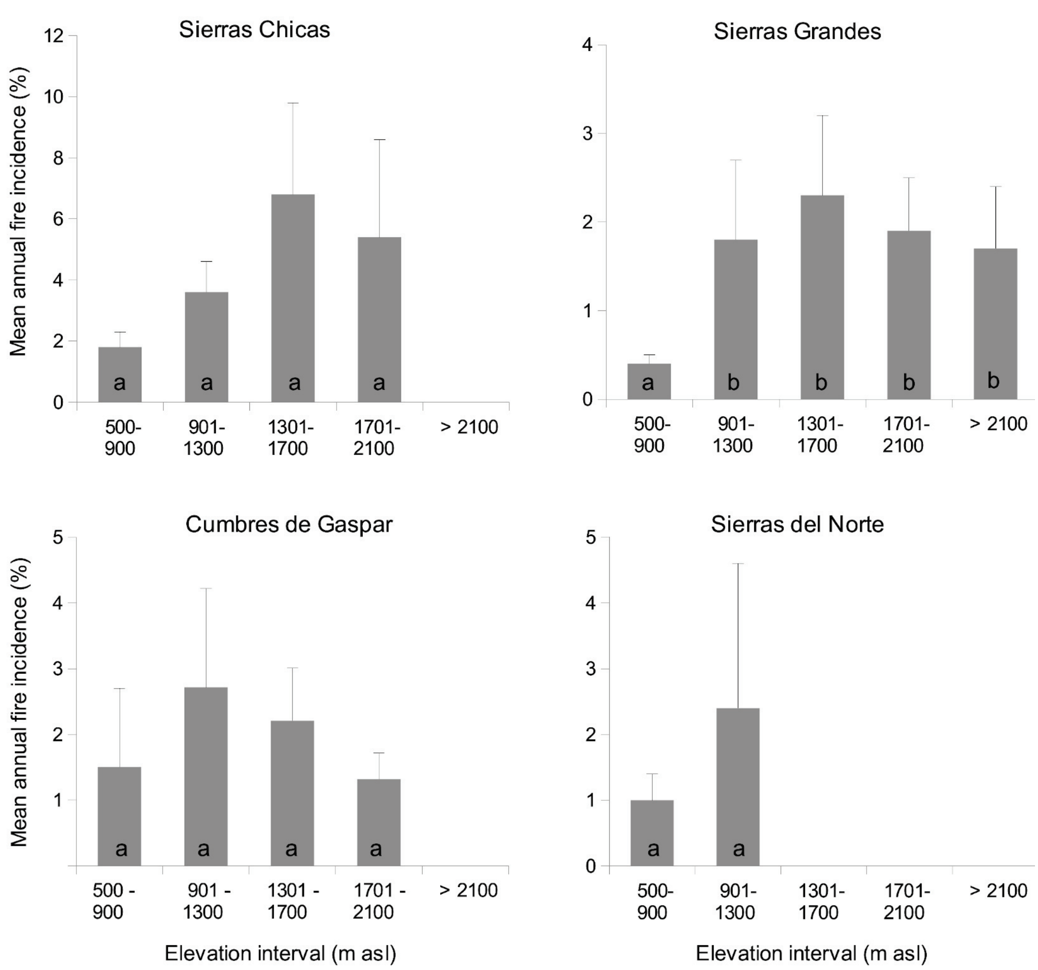

Figure 3. Mean annual fire incidence (%) and standard error per elevation interval in the four studied mountain systems in Córdoba (Argentina) between 1999 and 2017. Different letters indicate significant differences among intervals (P<0.05, n=18 years).

Figura 3. Incidencia media anual del fuego (%) y error estándar por intervalo altitudinal en los cuatro sistemas serranos estudiados en Córdoba (Argentina) entre 1999 y 2017. Letras diferentes indican diferencias significativas entre intervalos (P<0.05, n=18 años).

DISCUSSION

During the study period, fire activity was high in the mountains of Córdoba, as reported in previous studies (Argañaraz et al. 2015a). Our results indicate that wildfires occurred at all elevations almost every year; however, fire incidence was not homogeneous along the elevation gradient. It was maximum at intermediate elevations, displaying a hump-shaped pattern. Our descriptive results highlight the differential role that fire may play as a modulator of vegetation physiognomy along the elevation gradient (Giorgis et al. 2013, 2015; Kowaljow et al. 2019). Our description will contribute to provide a basis for discussing the multiple co-occurring factors which shape the vegetation response to elevation, and to build data-based hypotheses on the role of disturbance in mountains.

Fire incidence along the elevation gradient

The greater fire incidence observed at the 901-1300 m and 1301-1700 m elevation intervals is consistent with a sharp increase in the extent of grasslands above 900 m a. s. l. (Table 1) (Giorgis et al. 2013, 2017). Despite some variability in estimations among studies and sectors of the mountains, it is clear that below 900 m a. s. l. grasslands occupy less than 20% of the area, while above this elevation they cover far more extensions (Table 1). When not excessively grazed, grasslands tend to favor fire ignition and spread due to the accumulation of fine fuels, which are in general more flammable than the coarser fuels provided by woody species, trees in particular (Jaureguiberry et al. 2011; Argañaraz et al. 2018; Landi 2018; Kowaljow et al. 2019; Foster et al. 2020). In contrast, well conserved forests often limit fire ignition and spread because fine biomass accumulation and desiccation are reduced under the increased moisture and lower light conditions of the understory environment (Kunst and Bravo 2003; Tálamo and Caziani 2003; Giorgis et al. 2013; Paritsis et al. 2015; Tiribelli et al. 2018). In line with these antecedents, Argañaraz et al. (2015a) found that grasslands are proportionally more burned than forests in the Córdoba mountains.

In the Andes belt, above 1700 m a. s. l., despite the high grassland cover, fire incidence was lower. Here, geomorphology and climate may be the most important factors limiting fire ignition and/or spread (Renison et al. 2006; Argañaraz et al. 2015b). This belt is composed of steep escarpments, hilly and rocky uplands, deep valleys and dissected plateaus, resulting in a much more rugged and rocky landscape than those of the Chaco and transition belts (Cabido et al. 1987). Besides rocky outcrops, the area also has large surfaces of rock pavements and stonelands, resulting from erosion processes triggered by long-term livestock grazing and fires (Cingolani et al. 2008, 2013). These unburnable rocky areas cover a large proportion of the upper belt (16-19%) (Table 3), interrupting the spatial continuity of the fire-propagating matrix. This landscape feature limits fire spread and, in some cases, probably facilitates fire suppression activities. In fact, the largest burned areas in this belt occurred in sectors with lower proportion of unburnable surface (Figure 1; Annex 1). Additionally, deep valleys and ravines often stop the advance of fire due to their more humid conditions and low topographic position in the landscape (Renison et al. 2006). Climatic characteristics may also be playing a role in this upper belt. Low potential evapotranspiration and higher rainfall (Table 2) reduce soil water deficit, shortening the fire season, reducing the desiccation of fuels and the fire-prone weather conditions, as was reported in this and other mountains (Kasischke et al. 2002; Littell et al. 2009; Argañaraz et al. 2015a). Additionally, comparatively high soil moisture allows the occurrence of large extensions of grazing-maintained lawns dominated by short species (Cingolani et al. 2008). These lawns have very low standing biomass and litter, thus contributing to the limitation of fire spread (Vaieretti et al. 2013). Our result agrees with the lower fire activity observed in more humid areas, both locally (Argañaraz et al. 2015b) and globally (van der Werf et al. 2008; Pausas and Ribeiro 2013).

The low fire incidence observed in the lowest interval (500-900 m) was different than the expectations based on the drier conditions of low-mountain areas, which lead to longer fire seasons and a faster desiccation of fuels (Rogeau and Armstrong 2017). This low incidence could be partially related to the proximity of urban or interface areas, which are mostly concentrated in this interval (Gavier and Bucher 2004; Argañaraz et al. 2017). Even though at the local scale fire frequency is higher at relatively short distances from urban areas, the surfaces affected are often small, due to the earlier detection of smoke columns. This allows firemen to reach the area sooner, increasing the chances of controlling the fire (Argañaraz et al. 2015b). Additionally, as we mentioned above, the higher native forest cover in this interval compared to upper elevations, together with the expanding woody alien-dominated stands, may limit fire expansion in forested areas due to the lower fine fuel accumulation in the understory environment and higher fuel moisture (Gavier-Pizarro et al. 2012; Giorgis et al. 2016, 2017; Herrero et al. 2016; Argañaraz et al. 2016). A complementary explanation may be associated with the possible limitations to fine fuel productivity imposed by the lower rainfall and higher potential evapotranspiration in this interval, which decrease soil water availability for plants, as was proposed for this and other ecosystems (van der Werf et al. 2008; Argañaraz et al. 2015b).

Based on our fire database, we calculated the average fire return interval for each elevation interval, which ranged from 32 years (1300-1700 m) to 80 years (500-900 m). It is important to highlight that these intervals should be shorter at the local level, especially in those areas covered with more flammable vegetation (e.g., grasslands and grassy shrublands) and at relatively short distances to urban areas and roads (Argañaraz et al. 2015a, 2015b, 2017). For example, a dendroecological study performed approximately at 700 m a. s. l. close to a populated area reported six widespread fires over 82 years in a grass/shrub-dominated community. In turn, no widespread fires were detected in a nearby forest-dominated community for at least 85 years (Kowaljow et al. 2019).

Fire as a driver of vegetation distribution

Fires strongly reduce aerial biomass, and play a role in restricting forest distribution along the whole elevation gradient (Gurvich et al. 2005; Giorgis et al. 2013, 2017; Torres et al. 2014; Alinari et al. 2015; Lipoma et al. 2016; Kowaljow et al. 2019). Fire limits the expansion of both Chaco and Andes forests because small saplings or resprouting native trees grow at slow rates, about 5-20 cm per year, except in the first post-fire growth season when previously large trees may grow up to 1.5-2 m. The usually slow growth rate of native trees combined with a relatively high fire occurrence increases their chances of being burned before reaching maturity, as reported also for other systems (Marcora et al. 2008, 2013; Coop et al. 2010; Renison et al. 2015; Herrero et al. 2016; Vera 2016; Capó et al. 2016; Alinari 2017; Argibay and Renison 2018; Kowaljow et al. 2019). However, despite of wildfires having an effect along the whole gradient, our results suggest that their influence vary with elevation.

According to the observed pattern of fire incidence along our study gradient, the restriction imposed by fire to forest expansion is likely to be more severe at the transition belt (1300-1700 m a. s. l.) and the upper portion of the Chaco belt (901-1300 m a. s. l.) than at other elevations. Fires contribute to the persistence of early successional stages dominated by grasses and/or shrubs, which in turn contribute to fire spread (Kowaljow et al. 2019). Fires spreading across grasslands may even gradually reduce forest cover by burning mature individuals, which in our system are rarely taller than 10-14 m, at the grassland/forest border, or in open forests, where trees are surrounded by grasses and shrubs (Giorgis et al. 2017). In the transition belt forest cover is particularly low, and forest patches, when present, are of small size (Zak 2008; Giorgis et al. 2017; Cabido et al. 2018). In addition to the higher fire incidence, this low forest cover may also be related to a poorer performance of woody species at intermediate elevations, either under non-fire conditions (Marcora et al. 2008, 2013; Vera 2016; but see Lanza et al. 2018) or when recovering from a fire event. Studies monitoring the post-fire response of both Chaco and Andes dominant woody species along the elevation gradient coincided in observing higher mortality and/or slower post-fire recovery at the transition belt, compared with the same species growing at lower (Chaco) or higher (Andes) elevations, respectively (Alinari 2017; Argibay and Renison 2018).

In the Andes belt, forest cover is low, despite the decreased fire incidence compared with the transition belt. However, some relatively large patches of *Polylepis australis* stands can be found in areas far away from sources of long-term fire and livestock disturbance (Cingolani et al. 2008). Through simulations, this study found that under a low disturbance long-term scenario, forests would occupy five times more area in the Andes belt. The dominant tree species of these elevations, *P. australis* and *M. boaria*, are highly consumed by livestock (Giorgis et al. 2010; Marcora et al. 2013). As a consequence, livestock imposes a serious restriction to the growth and survival of individuals shorter than 2 m, strongly limiting forest expansion (Teich et al. 2005; Marcora et al. 2013; Cingolani et al. 2014; Renison et al. 2015; Giorgis et al. 2020). Thus, the combination between fire and livestock, and not only fire, may be restricting forest expansion in the Andes belt. When a fire reduces the size of *Polylepis australis* individuals, regrowth tissues are browsed by livestock, reducing biomass accumulation and survival (Alinari et al. 2015; Argibay and Renison 2018). In turn, when compared with Andes species, Chaco species are less palatable and livestock imposes a less severe limitation to their growth and survival (Torres and Renison 2015, 2016; Capó et al. 2016).

In the mountains of central Argentina, the combination of a slow forest recovery with a relatively high fire incidence associated with a strong feedback between vegetation and fire contributes to the persistence of a landscape dominated by early successional stages (Cingolani et al. 2013; Argañaraz et al. 2015a; Giorgis et al. 2017; Kowaljow et al. 2019). Similar positive feedbacks between fire and vegetation were described for other Chaco subregions and temperate forests of the southern hemisphere, where fire promotes the dominance of shade-intolerant and more flammable species than those present in forests (Tálamo and Caziani 2003; Blanco et al. 2014; Paritsis et al. 2015; Kitzberger et al. 2016; Tepley et al. 2018). Thus, at present, it is particularly important to limit human-induced fire ignitions and fire spread in order to favor the opportunities for shrublands to mature into native closed forests in all mountain belts. This is particularly important considering that mature forests also face other threats at present. Wildland-urban interface areas are expanding on the mountains (Argañaraz et al. 2017), leading to forest loss and decreasing the area available for forest maturation and expansion. Additionally, livestock may be combined with fire to prevent forest recovery, mainly in the Andes belt; but more studies are needed to assess the relative role of livestock *versus* fire along the whole elevation gradient. Simultaneously, the region is being invaded by almost 40 alien tree and shrub species, hampering the recovery of native forests after fire (Giorgis et al. 2011, 2016; Gavier-Pizarro et al. 2012; Giorgis and Tecco 2014; Herrero et al. 2016; Tecco et al. 2016).

Acknowledgements. We thank Secretaría de Recursos Hídricos de la Provincia de Córdoba for providing the water body layer and I. Barberá and D. Renison for thoroughly reading the manuscript, and for J. Brasca for editing English in a previous version. We also thank the editor and two anonymous reviewers for helpful comments on this manuscript. ASTER GDEM is a product of NASA and METI. This study was funded by grants to JPA from FONCyT (PICT 2017-1766), to AMC from CONICET - DFG, Programa de Cooperación bilateral - Nivel II - Ejecución 2015-2017, D3975, and CONICET-PIP 112-201201-00164, and grants to LMB from SECyT-Universidad Nacional de Córdoba and FONCyT (PICT 1338-2016).

References

Acosta, A., S. Díaz, M. Menghi, and M. Cabido. 1992. Patrones comunitarios a diferentes escalas espaciales en pastizales de las Sierras de Córdoba, Argentina. Revista Chilena de Historia Natural **65**:195-207.

Alinari, J. 2017. ¿Puede el fuego limitar la distribución altitudinal de las principales especies del bosque serrano de la provincia de Córdoba? PhD Thesis, Universidad Nacional de Córdoba, Córdoba, Argentina.

Alinari, J., A. M. Cingolani, A. R. von Muller, and M. Cabido. 2019. El tamaño de los individuos y el microambiente afectan el daño por fuego y la supervivencia en árboles del Chaco Serrano. Ecología Austral **29**:272-284. https://doi.org/10.25260/EA.19.29.2.0.841.

Alinari, J., A. von Muller, and D. Renison. 2015. The contribution of fire damage to restricting high mountain Polylepis australis forests to ravines: Insights from an un-replicated comparison. Ecología Austral **25**:11-18.

Archibald, S., C. E. R. Lehmann, C. M. Belcher, W. J. Bond, R. A. Bradstock, A.-L. Daniau, K. G. Dexter, E. J. Forrestel, M. Greve, T. He, S. I. Higgins, W. A. Hoffmann, B. B. Lamont, D. J. McGlinn, G. R. Moncrieff, C. P. Osborne, J. G. Pausas, O. Price, B. S. Ripley, B. M. Rogers, D. W. Schwilk, M. F. Simon, M. R. Turetsky, G. R. V. der Werf, and A. E. Zanne. 2018. Biological and geophysical feedbacks with fire in the Earth system. Environmental Research Letters **13**(3):1-19 [033003]. https://doi.org/10.1088/1748-9326/aa9ead.

Argañaraz, J. P., G. Gavier Pizarro, M. Zak, and L. M. Bellis. 2015a. Fire regime, climate, and vegetation in the Sierras de Córdoba, Argentina. Fire Ecology **11**:55-73. https://doi.org/10.4996/fireecology.1101055.

Argañaraz, J. P., G. Gavier Pizarro, M. Zak, M. A. Landi, and L. M. Bellis. 2015b. Human and biophysical drivers of fires in Semiarid Chaco mountains of Central Argentina. Science of The Total Environment **520**:1-12. https://doi.org/10.1016/j.scitotenv.2015.02.081.

Argañaraz, J. P., M. A. Landi, S. J. Bravo, G. I. Gavier-Pizarro, C. M. Scavuzzo, and L. M. Bellis. 2016. Estimation of live fuel moisture content from MODIS images for fire danger assessment in Southern Gran Chaco. IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing **9**:5339-5349. https://doi.org/10.1109/JSTARS.2016.2575366.

Argañaraz, J. P., M. A. Landi, C. M. Scavuzzo, and L. M. Bellis. 2018. Determining fuel moisture thresholds to assess wildfire hazard: a contribution to an operational early warning system. PLoS ONE **13**(10):e0204889. https://doi.org/10.1371/journal.pone.0204889.

Argañaraz, J. P., V. C. Radeloff, A. Bar-Massada, G. I. Gavier-Pizarro, C. M. Scavuzzo, and L. M. Bellis. 2017. Assessing wildfire exposure in the Wildland-Urban Interface area of the mountains of central Argentina. Journal of Environmental Management **196**:499-510. https://doi.org/10.1016/j.jenvman.2017.03.058.

Argibay, D. S., and D. Renison. 2018. Efecto del fuego y la ganadería en bosques de Polylepis australis (Rosaceae) a lo largo de un gradiente altitudinal en las montañas del centro de la Argentina. Bosque **39**:145-150. https://doi.org/10.4067/S0717-92002018000100145.

Bastarrika, A., M. Alvarado, K. Artano, M. P. Martínez, A. Mesanza, L. Torre, R. Ramo, and E. Chuvieco. 2014. BAMS: A Tool for Supervised Burned Area Mapping Using Landsat Data. Remote Sensing **6**:12360-12380. https://doi.org/10.3390/rs61212360.

Bastarrika, A., E. Chuvieco, and M. P. Martín. 2011. Mapping burned areas from Landsat TM/ETM+ data with a two-phase algorithm: Balancing omission and commission errors. Remote Sensing of Environment **115**:1003-1012. https://doi.org/10.1016/j.rse.2010.12.005.

Blanco, C. C., S. Scheiter, E. Sosinski, A. Fidelis, M. Anand, and V. D. Pillar. 2014. Feedbacks between vegetation and disturbance processes promote long-term persistence of forest-grassland mosaics in south Brazil. Ecological Modelling **291**:224-232. https://doi.org/10.1016/j.ecolmodel.2014.07.024.

Bowman, D. M., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D'Antonio, R. S. DeFries, J. C. Doyle, S. P. Harrison, and others. 2009. Fire in the Earth system. Science **324**:481-484. https://doi.org/10.1126/science.1163886.

Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. Journal of Arid Environments **67**:148-164. https://doi.org/10.1016/j.jaridenv.2006.09.027.

Cabido, M., and A. Acosta. 1988. Degradación en pastizales climácicos de las Sierras de Córdoba, Argentina. Zonación a partir del Pastizal de *Deyeuxia hieronymi* en Pampa de Achala. Documents Phytosociologiques **11**:573-581.

Cabido, M., R. Breimer, and G. Vega. 1987. Plant communities and associated soil types in a high plateau of the Córdoba mountains, central Argentina. Mountain Research and Development **7**(1):25-42. https://doi.org/10.2307/3673322.

Cabido, M., G. Funes, E. Pucheta, F. Vedramini, and S. Díaz. 1998. A chorological analysis of the mountains from central Argentina. Is all what we call Sierra Chaco really Chaco? Contribution to the study of the flora and vegetation of the Chaco: XII. Candollea **53**:321-331.

Cabido, M., S. R. Zeballos, M. Zak, M. L. Carranza, M. A. Giorgis, J. J. Cantero, and A. T. R. Acosta. 2018. Native woody vegetation in central Argentina: Classification of Chaco and Espinal forests. Applied Vegetation Science **21**:298-311. https://doi.org/10.1111/avsc.12369.

Capó, E. A., R. Aguilar, and D. Renison. 2016. Livestock reduces juvenile tree growth of alien invasive species with a minimal effect on natives: a field experiment using exclosures. Biological Invasions **18**:2943-2950. https://doi.org/10.1007/s10530-016-1185-3.

Caprio, A. C., and T. W. Swetnam. 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. United States Department of Agriculture Forest Service. General Technical Report INT **320**:173-179.

Cingolani, A. M., D. Renison, P. A. Tecco, D. E. Gurvich, and M. Cabido. 2008. Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. Journal of Biogeography **35**:538-551. https://doi.org/10.1111/j.1365-2699.2007.01807.x.

Cingolani, A. M., D. Renison, M. R. Zak, and M. Cabido. 2004. Mapping vegetation in a heterogeneous mountain rangeland using landsat data: an alternative method to define and classify land-cover units. Remote Sensing of Environment **92**:84-97. https://doi.org/10.1016/j.rse.2004.05.008.

Cingolani, A. M., M. V. Vaieretti, M. A. Giorgis, N. La Torre, J. I. Whitworth-Hulse, and D. Renison. 2013. Can livestock and fires convert the sub-tropical mountain rangelands of central Argentina into a rocky desert? The Rangeland Journal **35**:285-297. https://doi.org/10.1071/RJ12095.

Cingolani, A. M., M. V. Vaieretti, M. A. Giorgis, M. Poca, P. A. Tecco, and D. E. Gurvich. 2014. Can livestock grazing maintain landscape diversity and stability in an ecosystem that evolved with wild herbivores? Perspectives in Plant Ecology, Evolution and Systematics **16**:143-153. https://doi.org/10.1016/j.ppees.2014.04.002.

Colladon, L. 2018. Anuario pluviométrico 2012/13-2016/17, cuenca del Río San Antonio. Informe interno del CIRSA. Informe interno del CIRSA, Instituto Nacional del Agua.

Colladon, L., and I. Pazos. 2014. Anuario pluviométrico 1992/1993 - 2011/2012. Cuenca del Río San Antonio. Sistema del Río Suquía, provincia de Córdoba. Instituto Nacional del Agua, Buenos Aires, Argentina.

Coop, J. D., R. T. Massatti, and A. W. Schoettle. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science **21**:472-487. https://doi.org/10.1111/j.1654-1103.2009.01154.x.

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. González, M. Tablada, and C. W. Robledo. 2017. InfoStat, versión 2017. Centro de Transferencia InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas: new climate surfaces for global land areas. International Journal of Climatology **37**:4302-4315. https://doi.org/10.1002/joc.5086.

Foster, C. N., S. C. Banks, G. J. Cary, C. N. Johnson, D. B. Lindenmayer, and L. E. Valentine. 2020. Animals as agents in fire regimes. Trends in Ecology and Evolution **35**:346-356. https://doi.org/10.1016/j.tree.2020.01.002.

Gavier, G. I., and E. H. Bucher. 2004. Deforestación de las Sierras Chicas de Córdoba (Argentina) en el período 1970-1997. Academia Nacional de Ciencias. Miscelánea **101**:1-27.

Gavier-Pizarro, G. I., T. Kuemmerle, L. E. Hoyos, S. I. Stewart, C. D. Huebner, N. S. Keuler, and V. C. Radeloff. 2012. Monitoring the invasion of an exotic tree (*Ligustrum lucidum*) from 1983 to 2006 with Landsat TM/ETM+ satellite data and Support Vector Machines in Córdoba, Argentina. Remote Sensing of Environment **122**:134-145. https://doi.org/10.1016/j.rse.2011.09.023.

Giorgis, M. A., A. M. Cingolani, and M. Cabido. 2013. El efecto del fuego y las características topográficas sobre la vegetación y las propiedades del suelo en la zona de transición entre bosques y pastizales de las sierras de Córdoba, Argentina. Boletín de la Sociedad Argentina de Botánica **48**:493-513. https://doi.org/10.31055/1851.2372.v48.n3-4.7555.

Giorgis, M. A., A. M. Cingolani, D. E. Gurvich, P. A. Tecco, J. Chiapella, F. Chiarini, and M. Cabido. 2017. Changes in floristic composition and physiognomy are decoupled along elevation gradients in central Argentina. Applied Vegetation Science **20**:558-571. https://doi.org/10.1111/avsc.12324.

Giorgis, M. A., A. M. Cingolani, P. A. Tecco, M. Cabido, M. Poca, and H. von Wehrden. 2016. Testing alien plant distribution and habitat invasibility in mountain ecosystems: growth form matters. Biological invasions **18**:2017-2028. https://doi.org/10.1007/s10530-016-1148-8.

Giorgis, M. A., A. M. Cingolani, I. Teich, and M. Poca. 2020. Can livestock coexist with Polylepis australis forests in mountains of central Argentina? Setting thresholds for a land sharing landscape. Forest Ecology and Management **457**:117728. https://doi.org/10.1016/j.foreco.2019.117728.

Giorgis, M. A., M. L. Lopez, D. Rivero, and A. M. Cingolani. 2015. Cambios climáticos en las sierras de Córdoba (Argentina) durante el holoceno. Aportes a las reconstrucciones climáticas a través del análisis de silicofitolitos del sitio arqueológico El Alto 3. Boletín de la Sociedad Argentina de Botánica **50**:361-375. https://doi.org/10.31055/1851.2372.v50.n3.12526.

Giorgis, M. A., and P. A. Tecco. 2014. Árboles y arbustos invasores de la Provincia de Córdoba (Argentina): una contribución a la sistematización de bases de datos globales. Boletín de la Sociedad Argentina de Botánica **49**:581-603. https://doi.org/10.31055/1851.2372.v49.n4.9991.

Giorgis, M. A., P. A. Tecco, A. M. Cingolani, D. Renison, P. Marcora, and V. Paiaro. 2011. Factors associated with woody alien species distribution in a newly invaded mountain system of central Argentina. Biological Invasions **13**: 1423-1434. https://doi.org/10.1007/s10530-010-9900-y.

Gurvich, D. E., L. Enrico, and A. M. Cingolani. 2005. Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. Austral Ecology **30**:789-796. https://doi.org/10.1111/j.1442-9993.2005.01522.x. https://doi.org/10.1111/j.1442-9993.2005.01529.x.

Haugo, R. D., S. A. Hall, E. M. Gray, P. Gonzalez, and J. D. Bakker. 2010. Influences of climate, fire, grazing, and logging on woody species composition along an elevation gradient in the eastern Cascades, Washington. Forest Ecology and Management **260**:2204-2213. https://doi.org/10.1016/j.foreco.2010.09.021.

Hemp, A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. Global Change Biology **11**:1013-1023. https://doi.org/10.1111/j.1365-2486.2005.00968.x.

Herrero, M. L., R. C. Torres, and D. Renison. 2016. Do wildfires promote woody species invasion in a fire-adapted ecosystem? Post-fire resprouting of native and non-native woody plants in central Argentina. Environmental Management **57**:308-317. https://doi.org/10.1007/s00267-015-0616-8.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science **105**:367-368. https://doi.org/10.1126/science.105.2727.367.

Jaacks, G. 2019. Monitoreo de fuegos de vegetación en el Parque Nacional Quebrada del Condorito, Argentina. Informe de avance 2013-2018. Documento para el Expediente Nº 664 3.066/2013 de la Administración de Parques Nacionales (APN). Registro interno APN: 665 IF-2019-40838697-APN-PNQC#APNAC. Villa Carlos Paz, Córdoba, Argentina.

Jaureguiberry, P., G. Bertone, and S. Díaz. 2011. Device for the standard measurement of shoot flammability in the field. Austral Ecology **36**:821-829. https://doi.org/10.1111/j.1442-9993.2010.02222.x.

Kasischke, E. S., D. Williams, and D. Barry. 2002. Analysis of the patterns of large fires in the boreal forest region of Alaska. International Journal of Wildland Fire **11**:131-144. https://doi.org/10.1071/WF02023.

Kitzberger, T., E. Aráoz, J. H. Gowda, M. Mermoz, and J. M. Morales. 2012. Decreases in Fire Spread Probability with Forest Age Promotes Alternative Community States, Reduced Resilience to Climate Variability and Large Fire Regime Shifts. Ecosystems **15**:97-112. https://doi.org/10.1007/s10021-011-9494-y.

Kitzberger, T., G. Perry, J. Paritsis, J. Gowda, A. Tepley, A. Holz, and 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.

Körner, C. 2003. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer Science and Business Media. https://doi.org/10.1007/978-3-642-18970-8.

Kowaljow, E., M. S. Morales, J. I. Whitworth-Hulse, S. R. Zeballos, M. A. Giorgis, M. Rodríguez Catón, and D. E. Gurvich. 2019. A 55-year-old natural experiment gives evidence of the effects of changes in fire frequency on ecosystem properties in a seasonal subtropical dry forest. Land Degradation and Development **30**:266-277. https://doi.org/10.1002/ldr.3219.

Kunst, C., and S. Bravo. 2003. Ecología y régimen de fuego en la región chaqueña Argentina. Pp. 109-118 *in* C. Kunst, S. Bravo and J. Panigatti (eds.). Fuego en los ecosistemas argentinos. Ediciones INTA, Buenos Aires, Argentina.

Kurtz, F. 1904. Flora de Córdoba. Pages 270-343 *in* M. E. Río and L. Achával (eds.). Geografía de la Provincia de Córdoba, vol. 1. Compañía Sudamericana de Billetes de Banco, Buenos Aires, Argentina.

Landi, M. A. 2018. Caracterización del régimen de incendios, su relación con el clima y su efecto en la resiliencia y estructura de la vegetación. PhD. Thesis, Universidad Nacional de Córdoba, Córdoba, Argentina.

Lanza, M. G., M. P. Chartier, and P. I. Marcora. 2018. Relación clima-crecimiento radial de Polylepis australis en un gradiente altitudinal en las Sierras Grandes de Córdoba, Argentina. Ecología Austral **28**:278-290. https://doi.org/10.25260/EA.18.28.1.1.620.

Lipoma, M. L., D. E. Gurvich, C. Urcelay, and S. Díaz. 2016. Plant community resilience in the face of fire: experimental evidence from a semi-arid shrubland. Austral Ecology **41**:501-511. https://doi.org/10.1111/aec.12336.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916-2003. Ecological Applications **19**:1003-1021. https://doi.org/10.1890/07-1183.1.

Luti, R., M. A. Bertrán de Solís, M. F. Galera, N. Müller de Ferreira, M. Berzal, M. Nores, M. A. Herrera, and J. C. Barrera. 1979. Vegetación. Pp. 297-368 *en* Geografía física de la provincia de Córdoba. Boldt, Buenos Aires, Argentina.

Marcora, P. I., I. Hensen, D. Renison, P. Seltmann, and K. Wesche. 2008. The performance of Polylepis australis trees along their entire altitudinal range: implications of climate change for their conservation. Diversity and Distributions **14**:630-636. https://doi.org/10.1111/j.1472-4642.2007.00455.x.

Marcora, P. I., D. Renison, A. I. Pais-Bosch, M. R. Cabido, and P. A. Tecco. 2013. The effect of altitude and grazing on seedling establishment of woody species in central Argentina. Forest Ecology and Management **291**:300-307. https:

//doi.org/10.1016/j.foreco.2012.11.030.

Martínez, G. A., M. D. Arana, A. J. Oggero, and E. S. Natale. 2017. Biogeographical relationships and new regionalisation of high-altitude grasslands and woodlands of the central Pampean Ranges (Argentina), based on vascular plants and vertebrates. Australian Systematic Botany **29**:473-488. https://doi.org/10.1071/SB16046.

McKenzie, D., C. Miller, and D. A. Falk. 2011. Toward a theory of landscape fire. Pp. 3-25 *in* D. McKenzie, C. Miller and D. A. Falk (eds.). The Landscape Ecology of Fire. Springer Science and Business Media. https://doi.org/10.1007/978-94-007-0301-8_1.

Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology **86**:2705-2715. https://doi.org/10.1890/04-1850.

Metlen, K. L., C. N. Skinner, D. R. Olson, C. Nichols, and D. Borgias. 2018. Regional and local controls on historical fire regimes of dry forests and woodlands in the Rogue River Basin, Oregon, USA. Forest Ecology and Management **430**:43-58. https://doi.org/10.1016/j.foreco.2018.07.010.

Nogués-Bravo, D., M. B. Araújo, T. Romdal, and C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. Nature **453**:216-220. https://doi.org/10.1038/nature06812.

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.

Pausas, J. G., and E. Ribeiro. 2013. The global fire-productivity relationship: Fire and productivity. Global Ecology and Biogeography **22**:728-736. https://doi.org/10.1111/geb.12043.

Pausas, J. G., and E. Ribeiro. 2017. Fire and plant diversity at the global scale. Global Ecology and Biogeography **26**: 889-897. https://doi.org/10.1111/geb.12596.

Prado, D. E. 1993. What is the Gran Chaco vegetation in South America? I: A review. Contribution to the study of flora and vegetation of the Chaco. V. Candollea **48**:145-172.

Renison, D., M. P. Chartier, M. Menghi, P. I. Marcora, R. C. Torres, M. Giorgis, I. Hensen, and A. M. Cingolani. 2015. Spatial variation in tree demography associated to domestic herbivores and topography: Insights from a seeding and planting experiment. Forest Ecology and Management **335**:139-146. https://doi.org/10.1016/j.foreco.2014.09.036.

Renison, D., A. M. Cingolani, and R. Suárez. 2002. Efectos del fuego sobre un bosquecillo de Polylepis australis (Rosaceae) en las montañas de Córdoba, Argentina. Revista Chilena de Historia Natural **75**:719-727. https://doi.org/10.4067/S0716-078X2002000400007.

Renison, D., I. Hensen, R. Suárez, and A. M. Cingolani. 2006. Cover and growth habit of Polylepis woodlands and shrublands in the mountains of central Argentina: human or environmental influence? Journal of Biogeography **33**: 876-887. https://doi.org/10.1111/j.1365-2699.2006.01455.x.

Rogeau, M.-P., and G. W. Armstrong. 2017. Quantifying the effect of elevation and aspect on fire return intervals in the Canadian Rocky Mountains. Forest Ecology and Management **384**:248-261. https://doi.org/10.1016/j.foreco.2016.10.035.

Sparacino, J., D. Renison, A. M. Devegili, and R. Suárez. 2019. Wind protection rather than soil water availability contributes to the restriction of high-mountain forest to ravines. New Forests **51**:101-117. https://doi.org/10.1007/s11056-019-09722-z.

Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. Science **334**:230-232. https://doi.org/10.1126/science.1210465.

Syphard, A. D., T. J. Brennan, and J. E. Keeley. 2018. Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. Diversity and Distributions **25**:90-101. https://doi.org/10.1111/ddi.12827.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. Ecological Applications **17**:1388-1402.

Syphard, A. D., V. C. Radeloff, N. S. Keuler, R. S. Taylor, T. J. Hawbaker, S. I. Stewart, and M. K. Clayton. 2008. Predicting spatial patterns of fire on a southern California landscape. International Journal of Wildland Fire **17**:602. https://doi.org/10.1071/WF07087.

Tachikawa, T., M. Hato, M. Kaku, and A. Iwasaki. 2011. Characteristics of ASTER GDEM version 2. Pp. 3657-3660 *in* Geoscience and remote sensing symposium (IGARSS), 2011 IEEE international. IEEE. https://doi.org/10.1109/IGARSS.2011.6050017.

Tálamo, A., and S. M. Caziani. 2003. Variation in woody vegetation among sites with different disturbance histories in the Argentine Chaco. Forest Ecology and Management **184**:79-92. https://doi.org/10.1016/S0378-1127(03)00150-6.

Tecco, P. A., A. I. Pais-Bosch, G. Funes, P. I. Marcora, S. R. Zeballos, M. Cabido, and C. Urcelay. 2016. Mountain invasions on the way: are there climatic constraints for the expansion of alien woody species along an elevation gradient in Argentina? Journal of Plant Ecology **9**:380-392. https://doi.org/10.1093/jpe/rtv064.

Teich, I., A. M. Cingolani, D. Renison, I. Hensen, and M. A. Giorgis. 2005. Do domestic herbivores retard Polylepis australis Bitt. woodland recovery in the mountains of Córdoba, Argentina? Forest Ecology and Management **219**: 229-241. https://doi.org/10.1016/j.foreco.2005.08.048.

Tepley, A. J., E. Thomann, T. T. Veblen, G. L. W. Perry, A. Holz, J. Paritsis, T. Kitzberger, and K. J. Anderson-Teixeira. 2018. Influences of fire-vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. Journal of Ecology **106**:1925-1940. https://doi.org/10.1111/1365-2745.12950.

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.

Torres, R. C., M. A. Giorgis, C. Trillo, L. Volkmann, P. Demaio, J. Heredia, and D. Renison. 2014. Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina: Post-fire tree regeneration. Austral Ecology **39**:346-354. https://doi.org/10.1111/aec.12084.

Torres, R. C., and D. Renison. 2015. Effects of vegetation and herbivores on regeneration of two tree species in a seasonally dry forest. Journal of Arid Environments **121**:59-66. https://doi.org/10.1016/j.jaridenv.2015.05.002.

Torres, R. C., and D. Renison. 2016. Indirect facilitation becomes stronger with seedling age in a degraded seasonally dry forest. Acta Oecologica **70**:138-143. https://doi.org/10.1016/j.actao.2015.12.006.

Vaieretti, M. V., A. M. Cingolani, N. Pérez Harguindeguy, and M. Cabido. 2013. Effects of differential grazing on decomposition rate and nitrogen availability in a productive mountain grassland. Plant and Soil **371**:675-691. https://doi.org/10.1007/s11104-013-1831-9.

Vera, F. C. 2016. Crecimiento radial de Lithraea molleoides en relación con la altitud y con las características del micrositio en el Bosque Serrano de Córdoba. Tesis de Grado, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina.

van der Werf, G. R., J. T. Randerson, L. Giglio, N. Gobron, and A. J. Dolman. 2008. Climate controls on the variability of fires in the tropics and subtropics: climate controls on fires. Global Biogeochemical Cycles **22**. https://doi.org/10.1029/2007GB003122.

Whelan, R. J. 1995. The Ecology of Fire. Cambridge University Press.

Whittaker, R. H. 1956. Vegetation of the great smoky mountains. Ecological Monographs **26**:1-80. https://doi.org/10.2307/1943577.

Zak, M. 2008. Patrones espaciales de la vegetación de la provincia de Córdoba. Análisis complementario de información satelital y datos de campo. PhD Thesis, Universidad Nacional de Córdoba, Argentina.