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Wildfire dynamics and impacts on a tropical Andean oak forest

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Abstract. Wildfires have increasingly damaged Andean tropical forests. However, both a poor understanding of wildfire dynamics and ecosystem response limits awareness about the magnitude of the problem and design management strategies. We estimate the impacts and significant drivers of wildfires by dating and mapping recent wildfires in an Andean tropical forest area, the Iguaque mountains. A large part of Iguaque hosts a population of the only *Quercus* species in South America, *Quercus humboldtii*. We used remote-sensing, official reports and social mapping to reconstruct the recent history of wildfires and change in oak forest patches in Iguaque. Between 1990 and 2017, 25 wildfires were recorded, with fire intervals between 4 and 21 years. These events burned 28.4% of the Iguaque mountains and showed a significant increasing trend in extent. Wildfires mostly occurred in the south, during the driest months, and their number and extent showed substantial interannual variations related to El Niño–Southern Oscillation cycles. Wildfires contributed to a 45% reduction in oak forests along with the fragmentation of existing populations. Our study presents evidence of the extent and impact of wildfires in Iguaque and provides new insights on fire dynamics in Andean tropical forests.

Keywords: Andean forests, climate change, Colombia, deforestation, ENSO cycles, fragmentation, oak forest management, *Quercus humboldtii*, wildfire.

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Introduction

Wildfires are a significant driver of environmental change globally (Geist and Lambin 2001; Hosonuma *et al.* 2012) and affect the dynamics, structure and composition of plant communities and ecosystem services (Ahlgren and Ahlgren 1960; TNC *et al.* 2004). Although 21st century global trends suggest a reduction in human-caused burning in many seasonally dry tropical areas, due primarily to the expansion of developed agriculture in savanna regions (Andela *et al.* 2017), the number, frequency and extent of wildfires have increased in many forested (or formerly forested) areas worldwide (Simon *et al.* 2004; Tansey *et al.* 2008; Earl and Simmonds 2018). Wildfire extent and frequency have been positively correlated with population density, proximity to roads and suburban areas, accumulation of dead fine fuel and extreme weather conditions (Godoy *et al.* 2019; Guillaume *et al.* 2019). They have also been related to El Niño–Southern Oscillation cycles (ENSO; Barlow and Peres 2004; Bianchi *et al.* 2014).

Wildfires have affected 84% of the surface in the world's biodiversity hot-spots (TNC *et al.* 2004), and in Latin America alone, 51 million ha have burned in the last three decades (FAO 2005, 2013). However, wildfire records have only recently been maintained in most tropical Andean countries (Armenteras *et al.* 2020), and those records are often incomplete, scattered and, in some cases, contradictory regarding the affected area (Anaya-Acevedo and Chuvieco-Salinero 2010). For example, in the Colombian Andean region, records show that 295 300 ha burned between 2001 and 2007 (Anaya-Acevedo and Chuvieco-Salinero 2010). Official reports from Colombia have been available since 1998 (UNGRD 2018). Between 2002 and 2013, 12 978 wildfires were reported, affecting 619 300 ha (IDEAM 2004). In 2015 alone, 3985 wildfires were reported, affecting 150 000 ha in Colombia (García *et al.* 2016). Some studies have investigated wildfire dynamics in Colombia (Armenteras *et al.* 2005, 2009*a*, 2009*b*; Muñoz 2005; Amaya and Armenteras 2012; Barreto *et al.* 2017; Armenteras *et al.*

2019, 2020), but many lack information about the detailed dynamics of wildfires, their impact in tropical mountain zones, and their relationship with land use, climatic conditions and vegetation.

There is a need to better understand wildfire occurrence and dynamics in the tropical Andean region, where there have been significant changes in fire regimes during the last 2 million years, and especially since human settlement began in the Late Pleistocene (TNC *et al.* 2004; Armenteras *et al.* 2019, 2020). For example, in Colombia, Paleo-ecological records confirm large wildfires during hot phases of the Pleistocene and the Holocene (significantly 11 000 years ago; González *et al.* 1966; Van der Hammen 1966; Kuhry 1988). During pre-Columbian times, fire was used in the Cundiboyacense highlands to clear vegetation and expand crops (Patiño 1965, 1997; Márquez 2001). These practices intensified with European colonisation until the present times, with forest and páramo vegetation converted to pastures maintained by frequent fires (Fals Borda 2006; Mora 2012). In some areas of the Colombian Andes, wildfire frequency has increased since pre-Hispanic times from one event every 1000 years to one event every year owing to human intervention (Verweij 1995; Vargas-R 2002).

The Iguaque Mountains provide an example of the increasing frequency of wildfires in the Andean region. Its lowland areas have been used for intensive agriculture for a long time. Large extents of the mountain range were designated a National Park in 1977 because of their high socio-ecological value. Since then, the area has witnessed numerous wildfires, affecting soil stability, water quality and landscape structure (Villarreal *et al.* 2017). Additionally, wildfires may have reduced the extent of Andean oak (*Quercus humboldtii* Bonpl.) forest (Fernández-Méndez *et al.* 2016).

Quercus humboldtii is endemic to the northern Andes (Nixon 2006; Avella 2016). It is the southernmost species of this genus in the Americas, and belongs to the red oak group (subgenus *Erythrobalanus* (Nixon 2006)). Andean oak is distributed exclusively in the Panamanian Darien and Colombian Andes Mountains, distributed along a broad environmental gradient ranging from 750 to 3450 m in elevation and 700 to 3000 mm mean annual rainfall (Rangel *et al.* 2009; Rangel and Avella 2011). In the Colombian Andes, historical transformations have reduced at least 60% of the original distribution of *Q. humboldtii* (Rodríguez *et al.* 2004; Etter *et al.* 2006). Some remnants of these forests have been protected, but these measures have been insufficient to arrest deforestation, wildfires and the spread of invasive species (Avella 2010; Salazar *et al.* 2020).

Many *Quercus* species are fire-tolerant (Johnson *et al.* 2002), owing chiefly to the concentration of dormant buds near the root collar (Espelta *et al.* 2003). This trait facilitates rapid post-disturbance resprouting. Oak tolerance to fire depends on stem diameter, bark thickness, and fire intensity and frequency, and is thus highly dependent on species (Johnson *et al.* 2002; Pausas 2017; Casals *et al.* 2018). In North America, red oak species tolerate low to moderate fire intensities, and fairly long fire intervals (more than 14 years; Johnson *et al.* 2002; DeSantis *et al.* 2010). Trees with diameter at breast height (DBH) greater than 17.8 cm show a higher probability of surviving wildfires. The response of Neotropical oaks to disturbances such as fire is less well known. In Mexico and Costa Rica, some oak species survive logging and fire (Aus der Beek *et al.* 2006; Guariguata *et al.* 2006). Yet, depending on fire frequency, regeneration may be arrested (Bonfil 2006; González-Espinosa *et al.* 2006). In Colombia, *Q. humboldtii* resprouts up to 3 years after fire, but it is not clear which fire regime this species is adapted to, or what the effects of fire on its regeneration are (Salazar *et al.* 2020). Several studies have suggested that Andean forests in Colombia (including oak forests) are neither fire-prone nor fire-adapted (Páramo-Rocha 2011; Armenteras *et al.* 2020).

As in many forests of the tropical Andean region, the frequency and extent of wildfires in the Iguaque mountains have not been studied in detail. Their causes and consequences are mostly unknown. Knowledge on fire regime and its relationship with vegetation community composition, land use and climate is key to understand the temporal and spatial dynamics of *Q. humboldtii* forests, and could help to protect biodiversity and sustain human wellbeing in these areas (Syphard *et al.* 2008; Aguilar-Garavito *et al.* 2019).

Here, we present a quantitative analysis of wildfire dynamics in the Iguaque mountains, using three different methodological approaches. With this study, we aim to answer the following questions: (1) what is the frequency of wildfires in Iguaque? (2) Can we detect interannual trends in the magnitude and frequency of wildfires? (3) Is wildfire probability constant throughout the year and the mountain range? And (4) have wildfires affected the extent and spatial distribution of oak forest?

Methods

Study area

The Iguaque mountains (22 000 ha) are located in the Eastern Colombian Andes (5°36′02″–5°44′38″N and 73°22′57″–73°31′20″ W; Fig. 1), in Boyacá state. The protected area Santuario de Fauna y Flora Iguaque (SFFI; 2400 to 3890 m above sea level (asl); 6750 ha) is surrounded by a buffer zone at lower elevations (2200 to 2400 m asl).

The Iguaque mountains extend over 22 km along two crests separated by the Cane–Iguaque watershed and are formed by structural sandstones of the Arcabuco Formation. To the south, shale outcrops create hilly landscapes. The topography is strongly wavy and broken, with slopes steeper than 15%. Soils are shallow, acidic and moderately evolved (Villarreal *et al.* 2017). The average annual temperature and precipitation of the whole range are 18°C (mean maximum 22°C, mean minimum 10°C) and 810 mm. Rainfall follows a bimodal distribution, with maxima in March–May and September–November. The rainiest months are April–May, with 201 mm on average, and the driest months are December–February, with 40 mm on average. Additionally, the rains present a decreasing gradient towards the south-west (Villarreal *et al.* 2017).

Páramo and Andean forests cover the northern part of the Iguaque mountains. In contrast, owing in part to historical agricultural use and later abandonment, areas to the south and south-east are covered by herbaceous vegetation on slopes and open shrublands on flat areas. Open *Quercus humboldtii* forests are currently confined to narrow discontinuous forest fragments along streams and river canyons (Marín and Betancur 1997; Fernández-Méndez *et al.* 2016). The Park's buffer area presents a mosaic of herbaceous and shrubby vegetation, mixed with

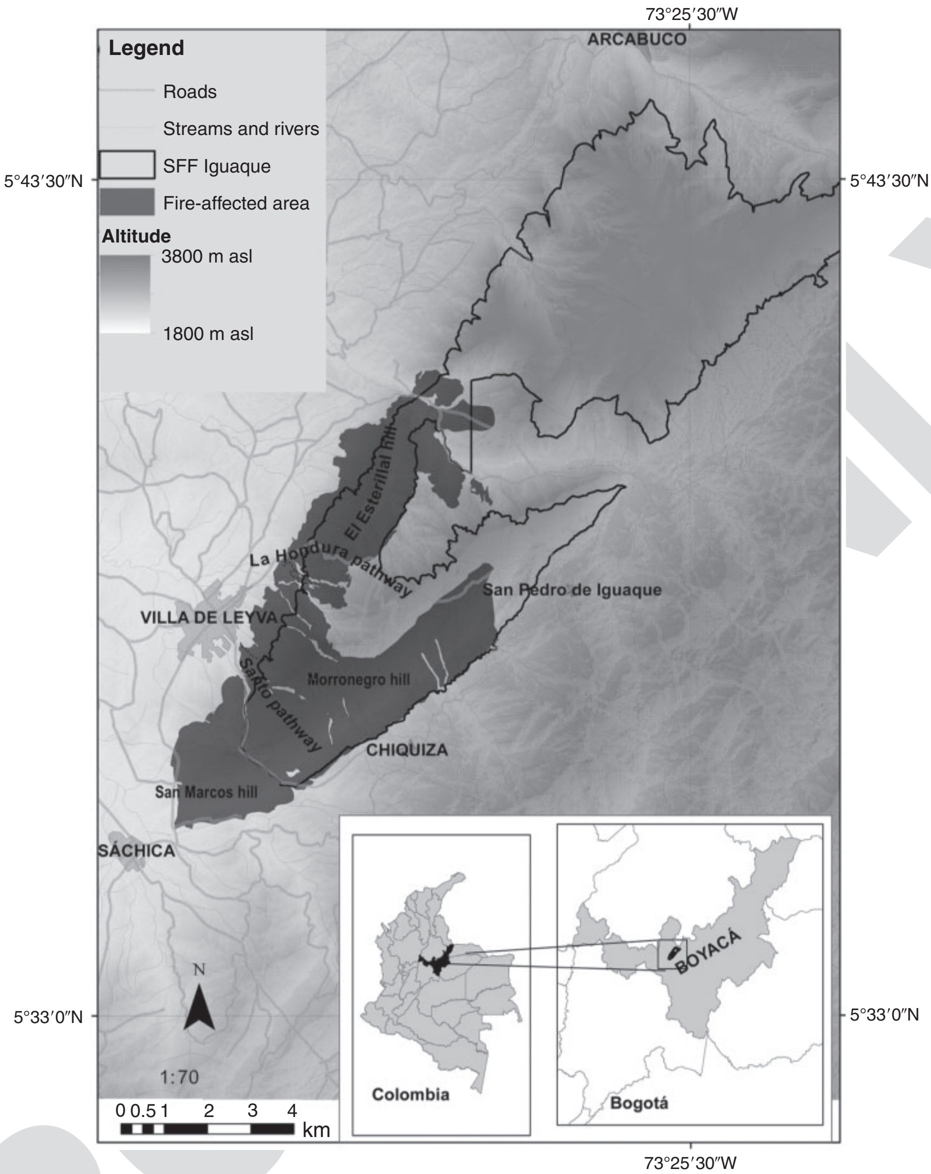

Fig. 1. Location of the Iguaque mountains in the state of Boyacá and Colombia.

pastures, farmland and recreational houses. Tourism activity has increased near Villa de Leyva over the last decades. This has intensified the demand for natural resources, mainly water, and promoted visitation by people who are not familiar with Iguaque. The situation may worsen in the near future as neighbouring villages pursue similar growth plans (Villarreal *et al.* 2017).

Wildfire occurrence and location

We used free remote sensing images and GIS (geographic information systems) to draw the boundaries of wildfires between 1991 and 2015 and estimate their extent (Landsat, Rapideye and Google Earth images from 1991, 2010 and 2015). We summarised this information in a 'remote sensing' GIS map. We reviewed official wildfire reports (SFFI 2006, 2014; 2016; Villa de Leyva 2012, 2014*a*, 2014*b*; UNGRD 2018; Villarreal *et al.* 2017). We summarised the information from both sources in an 'official report' GIS map.

In September 2015, we conducted semistructured interviews with 50 key informants, namely Park neighbours (31), public officers at the Villa de Leyva Mayor's Office (4), managers at SFFI (6) and local firefighters (9). We asked them to provide details on the dates and geographical extent of wildfires, including drawing a polygon for each wildfire using basic Iguaque topographic maps (1 : 25 000). We then summarised this information in the 'social wildfire' GIS map. We conducted our spatial analyses using *Arc-GIS 10* (ESRI 2015).

Trend in burnt area

We used a non-parametric Mann–Kendall test ($\alpha \leq 0.05$ and Z statistic $= 1.96$, obtained from the standard normal table) to

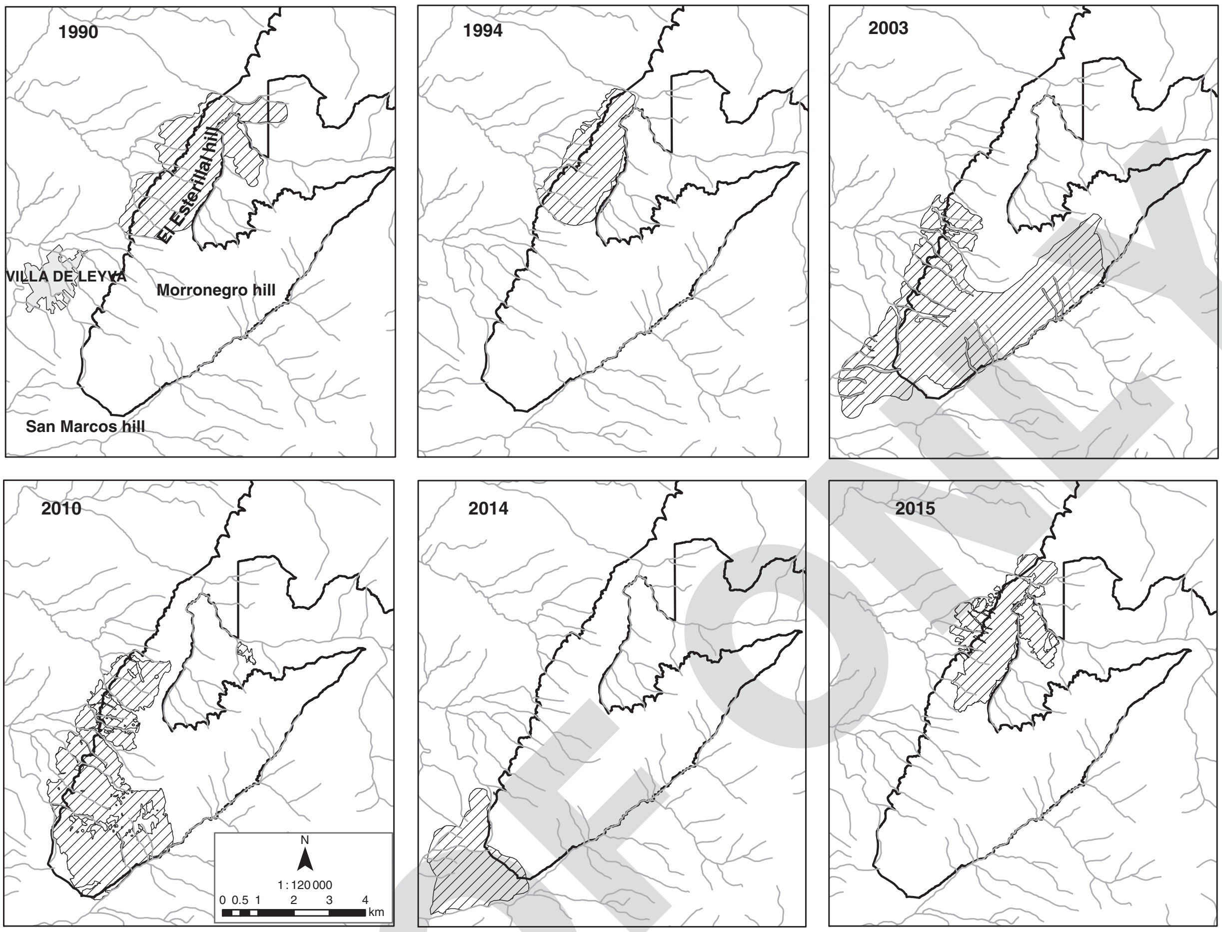

Fig. 2. Geographical extent of significant wildfires occurring in the Iguaque mountains (Colombia) between 1990 and 2015, estimated using remote-sensing images (Landsat, Rapideye and Google Earth).

detect temporal trends in burnt area. (Mann 1945; Kendall 1975). We employed the mk.test function in the *R* 'trend' package (R Core Team 2020; Thorsten 2020).

Wildfire frequency

We estimated wildfire recurrence using the information contained in remote-sensing, official-report and social wildfire maps utilising map algebra and Boolean operators (union) for multicriteria analysis (Franco 2011). We calculated the level of accuracy of the coincidence among maps obtained with the different data sources. Because we do not have field control points for past wildfire periods, we used the remote-sensing map as ground truth (reference map), and the recurrence of wildfires in official reports and social maps as classes (compared maps). We built a confusion matrix and calculated the kappa index (Chuvieco-Salinero 1990), using the count value per class, to estimate the correlations between the remote sensing map and the other maps.

Wildfires and climate

We explored the relationship between the number and extent of wildfires in Iguaque and ENSO cycles by using 336 monthly observations of the Ocean Niño Index (ONI) between 1989 and 2017 (NOAA 2018). We then used a variety of statistical tests to assess these relations, as the sample size was small and wildfire probability low. First, we calculated Pearson and tau Kendall associates correlation coefficients, as initial diagnostic methods, to evaluate the degree of a simple relationship between both phenomena: wildfires and ONI, in a parametric and non-parametric way respectively (Bratsas *et al.* 2018; R Core Team 2020). Second, the number of wildfires obtained from official reports and ONI data was sufficient to conduct time series analysis, including computation of the autocorrelation function (ACF) and the cross-correlation function (CCF). Monthly wildfire counts were compared with monthly ONI. As we found that the series was not stationary, we computed the differences between consecutive observations just once. This is known as differencing (Hyndman and Athanasopoulos 2018).

ACFs were examined for the wildfire counts and ONI data to assess serial autocorrelation, trends and seasonality. Stationarity tests were performed before comparing CCF and ONI (Dickey–Fuller stationarity test) (Said and Dickey 1984; Banerjee *et al.* 1993). To perform these analyses, we used the Dickey–Fuller test and the ACF and the partial autocorrelation function (PACF) to determine if the series were stationary. Further, finally, we

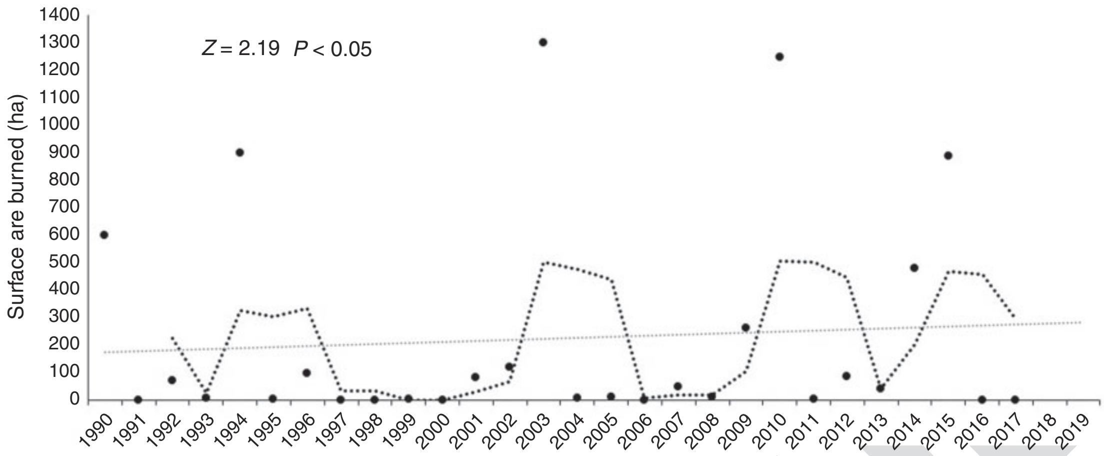

Fig. 3. Surface area burned annually (dots), surface area burned 3-year moving average (thick dotted line), and linear surface area burned trend (thin dotted line) in the Iguaque mountains (Colombia), estimated from official reports and validated by analysing remote-sensing images and personal interviews. Trend significance (*Z*, Mann–Kendall test) are shown.

applied the CCF. All analyses were implemented in the *R* package ‘tseries’ (Trapletti *et al.* 2018; R Core Team 2020).

Oak forest distribution and wildfires

We mapped the distribution of oak forests in the unburned and frequently burned areas of the Iguaque mountains using aerial photographs from 1970, and images from SPOT 2006 and Google Earth 2016. These maps were validated with data from a field survey. As access was difficult, we could not use a grid of random observations. However, the pattern of oak cover obtained with aerial photographs and satellite images was confirmed by observations made from spots where access was feasible.

We used the GIS and the formula of Puyravaud (2003) to calculate the following basic landscape metrics, and compare 1970, 2006 and 2016 images: (1) the area covered by oak forests; (2) the average size of forest patches; (3) the largest forest patch; and (4) the number of forest patches (McGarigal *et al.* 2012). We validated forest fires and oak forest boundaries by performing a supervised classification (maximum livelihood algorithm), with training areas selected from multispectral images (Chuvieco-Salinero 1990, 2008). Finally, we compared the four landscape metrics mentioned above between the unburned area and the burned area, using the Pearson chi-square test (chisq.test in the *R* ‘stats’ package) (R Core Team 2020), to assess the probability that any observed differences between the datasets were due to randomness.

Results

Wildfire occurrence, location, surface burned and trends

Using remote sensing images, we recorded 25 wildfires and 6236 ha burned in the Iguaque mountains between 1990 and 2017. The wildfire initiated on 24 February 2003 was the largest ever recorded in the mountain range, affecting 1300 ha (Fig. 2). The southern ridges were the most heavily affected by wildfires. Fire extent showed a significant increasing monotonic trend from 1990 to 2017 ($Z = 2.19$, $P < 0.05$, Fig. 3).

Only six of the twenty-five dated wildfires affected more than 260 ha each (Fig. 3) and they were concentrated in the southern and central parts of the study area. We considered these events the largest wildfires (600, 900, 1300, 1245, 477 and 887 ha; 24% of the total wildfires), and they occurred only once a year. In contrast, most wildfires were smaller (19 events of 1–260 ha, 76%), and coincided with other small wildfires occurring during the same year.

Wildfires recorded in our work coincided with the fire records reported by environmental authorities since 1990, and by the national information system since 1998. We also found records of additional wildfires from 1908, 1910, 1927, 1980 and 1986 in local reports from the Villa de Leyva Mayor’s office (SFFI 2006; Villa de Leyva 2012, 2014*a*), but those events were excluded from our analysis because their geographical borders could not be mapped. Wildfires occurred exclusively during the driest months (Fig. 4). A total of 15 (60%) and 10 (40%) of the wildfires occurred between 20 August and 20 September, and 1 January and 28–29 February respectively.

Interview participants reported 20 wildfires between 1990 and 2015. SFFI officers and firefighters mentioned wildfires occurring between 1940 and 1970, these being the oldest dates preserved in community memory. Wildfires were almost entirely anthropogenic. Interview respondents and official reports identified intentional causes such as uncontrolled agricultural and domestic waste burning (27%), hunting (13%) and retaliation aimed at environmental authorities (10%) as significant causes. More than one-third of the participants (36%) mentioned accidents caused by tourist bonfires, night torches and firework fires. Finally, 14% of the interviewees suggested that drought (8%), certain types of vegetation (i.e. pine, grass and common bracken, 4%), and lightning (2%) facilitated wildfires.

Wildfire frequency

Since 1990, the central part of the Iguaque mountains showed the highest wildfire recurrence, and the peripheral areas the lowest (Fig. 5). We found very high wildfire frequency around oak forest relicts – wildfires occurring in 1990, 1994, 2009, 2010 and 2015

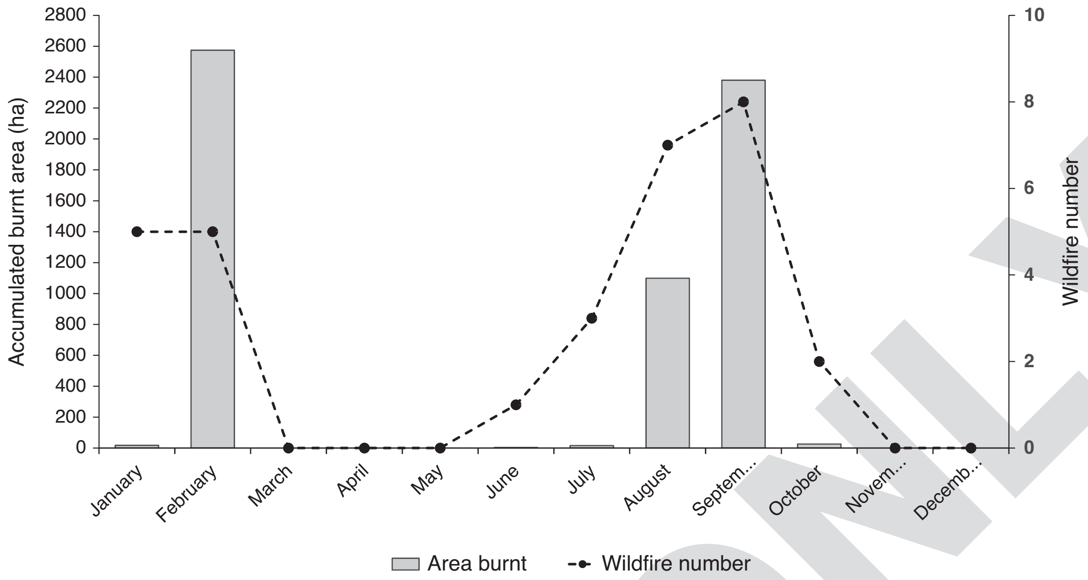

Fig. 4. Monthly wildfire occurrence and surface area burned in the Iguaque mountains (Colombia) between 1990 and 2017.

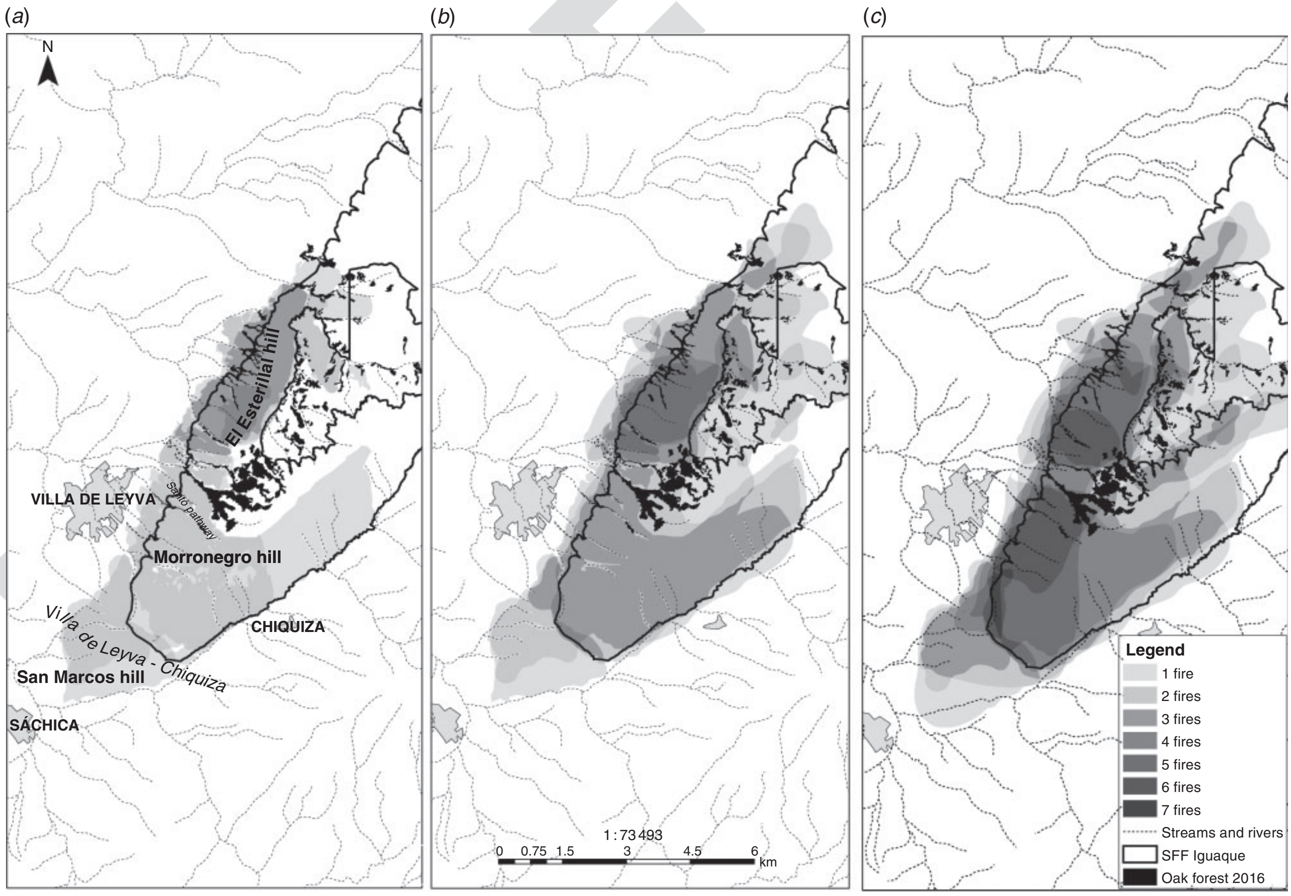

Fig. 5. Wildfire recurrence between 1990 and 2015 in the Iguaque mountains (Colombia). Estimates are based on three different sources of information: (*a*) remote-sensing images; (*b*) official reports; and (*c*) social maps.

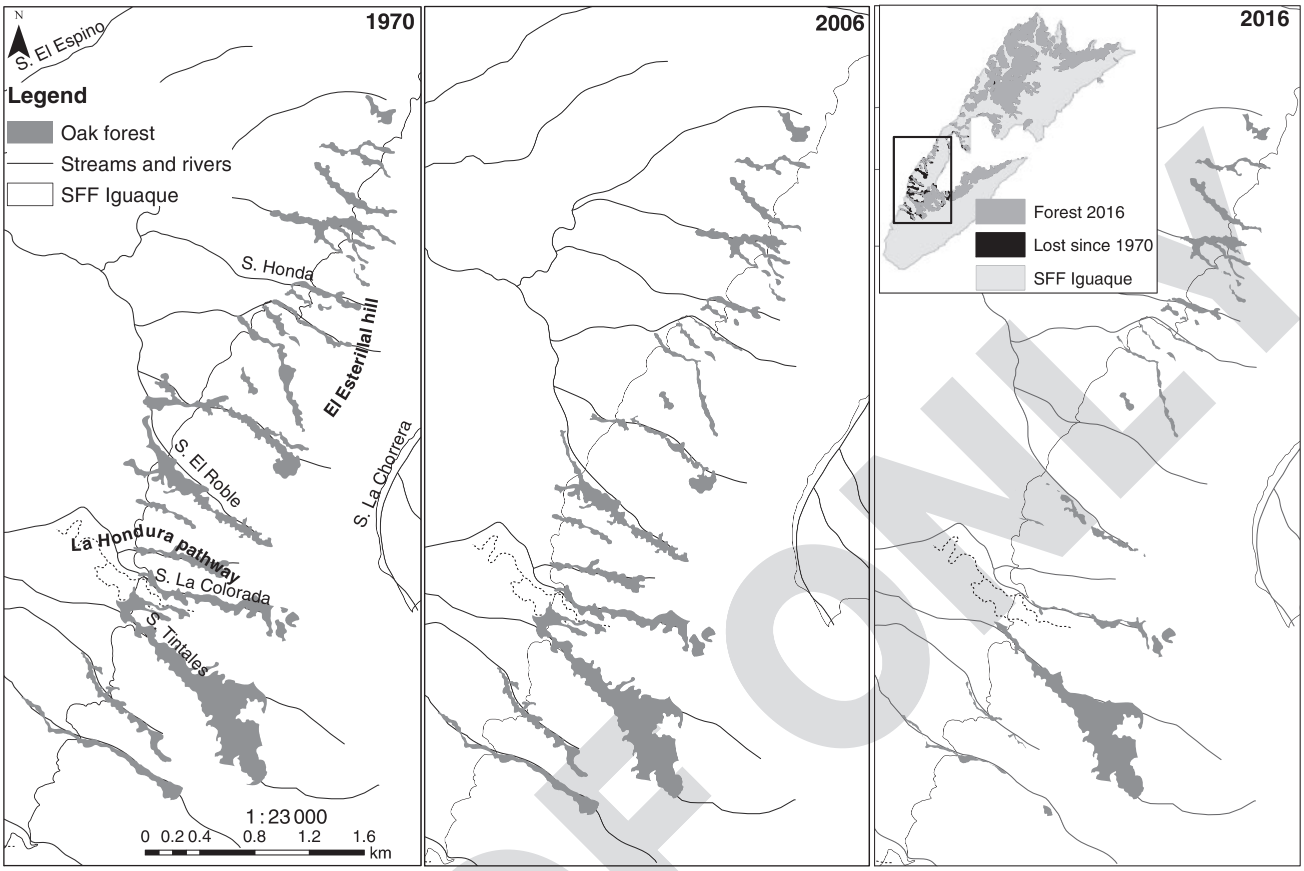

Fig. 6. Oak forest distribution in the south-western Iguaque mountains (Colombia) in 1970, 2006 and 2016.

directly impacted these forests. In the areas most affected by the fires, the social map showed a recurrence of seven fires. In contrast, the map of official reports and remote sensing images showed recurrences of five and four wildfires respectively.

The social maps showed four areas with a frequency of six and seven fires in 27 years (589 ha), seven areas with four and five wildfires (1403 ha), and a larger number of areas with one to three wildfires (3190 ha) (Fig. 5*c*). The analysis of maps obtained from official reports showed an intermediate frequency of wildfire compared with the other two maps, but a significant coincidence in the high-frequency areas. According to the interviewees, wildfires occurred almost annually since 1990 and were usually small in size. Both official reports and social maps showed a low degree of coincidence with the map derived from remote-sensing images (kappa index: 0.33 and 0.39; accuracy 33 and 39% respectively).

Wildfires and climate

We found a positive but weak correlation between ONI-ENSO and annual percentage of burned area in Iguaque (Pearson's $r = 0.15$, $P = 0.006$, $n = 346$) and a weak association between the number of wildfires and ONI-ENSO (Kendall's tau $= 0.076$, $P = 0.08$, $n = 346$) (Table S1, Supplementary material). The CCF (Fig. S1, Supplementary material) confirmed the existence of a seasonal pattern in both climate and wildfires, with several significant positive correlations ahead of and behind the lags.

Wildfires and oak forest distribution

The extent of oak forests in the south-western and western slopes of the Iguaque mountains was substantially reduced between 1970 (113 ha) and 2016 (51 ha; Fig. 6, Table 1). This decline was paralleled by fragmentation of the original population: the number of patches increased from 27 to 34 during this period, while the average patch size decreased from 1.65 to 0.32 ha. Similarly, the largest forest patch's surface area was reduced from 36 ha in 1970 to 26 ha in 2016.

Oak forest decline was restricted to the burned areas, as we found no evidence of wildfire in the northern range of the Iguaque mountains, and forest loss rate between 1970–2006 and 2006–16 in these areas was virtually zero.

We found a significant association between the previous occurrence of wildfires and (1) reduction in the surface area covered by oak forest (Pearson chi-square test d.f. $= 2$, $P << 0.0001$), and (2) the average size of forest patches (Pearson chi-square test d.f. $= 2$, $P << 0.0001$) in the Iguaque mountains burned areas.

Discussion

Wildfire dynamics and drivers

Wildfire frequency and extent in the southern sector of the Iguaque mountains showed substantial temporal variation. Even so, the burnt area showed a significant increasing monotonic

Table 1. Changes in the extent of oak forests since 1970, and main attributes of oak forests patches for the area most affected by wildfires (south-western ranges) and entire Iguaque mountains

	Wildfire-affected area			Iguaque mountains		
	1970	2006	2016	1970	2006	2016
Number of patches	27	27	34	44	39	29
Oak forest area (ha)	113	97	51	1860	1844	1798
Largest patch area (ha)	36	36	26	811	813	813
Average size of patch (ha)	1.7	1.4	0.3	26.2	28.2	29

trend between 1990 and 2017. This aligns with observations made in other regions of Colombia (IDEAM 2004; Armenteras *et al.* 2005; Pabón-Caicedo 2011; Rodríguez-Buriticá *et al.* 2017; Aguilar-Garavito *et al.* 2019; Armenteras *et al.* 2019), Latin America (Manta and León 2004; Chuvieco-Salinero *et al.* 2008; Armenteras *et al.* 2020) and some regions of the world (Boschetti *et al.* 2006; Chen *et al.* 2017; Earl and Simmonds 2018).

Wildfires in Iguaque followed the ENSO cycles: the largest wildfires predominantly occurred during ENSO years, and wildfire occurrence was weakly but significantly related to ONI. Large wildfires have often shown consistent relationships with ENSO dynamics: during La Niña, plant biomass increases, and with it the risk of wildfire during ensuing El Niño droughts (Kitzberger 2002; Fuller and Murphy 2006). Other studies describe ENSO effects on tropical wildfires (Kitzberger *et al.* 1997; Chen *et al.* 2017; Mariani *et al.* 2017), and indeed, ENSO may create the conditions for 20–30% of wildfires in tropical regions (Chen *et al.* 2017). Wildfires in Iguaque were concentrated mainly in the two periods of low rainfall (February and August–September), high temperatures and south-easterly trade winds. They coincided with the largest tourist date visitation numbers to Villa de Leyva (Villarreal *et al.* 2017; Google Trends 2020). These findings have important implications for the future of Iguaque ecosystems in the context of climate change and emphasise the need to develop a fire management program that integrates scenarios of climate change.

In addition to climate, other interrelated factors probably influenced the wildfire regime in Iguaque, including an increasing human population density (Pausas 2004; FAO 2005; Bianchi *et al.* 2014), land-use change (TNC *et al.* 2004), biomass accumulation and fuel continuity (Fuller and Murphy 2006; Bianchi *et al.* 2014). For 500 years, tree felling, slash-and-burn techniques, and intensive agriculture and grazing have shaped the Iguaque landscape (Fals Borda 2006; Mora 2012; Villarreal *et al.* 2017). After the designation of the Iguaque mountains as a protected area (SFFI) in 1977, abandonment of traditional land uses may have favoured colonisation by pioneer plant species and increased fuel accumulation and continuity (Fernández-Méndez *et al.* 2016; Salazar *et al.* 2020). Since 1977, farmers have not been allowed to clear vegetation for cropping and grazing, unregulated tourism has increased, and the resident population has decreased, thereby reducing the chances of wildfire control.

Our interviews revealed the existence of socio-environmental conflicts due to the designation of the protected area, which may have increased the risk of intentional ignition. Interviewees identified social conflicts and poor management of human activities in the buffer zone of the Park as significant causes of wildfires. Tourism has substantially increased in the study area over the last decades and has been suggested as a significant driver of wildfire frequency (Villa de Leyva 2012, 2014*a*, 2014*b*, 2016; Villarreal *et al.* 2017; Google Trends 2020). Determining the importance of social factors in the increase of wildfire is crucial to design effective management programs. These programs should involve strengthening the capacity for fire prevention, monitoring and firefighting, as well as expanding environmental education and awareness efforts. Management programs can promote conservation agreements between SFFI, landowners, farmers and the government, and thus strengthen the regulatory framework.

The origin of wildfires in Iguaque was largely anthropogenic. Thus, the increase in urban and peri-urban populations (51% between 2005 and 2018; DANE 2005, 2020), in addition to insufficient knowledge about forest dynamics and wildfire risk, has likely led to an increase in the frequency of ignition (Pechony and Shindell 2010; Knorr *et al.* 2016). This anthropogenic origin agrees with national and international reports for Colombia and elsewhere (MAVDT 2002; IDEAM 2004; Pausas 2004; FAO 2005; Parra 2011; Aguilar-Garavito *et al.* 2019; Armenteras *et al.* 2019, 2020).

Oak forest dynamics

A century ago, large extents of the southern watersheds of Iguaque were covered by dense, tall forests dominated by *Quercus humboldtii* and *Clusia multiflora* Kunth along streams, river canyons, ravines, plains and low hills (Marín and Betancur 1997; Rodríguez *et al.* 2005; Mendoza-Cifuentes 2017; Salazar *et al.* 2020). In the southern Iguaque mountains, sub-xerophytic shrubs were dominant on the slopes, and open, low oak forests covered the low hills (Mora 2012; Fernández-Méndez *et al.* 2016; Mendoza-Cifuentes 2017; Villarreal *et al.* 2017). Since then, the Iguaque landscape has profoundly changed owing to a reduction in the surface area covered by oaks, increased fragmentation of oak populations and the disappearance of forest patches (Fernández-Méndez *et al.* 2016; Mendoza-Cifuentes 2017; Salazar *et al.* 2020). These effects have been particularly intense in areas where wildfire recurrence was higher, especially where oak forests burned three to six times between 1990 and 2015, with fire return intervals of less than 21 years. The duration of the fire-free intervals in these areas may not be long enough to allow periodic oak recruitment (Johnson *et al.* 2002; Salazar *et al.* 2020; M. Aguilar-Garavito, unpubl. data). As a consequence, the current fire regime in Iguaque may favour the establishment of a homogeneous shrubby grassland with isolated old trees, put oak populations at risk and thus compromise forest resilience.

The incidence and effects of wildfires in the Iguaque oak forests have been reported elsewhere (Fernández-Méndez *et al.* 2016; Salazar *et al.* 2020) and support our results. However, this interaction has not been studied in other Colombian oak forests. Other studies have associated wildfires with a reduction in the surface area covered by other types of Andean Forest and páramos (Vargas-R 2002; IDEAM 2004; Muñoz 2005; Parra 2011; Amaya and Armenteras 2012; Rodríguez-Buriticá *et al.* 2017; UNGRD 2018; Aguilar-Garavito *et al.* 2019).

Quercus humboldtii is known to be a 'fire-persistent' tree that can resprout after a fire (Salazar *et al.* 2020). Many other *Quercus* species also exhibit fire resistance (Johnson *et al.* 2002; Espelta *et al.* 2003), and in Mediterranean and temperate ecosystems, some oaks species have replaced other trees that cannot withstand frequent or severe wildfires (DeSantis *et al.* 2010; Leverkus *et al.* 2014). Nevertheless, in the Iguaque mountains, *Q. humboldtii* did not respond positively to wildfires. We speculate that the resprouting ability was quickly depleted in this species owing to the high frequency of fire such that the oaks could not withstand the recurrent fires. However, further studies on *Q. humboldtii* morphofunctional and reproductive responses to wildfires are needed before fully understanding the impact of wildfire on the oak forests described in our study.

In Iguaque burned areas, the structure of the plant community has shifted towards botanically impoverished shrubby grasslands (Marín and Betancur 1997; Fernández-Méndez *et al.* 2016), where highly flammable alien species thrive (*Pteridium aquilinum* (L.) Kuhn, *Melinis minutiflora* P. Beauv., *Andropogon lehmanii* Pilg. and *Heteropogon contortus* (L.) P. Beauv. Ex Roem. and Schult) (Fernández-Méndez *et al.* 2016; Mendoza-Cifuentes 2017). They provide fuel loads ranging from 4 to 35 Mg ha^{-1} (Aguilar-Garavito *et al.* 2016). These formations correspond with Anderson (1982) fuel models Type 3 and 4: dense and tall grasslands and dense thickets or trees, which have a high horizontal and vertical continuity, and abundant live and dead fuel accumulation (Rothermel 1972; Albini 1976). Fire spreads rapidly across these vegetation fuel types, generating tall flames. These fuel models agree with the results of our interviews about fire behaviour.

The approach to the wildfire problem in Iguaque and the Andean oak forests should consider a paradigm shift in fire management, which has historically been focused on fire suppression. Our results suggest that past management approaches may be insufficient and should be complemented with other measures, such as the reduction of fuel loads in the boundaries between farms and the protected area, and in the boundaries between forests and other land-cover types (urban, grasslands, shrublands) (Baeza *et al.* 2002, 2006; Lloret 2004). Prescribed fire at appropriate intervals and intensities and applied on strategic areas eventually could be a tool, in the short term, to reduce fuel loads and maintain open forest habitat with suitable conditions for oak regeneration (Johnson *et al.* 2002). Less aggressive alternatives such as manual and mechanical removal of invasive plants should also be considered. Studies to evaluate the technical and socioeconomic feasibility of such measures and their impact on ecosystem and landscape diversity and function are necessary to design efficient management programs. Furthermore, vegetation management should focus on oak forest restoration by promoting oak recruitment and controlling invasive species.

Finally, the SFFI administration and the Mayor's Offices, environmental authorities and fire departments around the Iguaque mountains should improve fire prevention programs and educate local people and tourists about fire risk, prevention and management in the Iguaque mountains. Similarly, a landscape management strategy should include agricultural and peri-urban lands, the protected area and fuel quantity and continuity reduction. It is also necessary to be more efficient in identifying and penalising those who violate Colombian environmental legislation concerning wildfires (Prestemon *et al.* 2019). These measures could help develop a wildfire management policy to prevent socio-ecological damage and losses caused by future fires in the Iguaque mountains (Moreira *et al.* 2020).

Conclusions

Wildfires in the Iguaque mountains have been common in recent decades, particularly towards the south of the protected area. Using a combination of remote sensing, official reports and social maps, we estimated the extent and dynamics of wildfires in areas with missing or non-standardised records. Our methodological approach can be extended to other areas where wildfires have not been systematically documented. Complementary techniques, like the analysis of fire scars on *Quercus humboldtii* trunks, could further refine these maps, particularly for wildfires occurring before 1990.

Our findings indicate that wildfires in Iguaque are associated with climate dynamics and human activities, and wildfires will likely increase in the near future owing to climate change, land-use change and social habits. Wildfires have significantly contributed to reductions in the extent of oak forests and the fragmentation of their populations. Given the critical role that *Q. humboldtii* plays in community structure and ecosystem functioning, measures towards reducing the frequency and impact of wildfires and restoring degraded forests should be urgently pursued.

Our results suggest a combined effect of land-use changes, wildfires and increased tourism activities, accentuated in the last decade, are significant challenges for biodiversity management in the study region. Further, our study contributes to our understanding of wildfire regimes in Andean forests and Andean oak population dynamics. It provides essential insights towards designing wildfire management strategies and creating biotic and social communities that are adapted and resilient to global change.

Conflicts of interest

The authors declare no conflicts of interest.

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