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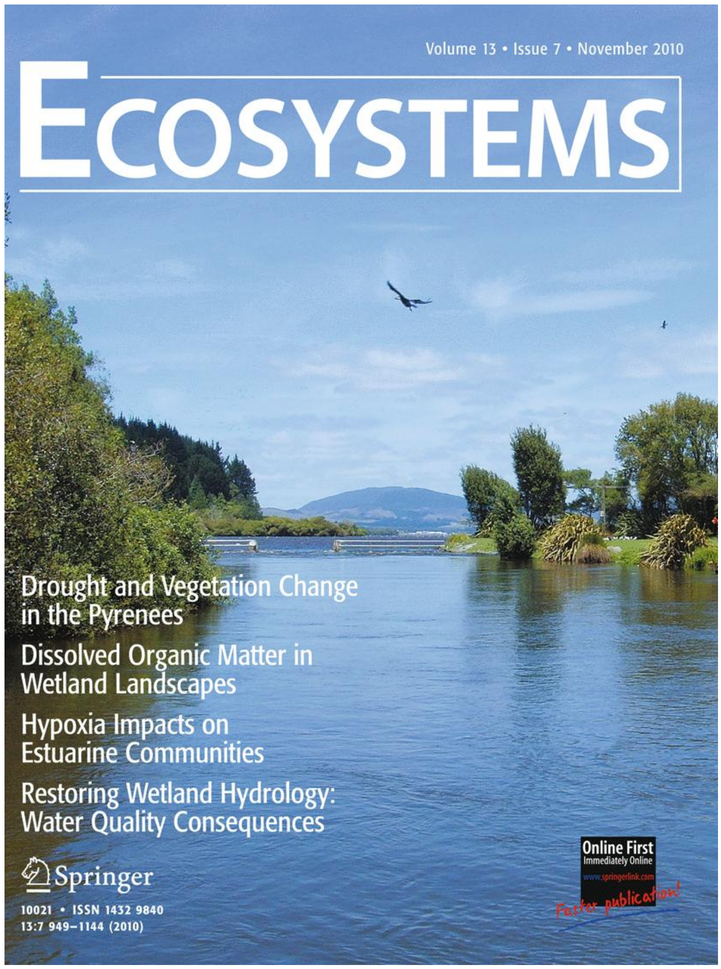

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ECOSYSTEMS

Fire-Mediated Forest Encroachment in Response to Climatic and Land-Use Change in Subtropical Andean Treelines

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Abstract

We used dendroecological techniques to analyze the effects of rainfall and grazing on fire regime and its implications for tree regeneration in subtropical mountains of northwestern Argentina during the 20th century, a period characterized by increasing rainfall and decreasing land-use intensity. We dated fire scars and establishment of *Alnus acuminata* (the dominant tree species) in six watersheds along a 600 km latitudinal range. We correlated fire frequency with rainfall records and performed Superposed Epoch Analyses to assess the relationship between rainfall and fire events during the century, and in two sub-periods: 1930–1965 (low rainfall, high grazing) and 1966–2001 (high rainfall, low grazing). We performed permutation analyses to assess the association between fire events and tree establishment, and to describe the spatial distribution of fires and forests in relation to hillslope aspect. Rainfall was associated with regional fires at interannual and decadal scales: fire probability increased after growing seasons with above-average rainfall and through the century, in concurrence with rainfall increase. The climatic control of fire was stronger under lower land-use intensity. Tree establishment was temporally associated with fire events, which occurred mainly in north facing slopes, where grassland cover is more extensive and forest colonization more likely. These results suggest that fire is limited by the availability of fine fuels, which is enhanced by high rainfall and reduced grazing; and tree establishment is limited by the competition with grasses. Consequently, increasing rainfall and decreasing grazing favored higher fire frequency, thus promoting forest encroachment during 20th century.

Key words: *Alnus acuminata*; climate change; dendroecology; grazing; forest expansion; land-use change; northwestern Argentina.

Introduction

Land use and climatic changes are the two most important components of global environmental change (Vitousek 1994; McCarty 2001; Foley and others 2005). Although global warming is the most conspicuous feature of climatic change, rainfall shifts may also have large ecological consequences (for example, Condit 1998; Dale and others 2001). Land-use change also exhibits two contrasting

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trends: while deforestation for agriculture expansion is the dominant pattern in tropical lowlands, some montane areas not suitable for modern agriculture are experiencing reductions in rural population and land-use intensity (Grau and Aide 2008). The complex ecological effects of the interactions between climate and land-use change are, in general, poorly understood. In Andean ecosystems, fire is a widespread disturbance that plays a key role in mediating the influence on ecosystems of both land use and climate. One particular landscape feature that is likely influenced by fire is treeline elevation and configuration (Young and León 2007). Although land use and climatic changes are expected to produce changes in fire and its effects on landscape dynamics, little research effort has been made to quantify these influences in tropical Andean ecosystems.

Fire is one of the most important disturbances in natural and seminatural environments, where it has the capacity to modify and shape landscapes (Bond and Keeley 2005; Bond and others 2005; Nowacki and Abrams 2008). Fire frequently plays a major role in defining the distribution of grasslands and woodlands. Often, frequent fires limit forest spread and favor grassland expansion over forested areas (Bond and Keeley 2005; Bond and others 2005; Carilla and Grau 2010). However, there are cases in which ground fires reduce competition for the establishment of water and light-demanding trees, thus favoring forest encroachment (Davis and others 2000; Grau and Veblen 2000; Hessl and Graumlich 2002). Hence, the net effect of fire on tree populations depends in part on the characteristics of the site and species involved.

Fire regime is the result of interacting anthropogenic, biological and climatic factors whose interactions often produce nonlinear responses (Veblen and others 1999; Guyette and others 2002). Individual fire occurrence is controlled by fuel availability, fuel moisture and ignition sources. In dry and mesic environments, fine biomass production is frequently conditioned by water availability through rainfall during previous growing seasons (for example, Veblen and others 1999; Grau and Veblen 2000). Rainfall can also prevent fire occurrence when fuel moisture is the limiting factor to fire ignition and spread (for example, Heyerdahl and others 2008). The anthropogenic controls on fire are also complex. On the one hand, ignition sources are expected to increase with land-use intensity when agriculture is not significant in the landscape (Veblen and others 1999; Guyette and others 2002). On the other hand, grazing by domestic animals typically reduces fine fuel availability, thus potentially reducing fire spread (Savage and Swetnam 1990; Belsky and Blumenthal 1997).

During the 20th century, two processes with potential consequences for fire ecology occurred in northwestern Argentina (NWA). First, annual rainfall rose (Minetti and Vargas 1997; Villalba and others 1998) with marked increases at the end of the 1950s and 1970s. Second, grazing by domestic animals and particularly sheep, the main economic activity in the montane systems, decreased in the second half of the century (Bolsi 1997). In the grassland-forest ecotones of the eastern mountain slopes of NWA, Grau (1985) used repeated photographs to record the expansion of forest over adjacent grasslands during the 20th century. Methods based on tree rings (dendroecology, Grau and Veblen 2000; Grau and others 2003) made it possible to evaluate the response of the regional fire regime to changes in climate and land use in the elevational range corresponding to the upper treeline in NWA; and to infer effects of fire on tree establishment and treeline dynamics.

We focused on four specific objectives: (1) to quantify the relationship between fire occurrence, and annual and seasonal patterns of rainfall, (2) to assess the trends in fire regime during the 20th century and its long-term association with changes in rainfall and grazing, (3) to quantify the association between fire events and tree establishment during the study period, and (4) to describe the spatial patterns of fires within the landscape. We hypothesized that rainfall controls fire occurrence through its effect on dry fine fuel availability (H1) and therefore we predicted that fire occurrence is associated with above-average rainfall in grasslands (P1.1). In addition, we expected that fire occurrence is positively correlated with growing season (summer) rainfall (P1.2), which increases fine fuel production; and negatively with the fire season (winter) rainfall (P1.3) due to a reduction in fuel moisture. Fuel availability is the result of the balance between rainfall, which controls fuel buildup, and grazing, which consumes fine biomass (H2). Thus, we expected an increase in regional fire frequency throughout the 20th century following an increase in fuel availability resulting from more rainfall and less grazing (P2.1). Additionally we expected that climatic control on fire frequency would be intensified as grazing intensity decreases (P2.2) because less grazing implies that fine fuel availability depends more on productivity than on harvest. Grasses compete with tree seedlings for water and light (H3) and consequently we expected an increase in tree establishment after fire events due to a reduction in interspecific competition for resources (P3). Finally we hypothesized that fine fuel distribution is controlled by topography (H4), so we expected that fires would be more frequent in north-facing slopes (P4), the topographic features that in the study area are mainly dominated by grasslands.

Methods

Study Area

The study was conducted in the upper montane forests of the subtropical humid forests (*Yungas*) of NWA between 2000 and 3000 m.a.s.l. The Argentine *Yungas* represent the southernmost extension of Andean tropical montane forests (Cabrera and Willink 1980); they extend across approximately 650 km, from approximately 22° on the border with Bolivia to approximately 28° in the province of Catamarca (Figure 1). At this elevational range, forests are largely dominated by *Alnus acuminata* (Betulaceae). This species usually represents more than 95% of the arboreal individuals (Bell 1991). *Alnus acuminata* is a light-demanding deciduous species that forms annual growth rings (Grau and others 2003). Forest patches alternate with grasslands and shrublands, in a savanna-like landscape (Giusti and others 1997; Grau 2005). The south-facing slopes are the most humid due to the lower annual insolation (Tian and others 2001). *Alnus acuminata* is a water-demanding species; in consequence, forests are mainly located on south-facing slopes and at the bottom of valleys where soil moisture is higher and protection from desiccating winds is better (Bell 1991). Through the comparison of historical photographs, Grau (1985) showed that forests expanded into grasslands during the second half of the 20th century.

The regional climate is characterized by a monsoonal rainfall regime, with more than 80% of the annual rainfall occurring between October and March (summer); winter is dry and relatively cold, including freezing temperatures and occasional

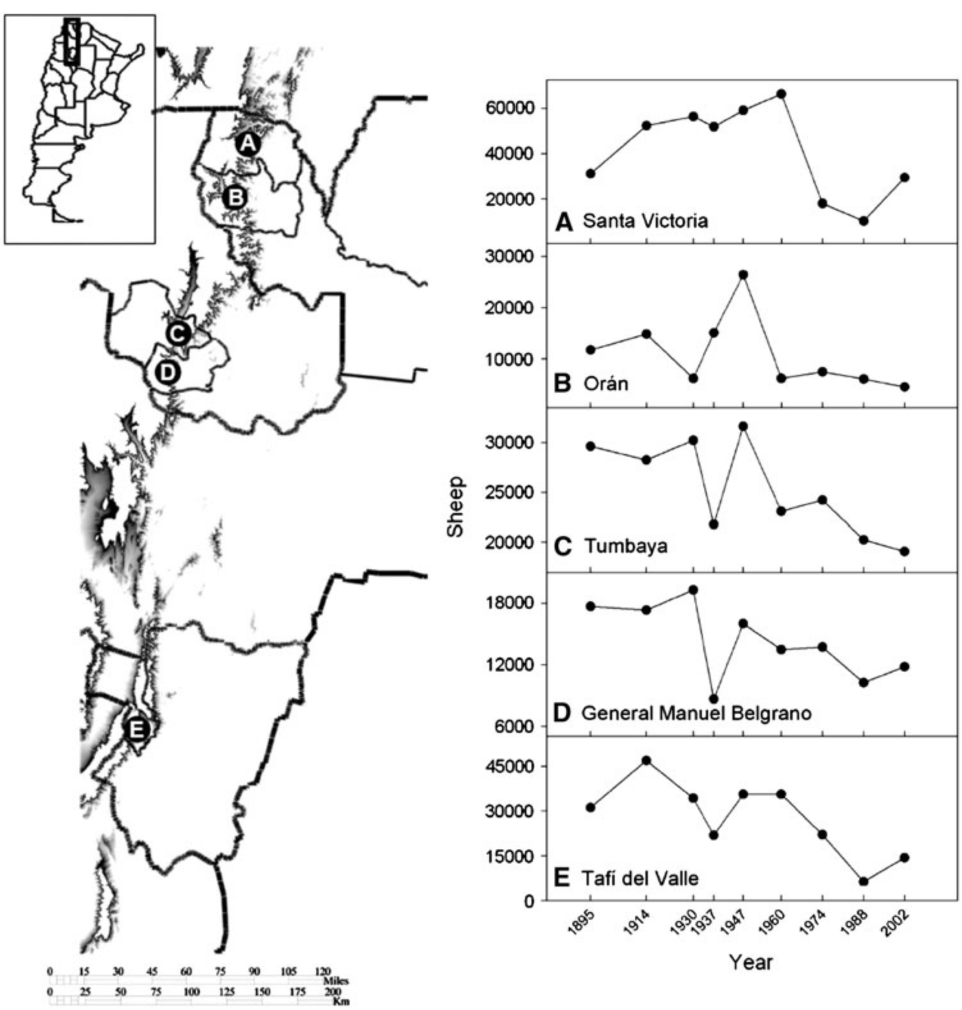

Figure 1. Digital elevation model of the study area between 2000 and 3000 m.a.s.l. (*left panel*). Each *dot* represents the location of the sampled watersheds, except for El Rincón and La Quebradita (both in Tafí del Valle) which are shown as a single dot due to their proximity. *Letters* inside the *dots* correspond with the figure at the *right panel*, showing changes in sheep abundances in the departments to which watersheds belong (see Table 1).

snowfalls. Tafi del Valle is the only location in this altitudinal belt that has systematic long-term (more than 50 years) meteorological data: it has an average rainfall of 422 mm y^{-1}, 91% of which falls between October and March. The average temperature of the hottest month (January) is 18.2°C and the average temperature of July is 8.1°C. During the second half of the 20th century an increase in annual rainfall was recorded at weather stations located on the plains of NWA with the main increases occurring at the end of the 1950s and 1970s (Minetti and Vargas 1997). This change was also reflected in local tree ring chronologies from montane forests (Villalba and others 1998).

The dominant land use in the study area is sheep and cattle ranching. Although cattle ranching also extends to lower elevational zones, sheep are largely restricted to high elevations (Grau and Brown 2000), and therefore changes in sheep density in departments (the smallest jurisdictional units for which statistical information is available, and which usually extend beyond the montane area) can be used as a proxy for change in grazing intensity in the montane area. However, comparisons between different watersheds cannot be done because the area of the departments and their proportion represented by the watershed are highly variable. In montane regions of NWA, the density of domestic animals decreased throughout the 20th century. Sheep density started to decrease in the 1930s, experienced a major stepwise reduction since 1960 and continued decreasing during the 1970s and 1980s (Bolsi 1997; Izquierdo and Grau 2009). Ground fires constitute the dominant disturbance (Grau 2001, 2005) and they are usually ignited by local people to promote grass regrowth with increased palatability and better nutritional properties for domestic animals. Most fires occur during the dry winter and early spring (Grau 2001). These fires spread mainly in grasslands but they can reach forest edges where they affect trees. When adult, *A. acuminata* (ca. >17 years) is a fire resistant species due to its thick bark. Younger trees are more sensitive to fires, and when affected by fires the proportions of killed, resprouting and unaffected individuals depend on their size, which is associated with their age (Grau and Veblen 2000).

In this study we surveyed six watersheds distributed along the latitudinal range (Figure 1; Table 1) to capture the regional variation in climate and land use. Cerro Bravo and San Andrés, both located in Salta Province, are the most northern and humid watersheds surveyed. Cerro Bravo supports high livestock density, whereas San Andrés supports a moderate intensity of land use. Volcán (Province of Jujuy) is the driest watershed studied and presents low land-use intensity. Yala (also in Jujuy) has a mesic rainfall regime with moderate land-use intensity. La Quebradita and El Rincón (valley of Tafí, Tucumán Province) both have a mesic rainfall regime and experienced a strong reduction in land-use intensity throughout the century.

Table 1. Location and Sample Characteristics of the Six Watersheds Studied

Watershed	Latitude Longitude	Province Department	Forested area (hectares)	Sampled sites	Sampled trees for establishment dating	Sites with fire scared trees	Fire events dated	Wedges of scarred trees
Cerro Bravo	22°15′ 64°46′	Salta Santa Victoria	389	30	301	14	43	39
San Andrés	23°07′ 64°55′	Salta Orán	270	30	269	2	3	4
Volcán	23°57′ 65°26′	Jujuy Tumbaya	126	30	267	6	16	21
Yala	24°05′ 65°29′	Jujuy Doctor Manuel Belgrano[a]	427	70	468	23	67	51
La Quebradita	26°49′ 65°42′	Tucumán Tafí del Valle[a]	249	30	280	5	26	14
El Rincón	26°57′ 65°28′	Tucumán Tafí del Valle[a]	136	75	718	17	33	35
Total			1597	265	2303	67	188	164

[a] *Departments that changed their spatial jurisdiction during the 20th century, for which the census information corresponding to their maximum area was taken into account.*

Sample Collection and Processing

The study was based on dendrochronological samples of *A. acuminata*; the dominant tree species, with reliable annual tree rings that can be used to date tree establishment and fire events (Grau and others 2003). In each watershed we walked randomly, and every 10 min or whenever we detected a tree with fire scar we stopped to take increment borer samples from the base of the nearest 6 to 10 trees. This sampling technique yielded an average minimum distance between sites of 149 m. The radius of each site depended on the density of available trees but it never exceeded 25 m. We repeated this protocol until at least 50% of the area of the watershed was surveyed. Increment borer samples were taken near the ground (typically less than 18 cm height) to get a complete ring series (that is, from sampling year to establishment year because most seedlings attain this height during the first growing season, Grau and Veblen 2000). In the sites where fire scars were present, we extracted wedges with a chainsaw (Arno and Sneck 1977) to date fire events. Fire scars can be recognized by their shape and height, and because generally they affect multiple trees (Grau and others 2003). We extracted up to five wedges from closeby scarred trees wherever they were available to confirm fire dates but in some cases, older fires were detected only on a single surviving tree. Each site was georeferenced with a GPS device. At least 30 sites and 300 trees were sampled in each watershed and rotten samples were discarded from the analyses, resulting in a varying number of increment borer samples in different watersheds (Table 1).

Increment borer samples and wedges were sanded with progressively finer sand paper to make the rings clearly visible. Samples were examined under an up to 45× magnifying glass and annual rings were counted backwards from the outermost ring (corresponding to the sampling year) to the innermost ring, adjacent to the pith, corresponding to the establishment year. When the pith was not hit by the sample, missing rings were estimated by geometrical inference up to a maximum of 10 years (Duncan 1989); samples that surpassed this deviation were discarded from the analyses. From a total of 2558 increment borer samples, 38.9% hit the pith and less than 0.5% were discarded due to high deviation. Establishment was assigned to the year when the growing season started. When grassland fires burn the base of tree trunks, a portion of cambium is killed but adjacent cambium can survive and continue to grow forming healing tissue with a lobular shape that permits fires to be dated. The rings of fire wedges were also counted backwards up to the first ring with charred wood and normal (not lobular) growth. Fire dates were assigned to the calendar year in which the healing tissue began to form because most fires take place during austral winters after annual growth has ceased (Grau and Veblen 2000; Grau and others 2003). Some wedges presented multiple fire scars; therefore the number of fire events dated is larger than the number of scarred trees sampled. No statistical cross-dating was performed because ring series were very short (Hessl and Baker 1997; Elliott and Baker 2004) and the deformation of annual rings close to fire scars generates highly variable growth patterns that prevent statistical cross-dating in short time series. However, visual cross-dating of increment borer samples of tree age was performed based on indicator years or groups of years (that is, years of unusually high or low growth). As a result, single year corrections were made in a small proportion of increment borer samples comparing each sample with other samples from the same watershed. We also tried visual cross-dating of fire scars, but no corrections were needed in fire scar wedge dating because annual rings were clearly visible in their broad surface and *A. acuminata* does not present false or missing rings (Grau and Veblen 2000; Grau and others 2003). Previous research found that there was a perfect temporal matching between fires dated with dendrochronological techniques using *A. acuminata* and those dated using satellite imagery (Grau and others 2003). We did not determine the season of fire occurrence with dendrochronological techniques because to our knowledge there are no studies on the anatomy of the growth rings of *A. acuminata* that would make this kind of assessment possible.

Data Analysis

We dated all the sampled fire scars and defined ''fire events'' as those recorded in any site and any year (that is, two or more simultaneous fires recorded in the same site were considered as a single event). Most fire events were recorded in more than one wedge, but some older fire events were recorded in only one surviving tree. We kept these dates to avoid a temporal bias due to loss of information resulting from tree death. Even though this definition does not imply that simultaneous fire events in a watershed are independent events because we cannot determine their source, it constitutes an objective way of quantifying a proxy for fire influence in the landscape. Moreover, most synchronous fires were dated in nonadjacent sites suggesting that they were independent events. To analyze regional fire events, which are more likely to be climatically controlled (Veblen and others 1999; Gavin and others 2007), a composite regional fire chronology was generated taking into account only those years in which at least 10% of the sites recording fire in each watershed burned in at least two watersheds. At the regional scale we generated a ''fire index'' to control for the decreasing number of potential fire-recording trees through time. Potential fire recorder trees decrease going backward into time due to tree mortality, so we computed the fire index as the ratio between total number of fire events and the number of trees that had established before the event year and were sampled in the survey.

To assess the short-term relationship between regional fires and rainfall (H1) we used two time series of rainfall indices. (1) The scores of the first component of a Principal Components Analysis performed with rainfall records from eight stations distributed in NWA foothills (Salta and Metan in Salta province, La Quiaca and San Salvador de Jujuy in Jujuy province, Trancas, San Miguel de Tucumán and Famaillá in Tucumán province, and San Fernando del Valle de Catamarca in Catamarca province) from 1930 to 2001. To summarize the rainfall information of the complete growing season we summed up the rainfall from October of the previous year (year −1) to March of the current year (year 0) for each weather station, and we assigned it to the current year, the one that begins in January of the growing season. (2) In addition, we used the rainfall record from S.M. de Tucumán, the longest and most reliable of the region, to discriminate summer and winter rainfall. In this case, we did not use all the regional weather station records due to the possible asynchrony in annual rainfall regime and seasonal patterns along the region (for example, rainy season may have different length, beginning or ending dates, increasing the error in the assessment of fire–climate relationships). These time series constitute proxies of the regional interannual variation of rainfall but they do not represent the actual amount of rainfall of the study area, where weather stations are lacking. To assess the predicted effect of rainfall variability on the occurrence of fires (P1.1), taking into account the temporal autocorrelation of rainfall through the time series, we performed Superposed Epoch Analyses (SEA, Prager and Hoenig 1989). SEA compares the mean of observed values of some attribute (that is, rainfall) in a time window around a particular event, with the values expected under the assumption of no causal relationship between the attribute and the event. The observed mean is considered for every year of the window and compared with an expected value, obtained through multiple permutations from the time series which are generated randomly with Monte Carlo methods. This permutation is used to generate confidence intervals to be compared with the observed values. In this case the compared attribute is rainfall; the events are regional fires and the time window considered begins 3 years prior to the regional fire event and ends 1 year after it. We considered the regional fire chronology as the response variable, because regional fires are climatically controlled in contrast with single fire events which might be affected by local conditions (Veblen and others 1999; Heyerdahl and others 2001; Gavin and others 2007); and regional rainfall as the controlling factor. In addition, to assess P1.2 and P1.3 about the differential influence of summer and winter rainfall on fire occurrence we performed SEAs considering winter and summer rainfall of S.M. de Tucumán as the controlling factors and the regional fire chronology as the response variable.

Sheep densities experienced a general decrease throughout the 20th century in NWA (Bolsi 1997; Izquierdo and Grau 2009), with a stepwise reduction in the 1960s (Figure 3) and thus, to evaluate H2, we split the 1930–2001 period into two symmetrical sub-periods: (1) 1930–1965, characterized by high sheep density and low precipitation; and (2) 1966–2001, characterized by reduced sheep densities and high rainfall. To evaluate the effect of rainfall on the temporal trend of fire frequency predicted by P2.1 we performed correlations between 5-year moving averages of fire index and 5-year moving averages of regional rainfall. Moving averages facilitate the detection of temporally accumulated effects but have the disadvantage of autocorrelation between observations, which would affect the statistical significance of the test. To overcome this problem we generated 10,000 correlation coefficients through Monte Carlo simulations. For each simulation we reshuffled fire index and annual rainfall, we computed their five-year moving averages and we calculated the correlation coefficient of the averaged time series. We ranked the simulated coefficients and we compared the 95th and 99th percentiles with the observed coefficient to evaluate the significance level of the observed correlation coefficient (McCabe and others 2004). We performed a Mann–Whitney U test to compare regional rainfall indices between the two sub-periods. To evaluate the effect of rainfall on fire regime we performed nonparametric correlations between regional rainfall and fire index for the complete period of time and within the two sub-periods. To evaluate changes in fire regime between the two sub-periods, we assessed the differences in fire indices between them with a nonparametric Mann–Whitney *U* test and we compared changes in median fire intervals between sub-periods of the composite fire series assuming a Weibull distribution. Finally, to assess whether climatic control on regional fire occurrence changed through time due to changes in grazing pressure (P2.2), we performed independent SEAs to analyze the relationship of rainfall-regional fire within the two sub-periods.

To evaluate the effect of fire events on tree establishment (P3) at the fire sites we conducted a permutation analysis to combine the age structure and the fire dates of each site. We calculated the average tree establishment in sites affected by fires in a time window of 21 years centered in each fire event. *Alnus acuminata* is a pioneer species that establishes shortly after disturbances, but there is no information about the temporal lag between disturbance and colonization. Thus, we used a window that included up to 10 years after the event to explore this time lag. We also considered the previous 10 years to explore possible nonrandom patterns with no relation to fire events and to detect below average establishment, which could suggest that fires eliminate juveniles (Grau and Veblen 2000). We constructed a null model by permuting tree establishment with Monte Carlo methods 1000 times. In each permutation we redistributed fires randomly in space (sorted by sites) but not in time (sorted by years) because fires and establishment increased throughout the century. From this permutation procedure we obtained an expected number of establishments for each year of the analyzed time window and its corresponding confidence intervals, which we compared with the observed establishment around fire years.

To analyze the spatial distribution of fires we compared the hillslope aspects of sampled fire sites with those of *A. acuminata* forests. Because in our sampling strategy fires are recorded in *A. acuminata* trees, the likelihood of detecting any single fire event depends on the number of affected trees which in turn depends on the existence of forests. Thus, the spatial distribution of recorded fires is highly correlated with the spatial distribution of the forest. If all forested sites were equally prone to fire occurrence, there would be no difference between the observed distribution of fires and that predicted by the forest distribution. On the contrary, if there are differences in the flammability between topographical locations, fire scars will be more frequent in trees located in some specific hillslope aspects. To evaluate P4, a 90-m grid size aspect map was generated from a digital elevation model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM). To calculate the aspect of pixels of the DEM, a square window of 3×3 pixels was centered in every pixel. A plane was fitted to the window and the aspect of the plane was assigned to the central pixel, 0° for the north-facing slopes and 180° for the south-facing slopes. The aspects of fire sites were grouped in 20° intervals. Hillslope aspect values were transformed to their cosine to obtain their north–south component (that is, north-facing aspects score 1 and south-facing aspects score −1). To generate a distribution of expected aspect values, we performed 1000 Monte Carlo simulations taking *n* fires (that is, the number of observed fires) from all the possible sites (that is, forest sites). Finally, this distribution with its confidence intervals was compared with the averaged aspect of fire sites.

Results

In the six surveyed watersheds, we sampled a total of 265 sites to describe the age structure of *Alnus* forests (Table 1). In 67 of these sites, we found 267 scarred trees representing 188 fire events (average of 2.78 fire events per site). The oldest dated fire event took place in 1935. Regional fire events tended to occur during rainy periods because the mean annual rainfall of the 5 years of the analyzed window positively deviated from the expected average, and in the fire year (year 0) this deviation was statistically significant (Figure 2A) as predicted (P1.1). Rainfall in S.M. de Tucumán during the growing season previous to regional fire years (year 0) was higher than average at a marginally significant probability level ($P < 0.06$, Figure 2B), as predicted by P1.2; but contrary to P1.3, winter rainfall also deviated positively from the historical average for years 0 and −2 suggesting that fuel desiccation is not a limiting condition for regional fire occurrence (Figure 2C).

We observed that the five-year moving average of the fire index oscillated with a quasi-cycle of approximately 10 years (Figure 3). In agreement with P2.1, fire index was positively correlated with calendar year along the complete study period, indicating an increase of fire incidence in the landscape through the century. This increase in fire frequency through time was weak and not significant during the 1930–1965 sub-period, but became steeper ($r = 0.36$) and statistically significant

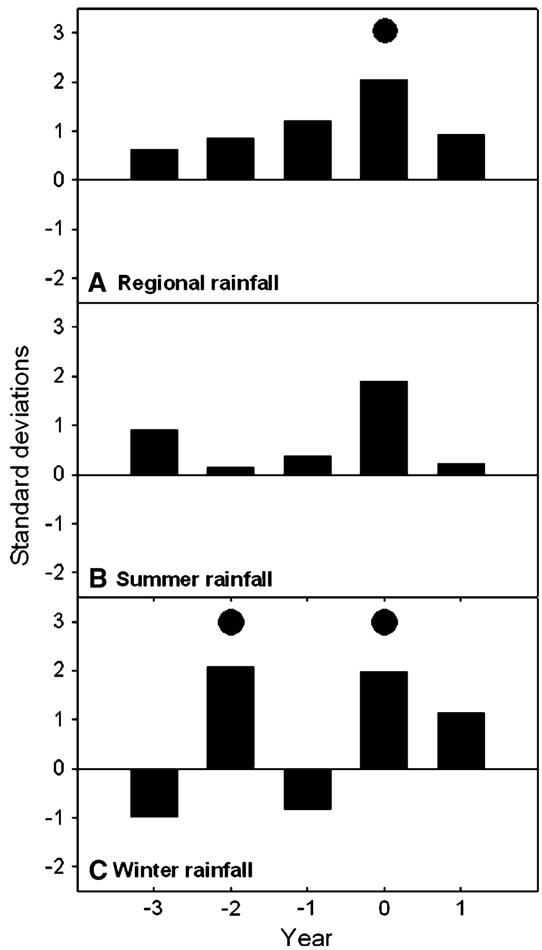

Figure 2. Rainfall departures (in standard deviation units) from expected average regional rainfall (**A**), and San Miguel de Tucumán summer (**B**) and winter (**C**) rainfall records. Regional fire years are defined as those in which at least 10% of the fire sites were burned in two or more watersheds. *Black dots* indicate statistically significant deviations from the expected average ($P < 0.05$) estimated through 1000 Monte Carlo simulations based on the observed number of fire years ($n = 20$). Year 0 is the year of fire occurrence.

between 1966 and 2001 (Table 2). The correlation between the 5-year moving average of fire index and 5-year moving average of regional rainfall was positive and significant during the entire period of time ($r = 0.39$, $P < 0.01$) but it was not significant within the two sub-periods (Table 2). Mean fire index and regional rainfall were significantly higher (Mann–Whitney U test, $P = 0.0007$) in the second sub-period suggesting that even though rainfall does not control fire index tightly it could be favoring a more intense fire regime (Table 2). Of the 20 years that presented regional fire events (those in which at least 10% of the recording sites were burned in at least two watersheds, Table 2; Figure 3B) only five occurred during the first subperiod, compared to 15 during the second subperiod. The median Weibull interval was 30% shorter in the second subperiod than in the first one (Table 2). As predicted by P2.2 the relationship between rainfall and fire occurrence was stronger during the second subperiod, although this difference was not statistically significant (Table 2). Between 1930 and 1965, rainfall during regional fire years did not differ from the average rainfall, and followed two relatively dry years (Figure 4A). In contrast, in the post 1965 period regional fires occurred during years of above-average rainfall (Figure 4B), more consistently with the pattern of the whole period.

In support of H3, the permutation analysis showed that *A. acuminata* establishment was associated with fire events: establishment was significantly above the mean during the fire year, as well as the following and previous years. Between years −10 to −2 (that is, prior to a fire occurrence), tree establishment generally deviated positively from expected values, whereas in the subsequent years (years 2–10), tree establishment was in general below the expected average (Figure 5).

Supporting H4, the spatial distribution of sampled fires differed from that expected from the distribution of *A. acuminata* trees in the landscape. The location of fire-scarred trees was significantly ($P < 0.01$) biased toward north facing in comparison to south-facing slopes, and there were no significant differences between east and west aspects (Figure 6).

Discussion

Fires in NWA montane treelines tend to occur during rainy periods (Figure 2A), generally supporting our first hypothesis. Regional fires took place during the dry season following a growing season with above-average rainfall, as explained by enhanced fuel production (for example, Veblen and others 1999; Grau and Veblen 2000, Figure 2B). All winters appear to be dry enough to carry fire, because they were also positively associated with above-average rainfall during winter (Figure 2C); a likely spurious positive association derived from the positive effect on fuel production of rainfall of the previous summer, which in turn is temporally correlated with winter rainfall. In summary, rainfall during the growing season (90% of the total annual rainfall) affects regional fire probability. Our results are consistent with many studies in semi-arid environments, where the climate effect on fire frequency is stronger through the control of fuel

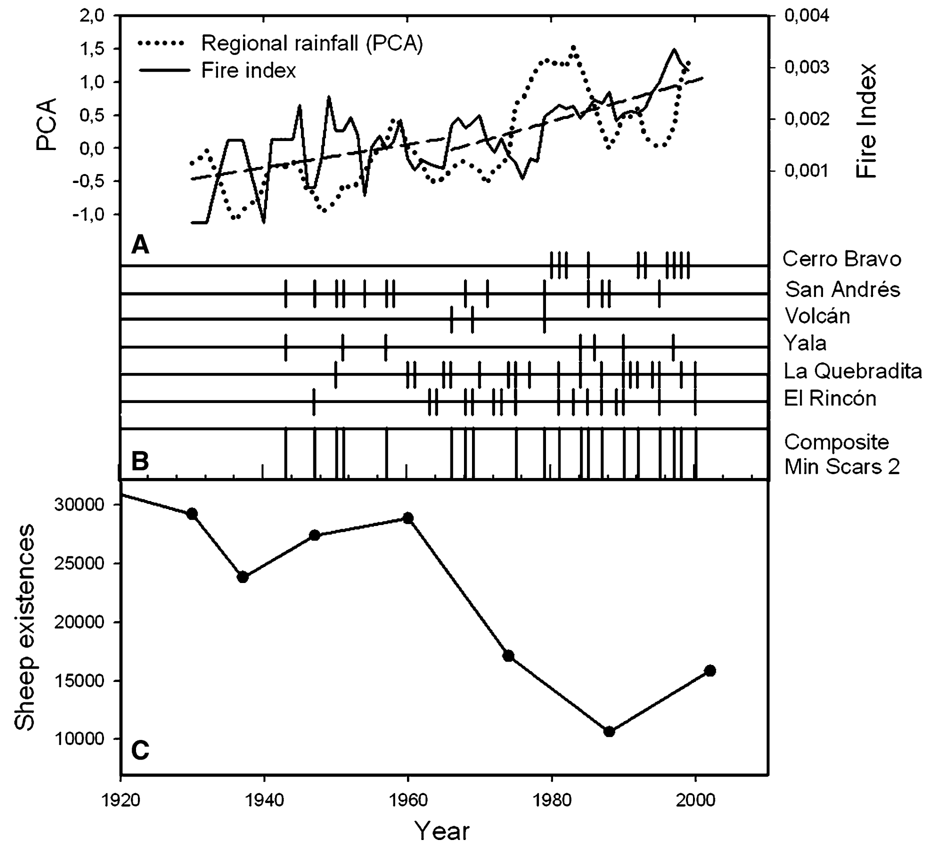

Figure 3. **A** Five-year moving average of fire index in montane forest-grassland ecotones in NWA (*solid line*) and five-year moving average of regional rainfall index (see text for methodological explanations). *Straight lines* represent the regression of calendar year and fire index for the two sub-periods considered (1930–1965 and 1966–2001). **B** Fire chronologies for each of the six studied watersheds. *Vertical lines* represent years in which at least 10% of the fire sites were burned. The regional composite chronology at the bottom represents years in which at least 10% of the fire sites were burned in at least two watersheds. **C** Sheep average existences throughout the 20th century in the five departments that include the six studied watersheds.

Table 2. Main Features of the Fire Regime in the Study Area between 1930 and 2001, and in the Two Subperiods (Pre and Post 1965)

	Average rainfall index standard deviation	Correlation between FI and year *P*	Correlation index between 5YMA of FI and regional rainfall	Weibull median fire interval	Average fire index standard deviation	Number of regional fires
1930–2001	0.074	0.334	0.394*	1.67	0.00166	20
	0.998	0.004			0.00161	
1930–1965	−0.370[a]	0.124	−0.069	1.09	0.00123[a]	5
	0.703	0.471			0.00188	
1966–2001	0.419[b]	0.363	0.167	1.25	0.00209[b]	15
	1.019	0.030			0.00115	

5YMA 5-year moving average, FI fire index (the ratio between fire events dated in a particular year and the number of potential recorder trees already established in that year).
**Significance at $P < 0.01$. [a,b]Statistically significant differences ($P < 0.05$) between groups when letters are different.*

formation rather than of fuel desiccation (for example, Kitzberger and others 1997; Veblen and others 1999; Grissino-Mayer and Swetnam 2000; Gavin and others 2007). Although fires are accurately dated using the rings of *A. acuminata* (Grau and others 2003), fire scars were visually cross-dated (though no corrections were needed) and more than 75% of the fire events were recorded in more than

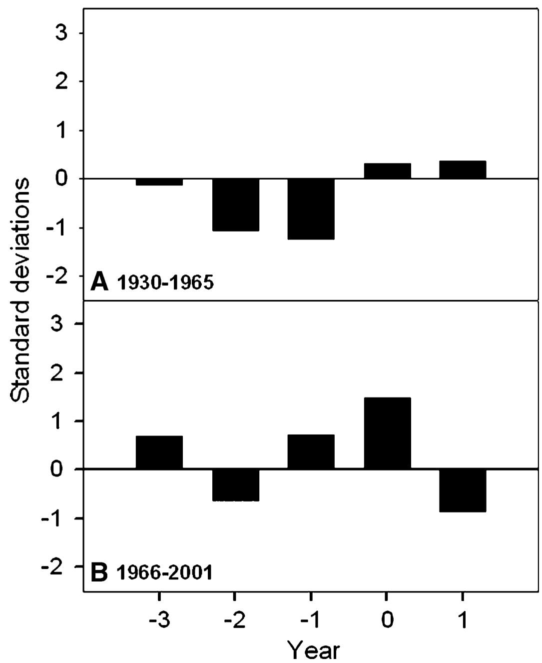

Figure 4. Rainfall departures (in standard deviation units) from average regional rainfall for windows from 3 years prior to 1 year after fire years (see definition in text), in the two studied sub-periods: **A** 1930–1965, $n = 5$; **B** 1966–2001, $n = 15$.

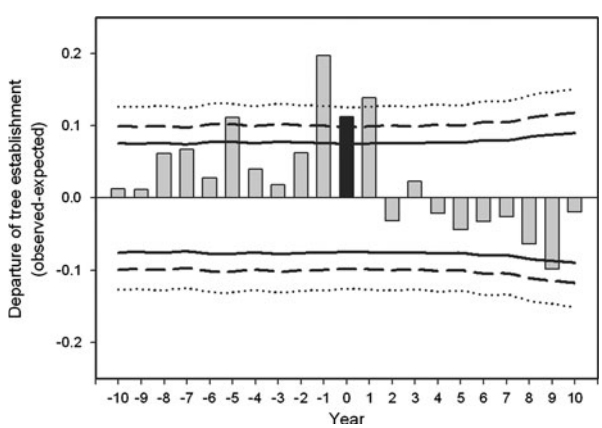

Figure 5. Departures of tree establishment in fire sites with respect to the null model (no relationship between fire and establishment). *Vertical bars* represent establishment departures during years in relation to the local fire event year, indicated with a *black bar*. Confidence intervals are represented with *solid* (95%), *dashed* (99%), or *dotted* (99.9%) *lines*.

one tree, dendrochronology-based studies are imperfect due to information loss through time. It is possible that more accurate studies (for example, using satellite imagery) would find a stronger association between rainfall and fire events.

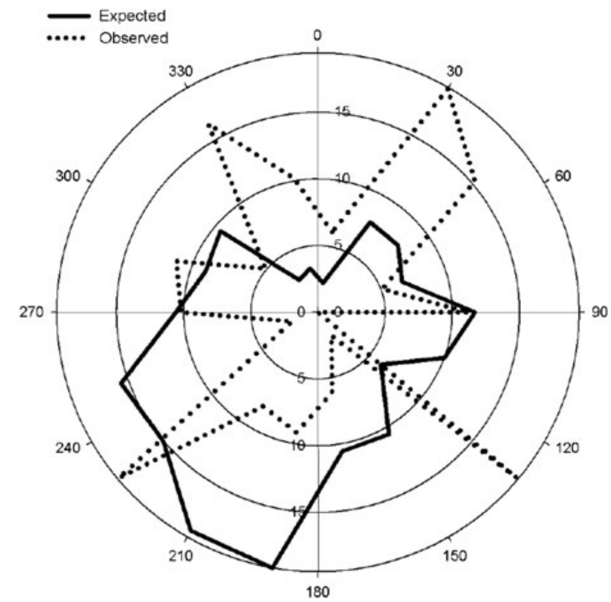

Figure 6. Observed and expected fire frequency in different hillslope aspects classified in 20° intervals. Each fire is considered individually and thus a sampling place may be counted more than once. Expected frequency is based on the location of *Alnus acuminata* forests.

In support of our second hypothesis, fire regimes changed through the 20th century to a higher fire frequency in response to climatic and land-use changes. Climatic influences on regional fire regime became stronger as rainfall increased and, probably more importantly, as grazing decreased (Table 2; Figure 3). This pattern also suggests that fuel availability is a key limiting factor to fire occurrence. Fine fuel availability is the result of the balance between production (mainly limited by water availability) and removal, mainly due to grazing. During the 1930–1965 sub-period (characterized by high sheep densities), there was no association between rainfall and fire occurrence, suggesting that grazing controlled fuel availability through harvest and masked the effect of water availability (Figure 4A). In contrast, rainfall control on fire occurrence was detectable after 1965, when rainfall was higher and grazing less intense (Figure 4B). These kinds of shifts in fire regime and climate–fire associations were previously observed in North America: an increase in livestock and other human activities limited fire spread due to fuel consumption and fragmentation in the central United States (Guyette and others 2002), and a change in the climate-fire relationship observed in California was related to a change in livestock pressure (Fry and Stephens 2006) in the mid of 19th century.

Our results do not necessarily imply that climatic control will be stronger under a further reduction in land-use intensity. In our system, fire ignitions are mainly anthropogenic (Grau and Veblen 2000), so they are expected to decrease with decreases in the rural population and land-use intensity (Guyette and others 2002). Because we observed an increase in fire frequency through the century (Figure 3; Table 2), fire ignitions do not seem to be a limiting factor to regional-scale fire occurrence. However, further reductions in ignition sources could fall below the threshold necessary to burn all the fire-prone sites, thus increasing the relative importance of anthropogenic ignition sources in relation to climatic controls. On the other hand, fires that expand over vast areas may occur with continuous abundant fuel and optimal climatic conditions. It is likely that if current land use and climatic trends continue, the concurrence of more rainfall, less grazing and less ignitions sources, may favor extensive areas with continuous fuel, thus producing a fire regime more dominated by infrequent, larger and more intense fires.

Our results support the idea that fires play a major role in the expansion of forests over grasslands in NWA montane forests, consistent with Grau and Veblen (2000). Tree establishment was significantly higher during years −1, 0 and 1 in relation to fire events (Figure 5). *Alnus acuminata* is a pioneer species that cannot establish under a forest canopy, therefore the increase in tree establishment in relation to fire likely implies an expansion of the forest rather than a replacement of older trees, which are not killed by fires after 5–20 years old (Grau and Veblen 2000). Enhanced establishment during the fire and subsequent year is likely explained by the elimination of competing aerial biomass of nonforest vegetation; a stage that is frequently the bottleneck to tree invasion into grasslands (Sankaran and others 2004). The enhanced recruitment of trees observed after fire should not be attributed to the resprouting of young trees affected by fires (Grau and Veblen 2000) because we observed that in the previous 9 years, establishment is also above average suggesting that fire events did not affect recently established trees negatively. There is no clear explanation for the high level of establishment in year −1, and it can potentially be attributed to dating errors in increment borer samples (for example, establishment occurring during year 0 is mistakenly assigned to year −1). However, the fact that this signal is detected in spite of the error in establishment dating and imperfect fire reconstruction due to the limitations of dendrochronological techniques (for example, loss of data along time, biased sampling toward intense fires, and so on) suggests that fire is at least one of the processes favoring tree establishment.

In addition, fires that are intense enough to scar trees, take place more frequently in north-facing slopes (Figure 6), which are generally dominated by grasslands (Bell 1991). Therefore, fires affect only a smaller proportion of *Alnus* forest and, in contrast, tend to occur frequently in the ecotone between grasslands and forests. The fact that fire frequency has increased on the landscape throughout the 20th century (Figure 3), when forests encroached (Grau 1985) provides further support to the hypothesis of a positive effect of ground fires on forests. A similar pattern has been observed on the ecotones between quaking aspen and high elevation meadows of the Teton National Forest in western Wyoming (Hessl and Graumlich 2002), where this tree species depends on fire occurrence to expand into grassland and where fire exclusion has inhibited its expansion. In the Canadian Rockies, the establishment of other pioneer species such as *Pinus contorta* and *Picea engelmannii* was enhanced after fire occurrence (Johnson and Fryer 1989); and, consistently, long-term studies combining pollen and charcoal analyses in two lakes of Switzerland showed that *Alnus glutinosa*, a fire resistant species of the same genus, increased its relative abundance during periods with high fire incidence on the landscape (Tinner and others 1999). So, although fire generally limits forest encroachment (Bond and Keeley 2005; Bond and others 2005; Carilla and Grau 2010), under some circumstances it can have the opposite effect. In our case study, the current level of fire frequency has two effects. On the one hand, fire is frequent enough to generate many time windows with suppressed interspecific competition for successful seedling establishment. On the other hand, the fire interval is long enough to allow trees to grow to a size at which they are fire resistant (Grau and Veblen 2000).

Increased rainfall, thus, appears to have two types of positive effects on forest expansion in NWA treelines: directly, higher moisture availability favors tree growth (Morales and others 2004) and establishment; and indirectly, moisture availability enhances fine fuel production and promotes more fire, which reduces competition with nonforest vegetation (Grau and Veblen 2000). Grasslands are located mostly in the drier north-facing slopes and the competition between grasses and *Alnus* seedlings for water would be more restraining than in wetter environments. It has been suggested that biological invasions are favored by an increase in resource availability through a reduction in the resource uptake of the established community (that is, disturbances) or through an increase in the resource supply (Davis and others 2000). In our study area both processes occurred simultaneously: rainfall (water supply) and fire incidence (competition reduction) increased throughout the 20th century (Figure 3). However, as both processes are collinear, and likely interact generating nonlinear responses, it is difficult to evaluate the relative contribution of each process to forest expansion.

Forest encroachment in the Argentinean montane system was mediated by a circumstantial combination of climatic, land use, and fire regime conditions, which might have no linear effects on the system due to the complexity of their interactions. Increasing rainfall in NWA seemingly favored tree establishment because *A. acuminata* is a water demanding species (Bell 1991) but, on the other hand it also favored grass growth, which competes with tree seedlings for light and water. Fire depends on fuel availability and it burns mainly grasses without affecting older and bigger trees, thus favoring tree establishment by a reduction in interspecific competition. However, because *Alnus* trees are resistant to fire at between 5 and 20 years of age (Grau and Veblen 2000); if the fire return interval fell below that range, it could negatively affect forests and lead to grassland expansion. Livestock likely have similarly ambiguous effects on tree-grass dynamics: grazing reduces competition for tree establishment but at the same time domestic animals damage seedlings inhibiting forest encroachment, as was observed in an experimental approach (Aráoz 2009). Grazing also affects fire frequency because livestock consume grass biomass that is the potential fuel for fires. So under a scenario of reduced land-use intensity fires may attain a frequency that could lead to forest shrinkage. An experimental analysis of germination, seedling survival, and fuel accumulation with and without livestock exclusion would probably shed some light on the relative weight of climate change and land-use change on forest encroachment.

Our results have consequences for ecosystems management in the context of relatively rapid environmental changes. NWA montane forests are complex semi-natural systems, in which human activities affect ecological processes through fire and grazing. Although climate cannot be controlled, grazing mediates the influence of climate on fires, and grazing management may affect the fire regime, and consequently, it may modify the effects of climate change on landscape configuration and ecosystem functioning. It has been suggested that reductions in land-use intensity may have important implications for the recovery of ecosystems in Latin America (Aide and Grau 2004; Grau and Aide 2008). This paper sheds light on the complex interactions between natural and social systems involved in the ecological consequences of land-use disintensification and its interactions with climate change.

The ecological effects of the interactions between climate change and land-use change mediated by fire regimes are likely to play a key role in the dynamics of tropical and subtropical Andean ecosystems, but they are poorly studied largely due to the lack of long-term studies. Our study system, with its potential for multidecadal records of fire and tree establishment based on dendrochronology (Grau and Veblen 2000; Grau and others 2003; Carilla and Grau 2010) provided the opportunity to quantitatively analyze how land-use and climate change interact to control fire regimes, and potentially affect landscape configuration in neotropical mountains. In this case, land-use disintensification coupled with increasing rainfall has favored more fires with a stronger climatic control, and this is likely favoring forest expansion into grassland areas. The interactions between climate, land use, and vegetation dynamics generate nonlinear responses (for example, fires respond to rainfall only when grazing falls below a threshold), and feedbacks (for example, resulting changes in forest distribution, partially controlled by fire, may change fire regimes dramatically by affecting fine fuels distribution). Such complex interactions need to be studied by further empirical work coupled with spatially explicit dynamic models to understand the responses of these montane ecosystems to ongoing and future land-use and climatic changes.

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REFERENCES

Aide TM, Grau HR. 2004. Globalization, migration, and Latin American ecosystems. Science 305:1915–16.

Aráoz E. 2009. Dinámica del bosque de alisos en el noroeste de Argentina en respuesta al cambio climático y de uso de la tierra. Tesis doctoral de la Universidad Nacional de Tucumán. Inedit. 124 pp.

Arno SF, Sneck KM. 1977. A method for determining fire history in coniferous forests of the mountain west. U.S. Department of Agriculture Forest Service General Technical Report Int-42.

Bell DA. 1991. Distribución del bosque de aliso de cerro, *Alnus acuminata* (Betulaceae) en la provincia de Tucumán, Argentina. Boletín de la Sociedad Argentina de Botánica 27:21–30.

Belsky AJ, Blumenthal DM. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conserv Biol 11:315–27.

Bolsi A. 1997. La actividad ganadera en el noroeste argentino. In: Bolsi A, Ed. Problemas Agrarios del Noroeste Argentino. San Miguel de Tucumán, Argentina: Universidad Nacional de Tucumán-Junta de Andalucía. p 149–79.

Bond WJ, Keeley JE. 2005. Fire as a global ''herbivore'': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–94.

Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fires. New Phytol 165:238–525.

Cabrera AL, Willink A. 1980. Biogeografía de América Latina. Organization of American States, Washington, DC, 122 p.

Carilla J, Grau HR. 2010. 150 years of tree establishment, land use and climate changes in montane grasslands, NW Argentina. Biotropica 42:49–58.

Condit R. 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. Clim Change 39:413–27.

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irlan LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM. 2001. Climate change and forest disturbances. Bioscience 59:723–34.

Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–34.

Duncan R. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacycarpus dacrydioides*). N Z Nat Sci 16:31–7.

Elliott GP, Baker WL. 2004. Quaking aspen (*Populus tremuloides* Michx.) at treeline: a century of change in the San Juan Mountains, Colorado, USA. J Biogeogr 31:733–45.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Howard EA, Holloway T, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK. 2005. Global consequences of land use. Science 309:570–4.

Fry DL, Stephens SL. 2006. Influence of humans and climate on the fire history of ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. For Ecol Manag 223:428–38.

Gavin DG, Hallett DJ, Hu FS, Lertzman KP, Prichard SJ, Brown KJ, Lynch JA, Bartlein P, Peterson DL. 2007. Forest fire and climate change in western North America: insights from sediment charcoal records. Front Ecol Environ 5:499–506.

Giusti L, Slanis A, Aceñolaza PG. 1997. Fitosociologia de los bosques de aliso (*Alnus acuminata* H.B.K. ssp. *acuminata*) de Tucumán (Argentina). Lilloa 38:93–120.

Grau A. 1985. La expansión del aliso del cerro (*Alnus acuminata* H.B.K. ssp. a*cuminata*) en el noroeste de Argentina. Lilloa 36:237–47.

Grau HR. 2001. Regional-scale spatial patterns of fire in relation to rainfall gradients. Glob Ecol Biogeogr 10:133–46.

Grau HR. 2005. Dinámica de bosques en el gradiente altitudinal de las Yungas Argentinas. In: Arturi M, Frangi J, Goya J, Eds. Ecología y Manejo de los Bosques Argentinos. La Plata, Argentina: Universidad Nacional de La Plata.

Grau HR, Aide TM. 2008. Globalization and land use transitions in Latin America. Ecol Soc 13:16. http://www.ecologyandsociety.org/vol13/iss2/art16/.

Grau A, Brown AD. 2000. Development threats to biodiversity and opportunities for conservation in the mountain ranges of the upper Bermejo River basin, NW Argentina and SW Bolivia. Ambio 29:445–50.

Grau HR, Veblen TT. 2000. Rainfall variability, fire and vegetation dynamics in neotropical montane ecosystems in northwestern Argentina. J Biogeogr 27:1107–21.

Grau HR, Easdale TA, Paolini L. 2003. Subtropical dendroecology-dating disturbances and forest dynamics in northwestern Argentina montane ecosystems. For Ecol Manag 177:131–43.

Grissino-Mayer HD, Swetnam TW. 2000. Century-scale climate forcing of fire regimes in the American southwest. The Holocene 10:213–20.

Guyette RP, Muzika RM, Dey DC. 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5:472–86.

Hessl AE, Baker WL. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. Arct Alp Res 29:173–83.

Hessl AE, Graumlich LJ. 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. J Biogeogr 29:889–902.

Heyerdahl EK, Brubaker LB, Agee JK. 2001. Spatial controls of historical fire regimes: a multiscale example from the interior west, USA. Ecology 82:660–78.

Heyerdahl EK, Morgan P, Riser JP. 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), Northern Rockies, USA. Ecology 89:705–16.

Izquierdo AE, Grau HR. 2009. Agriculture adjustment, land-use transition and protected areas. J Environ Manag 90:858–65.

Johnson EA, Fryer GI. 1989. Population dynamics in lodgpole pine-engelmann spruce forests. Ecology 70:1335–45.

Kitzberger T, Veblen T, Villalba R. 1997. Climatic influence on fire regime along a rain-forest to xeric woodland gradient in northern Patagonia, Argentina. J Biogeogr 24:35–47.

McCabe GJ, Paleck MA, Betancourt JL. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. Proc Natl Acad Sci 102:4136–41.

McCarty JP. 2001. Ecological consequences of recent climate change. Conserv Biol 15:320–31.

Minetti JL, Vargas WM. 1997. Trends and jumps in the annual rainfall in South America, south of the 15ºS. Atmosfera 11:205–21.

Morales MS, Villalba R, Grau R, Paolini L. 2004. Rainfall-controlled tree growth in high elevation subtropical treelines. Ecology 85:3080–9.

Nowacki GJ, Abrams MD. 2008. The demise of fire and ''mesophication'' of forests in the eastern United States. Bioscience 58:123–38.

Prager MH, Hoenig JM. 1989. Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel. Trans Am Fish Soc 118:608–18.

Sankaran M, Ratnam J, Hanan NP. 2004. Tree-grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. Ecol Lett 7:480–90.

Savage M, Swetnam TW. 1990. Early 19th-century fire decline following sheep pasturing in a navajo ponderosa pine forest. Ecology 71:2374–8.

Tian YQ, Davies-Colley RJ, Gong P, Thorrold BW. 2001. Estimating solar radiation on slopes of arbitrary aspect. Agric For Meteorol 109:67–74.

Tinner W, Hubschmid P, Wehrli M, Amman B, Conedera M. 1999. Long term forest fire ecology and dynamics in Southern Switzerland. J Ecol 87:273–89.

Veblen TT, Kitzberger T, Villalba R, Donnegan J. 1999. Fire history in northern patagonia: the roles of humans and climatic variation. Ecol Monogr 69:47–67.

Villalba R, Grau HR, Bonisegna JA, Jacoby GC, Ripalta A. 1998. Tree-ring evidence for long-term precipitation changes in subtropical South America. Int J Climatol 18:1463–78.

Vitousek PM. 1994. Beyond global warming: ecology and global change. Ecology 75:1861–76.

Young KR, León B. 2007. Tree-line changes along the Andes: implications of spatial patterns and dynamics. Philos Trans R Soc B 362:263–72.