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SPECIAL FEATURE: SUSTAINABILITY ON THE U.S./MEXICO BORDER

Linking old-growth forest composition, structure, fire history, climate and land-use in the mountains of northern México

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Abstract. Old-growth forests are biologically and ecologically valuable systems that are disappearing worldwide at a rapid rate. México still holds large areas covered by temperate forests in the mountains of the Sierra Madre Occidental, but few of these retain old-growth characteristics. We studied four sites with remnant old-growth forests in Mesa de las Guacamayas, a site in the Sierra Madre Occidental in northwestern Chihuahua, to assess their composition, structure, and age characteristics. Overstory tree densities and basal areas at each site were based on measurements of all trees >1.3 m tall. The overstory was dominated by large *Pinus durangensis*, *P. strobiformis*, and *Pseudotsuga menziesii* (270–335 trees ha^{-1}, basal area 24–42 m^2 ha^{-1}), with a subcanopy formed mostly of oaks. This species composition, combined with the lack of vertical structural development, and thus of fuel ladders, suggests that these forests are relatively resistant to severe wildfire. We evaluated forest attributes in the context of local fire regimes and regional climatic patterns, and found that frequent disturbance by surface fires has been part of the study sites' histories for at least 250 years. While climate was a driver of fire regimes historically in this mountain range, humans appear to have played a role in interruptions of the fire regime in the second half of the 20th century. Age distributions showed recruitment to the canopy over ~250 years, while fires in the four sites recurred every 6–12 years. Temporary interruption of the fire regime in the mid-20th century at three sites was associated with increased tree establishment, especially by broadleaved species. One site had an uninterrupted fire regime and showed continuous tree establishment, consistent with the self-reinforcing role of frequent fire in regulating live and dead fuel loads. Remnant old-growth forests such as those we sampled are becoming increasingly rare in the Sierra Madre Occidental. The biodiversity and ecological processes that they support are highly threatened and their conservation must be made a priority in the U.S.-México borderlands.

Key words: old growth; pine-oak forests; *Rhynchopsitta pachyrhyncha*; Sierra Madre Occidental; Special Feature: Sustainability on the U.S./Mexico Border.

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Introduction

Old-growth forests (OGFs) differ from secondary forests in a broad range of ecological and biological characteristics (Wirth et al. 2009). For example, they often have more diverse plant communities (Burrascano et al. 2009, D'Amato et al. 2009), increased stratification complexity, and higher amounts of snags, logs, and large live trees (Binkley et al. 2007). Old-growth forests provide key habitat for species that are not found in secondary or harvested forests (Lammertink et al. 1998, Miller and Chambers 2007) and act as sinks in terrestrial carbon dynamics (Carey et al. 2001, Luyssaert et al. 2008, Keeton et al. 2010). They also can provide information regarding processes that may affect ecosystems over time, such as climate, fire, and other disturbances (Swetnam 1993, Swetnam and Baisan 2003, Kaufmann et al. 2007, Fulé et al. 2012). However, the area covered by OGFs has decreased dramatically worldwide in the past century (Boucher et al. 2009, Wirth et al. 2009). By 2009 it was estimated that only 23% of the world's forests remained intact, with most of the remnant old-growth concentrated in boreal and tropical latitudes (Wirth et al. 2009). México has not escaped the global trends of accelerated forest cover loss and degradation (Challenger et al. 2009, Sánchez Colón et al. 2009). Between the 1970s and 2002, México's temperate forest cover decreased by 25% and became increasingly fragmented, mostly due to agricultural clearing (Sánchez Colón et al. 2009).

The Sierra Madre Occidental (SMOc) supports the largest continuous area of temperate to subtropical forests in México (Challenger and Soberón 2008). It runs in a north-south direction over approximately 1200 km of the country's Northwest, varying in width from 200 to 400 km. The SMOc is one of the least studied biotic provinces in México, due to its remoteness, rugged terrain, difficult access, and a long history of social instability (Felger and Wilson 1994). Despite the limited information about its biological and ecological systems, it has been estimated that temperate forests of the SMOc have a plant endemism rate of 70%, the highest identified for all vegetation types in México (Felger et al. 1997). Its temperate forests also offer unique opportunities to study systems with maintained fire frequencies that in some cases have remained unaltered into the 21st century (Fulé et al. 2011, Fulé et al. 2012).

Forests with uninterrupted fire regimes can be more resistant to severe fire and are more heterogeneous than those in which fires have been suppressed (Stephens and Fulé 2005). While fire suppression policies have been in place in México since the early 1900s (Rodríguez Trejo 1999), loose enforcement and relatively sparse resources—compared to the United States—have allowed historical fire regimes to continue up to the present in some remote sites of the SMOc (Heyerdahl and Alvarado 2003, Stephens et al. 2008, Fulé et al. 2011, Fulé et al. 2012). Previous studies in the SMOc suggest a strong relationship between fire occurrence and large-scale climatic patterns, such as the El Niño Southern Oscillation. Fire years coincide with dry years and are often preceded by wet years that promote accumulation of fine fuels (Heyerdahl and Alvarado 2003, Fulé et al. 2005, Cerano Paredes et al. 2010).

The natural conditions of forests in the mountains of the SMOc in Chihuahua are closely associated with centuries of continuous human use and management. Prior to the arrival of Europeans in the 16th and 17th centuries, these forests were part of the territories of various indigenous groups (Lartigue 1983, Challenger 1998). Evidence from *trincheras* (retaining walls built with rocks) suggests that humans have occupied the *sierras* of northern Chihuahua since pre-Hispanic times (Herold 1965, Howard and Griffiths 1966). While indigenous people in the SMOc continue to use fire and other forest management practices (LaRochelle and Berkes 2003, Fulé et al. 2011), commercial forestry has been the most important agent of human-induced change in the SMOc since the early 1900s (Challenger et al. 2009). To date, Chihuahua remains one of the most important timber-producing states in México (CONAFOR 2009).

By the end of the 20th century, changes in age and structural characteristics in forests of the SMOc were so dramatic that two different studies (Escalante 1996, Lammertink et al. 1998) reported that only ~1% of the area once covered by OGFs remained in the region. The Imperial Woodpecker, Mexican Grizzly Bear, and Mexican Wolf were extirpated from the SMOc in the 20th

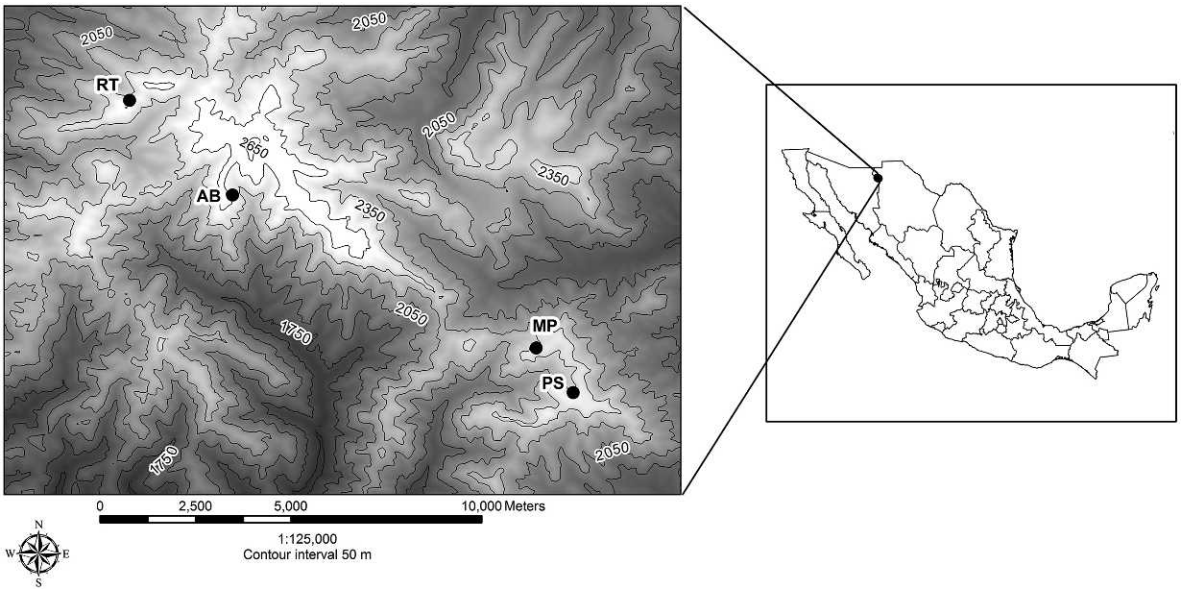

Fig. 1. Location of the Mesa de las Guacamayas study area in the state of Chihuahua, México. Study site names and codes are: MP, Mesa Prieta; PS, Mesa Prieta Sur; RT, Rincón de las Tinajas; and AB, El Abeto.

century, due in part to habitat loss and fragmentation, increased human presence and hunting (Challenger 1998). Thick-billed Parrots, called *guacamayas* in Spanish, have been extirpated from other mountain ranges in México. Breeding populations are found in the mountains of the SMOc, and they are legally recognized as an endangered species (SEMARNAT 2010). Thick-billed Parrots favor old-growth habitat for nesting and breeding (Monterrubio-Rico and Enkerlin-Hoeflich 2004), and thus they are especially susceptible to changes in forest structure to the extent that the recent decline in their populations has been attributed to habitat reduction (Lammertink et al. 1998, Monterrubio-Rico and Enkerlin-Hoeflich 2004).

Unlogged sites provide a unique opportunity to study interactions among forest development, fire, and large-scale climatic processes in OGFs. We studied four old-growth sites at Mesa de las Guacamayas in northwestern México, measuring forest structure, composition, age distribution, tree regeneration, surface and canopy fuels, and the characteristics of large snags. We used these data, together with fire history information from a companion study (Fulé et al. 2012), to answer the following questions: (1) What are the attributes of the structure and floristic composition of the overstory, regeneration, and fuel loads? (2) What are the interactions of fire, regional climatic variability, and human-induced land-use changes across a ~250 year timeline in the landscape represented by the four study sites?

Methods

Study area

The Mesa de las Guacamayas (MDG) mountain range is located at the northern end of the SMOc in northwestern Chihuahua, México (Fig. 1). It is part of Ejido Cinco de Mayo, a communal holding of ~25,000 ha of forests and grasslands created through the allocation of federal land by a presidential decree executed in 1972 (RAN 2010). Large concessions in the region were granted to various lumbering operations in the first half of the 20th century (Palomares Peña 1991), but we were unable to confirm if the forests of MDG were included in these. In the 1960s, at least one sawmill was established in the site, operating until *ejido* formation in the 1970s. The *ejido* continued to log its more accessible forests as recently as the late 1990s (Campos, *personal communication*). Only one family lives at MDG year-round, and current uses include light

grazing by cattle and equines.

Conifer species that form the overstory in the sampled sites are in the Cupressaceae (*Juniperus deppeana* Steud. and *Cupressus arizonica* Greene) and Pinaceae (*Abies* sp., *Pinus durangensis* Martınez, *P. strobiformis* Engelm. (synonymous with *P. ayacahuite* var. *brachyptera* Shaw), and *Pseudotsuga menziesii* (Mirb.) Franco). Broadleaved species in the four sites belong to four families: *Robinia neomexicana* A. Gray (Fabaceae); *Quercus coccolobifolia* Trel., *Q. durifolia* Seemen, *Q. gambelii* Nutt., *Q. grisea* Liebm., *Q. mcvaughii* Spellenb., *Q. sideroxyla* Hum. & Bonpl. and *Q. viminea* Trel. (Fagaceae); *Fraxinus velutina* Torr. (Oleaceae); and *Prunus* sp. (Rosaceae).

Parent material in Mesa de las Guacamayas is of volcanic origin, formed mostly of rhyolitic ignimbrites (Ferrari et al. 2007). Predominant soils are Phaeozems and Regosols, with Lithosols present in small pockets (Unidad Forestal Casas Grandes-Babícora 1999). Weather records for the region are sparse and incomplete; the nearest weather station is Guapoca (located ~90 km to the SE of the site at 1260 m of altitude). Data for the period 1961–1998 show that mean annual values were 584.6 mm for precipitation, 15.9°C for temperature, 6.3°C for minimum temperature and 25.6°C for mean maximum temperature (CSM N.A., Estaciones climatológicas del sistema CLICOM. Comisión Nacional del Agua, Subdirección General Técnica, Coordinación del Servicio Meteorológico).

Field methods

We searched the study area on foot, looking for forest stands dominated by *Pinus* spp. and *Pseudotsuga menziesii* with no signs of harvesting (Fig. 2). We identified four such sites: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB) (Fig. 1). We established ten plots on a 100×100 m sampling grid ($N = 40$ plots) at each study site, on steep, north-facing slopes (Table 1). MP and PS were accessible only by foot, AB was at the end of a logging road and RT was on the side of a secondary road.

We used circular fixed-area plots located at each grid point to obtain data about the structure, composition and age of the overstory, and the regeneration stratum. Plots for overstory measurements were 200 m^2 (7.98 m radius) and 40 m^2 for nested regeneration plots (3.57 m radius). We marked each plot center permanently and recorded elevation, slope, and aspect.

We identified tree species in the field using regional field guides for *Pinus* (Farjon et al. 2000) and *Quercus* (Spellenberg 2001). We collected botanical specimens for all species and deposited a full set of our collections (M. Joe and C. Cortés 2009) at ASC, the Deaver Herbarium of Northern Arizona University. We considered *Robinia neomexicana* as a tree since it reached tree height and was part of the subcanopy stratum. We recorded the species of each tree or snag (for some decaying snags we could record only the genus), and diameter at breast height (DBH, 1.3 m) of all (live and dead) trees and snags >1.3 m tall in each 200 m^2 plot. We also recorded total tree height and canopy base height, and condition class of each stem using the nine-class system described by Thomas (1979). We tallied all saplings or shrubs <1.30 m tall, in each 40 m^2 subplot using three height classes (1–40 cm; 41–80 cm, >80 cm). We used increment borers to core all trees >30 cm DBH as well as a 10% subsample of randomly selected smaller trees in each plot. Coring height was at 10 cm above ground level to minimize age variation to coring height. If trees were too small to core (<10 cm DBH), we cut a stem section at 10 cm above ground level.

To assess fuel loads at the four sites we used the method described by Brown (1974), establishing 15-m planar transects in a random direction from each plot center ($N = 40$). We tallied woody fuels in the first 5 m of the transect using standard size classes: 1-hour timelag fuels (0–0.62 cm diameter), 10-hour timelag fuels (0.63–2.53 cm diameter), and 100-hour timelag fuels (2.54–7.61 cm). We measured all dead and live 1000-hour timelag fuels (>7.61 cm at the narrowest point), and the depth in cm of the organic (duff and litter) layers every 5 m. We recorded the presence or absence of canopy cover by vertical projection every 1 m along the transect. We collected and crossdated 157 partial cross-sections from fire-scarred trees on the four sites and used them for fire history analyses (Fulé et al. 2012).

Laboratory methods and data analysis

Botanists at ASC determined the identity of botanical specimens. Some specimens were sent

Fig. 2. Old-growth forest at the Mesa Prieta Sur (MP) study site in Mesa de las Guacamayas. Left: Typical canopy structure of live standing trees and large snags; large logs on forest floor. Right: Fire-scarred pines on the foreground, subcanopy of broadleaved trees, a clump of younger trees to the left, and large dead fuels on the ground.

to other herbaria for identification or verification due to the lack of a recognized scientific flora for the region. We calculated basal area (BA, m^2 ha^{-1}) and tree density (number of trees ha^{-1}) for all living and dead trees by species, and regeneration density per species group per height class. Given the high BAs of *Pinus durangensis*, *P. strobiformis* and *Pseudotsuga menziesii*, we treated

Table 1. Physical and biological characteristics at the four sampling sites at Mesa de las Guacamayas, Chihuahua.

Site†	Latitude (N)	Longitude (W)	Slope (%)	Elevation (m asl)	Tree species richness	Establishment‡	Indicator species§
MP	30°30′	108°32′	**59.8** (20–72)	**2375** (2250–2550)	**2.6** (1, 4)	1793	PIST
PS	30°29′	108°32′	**46.2** (4–76)	**2409** (2350–2447)	**2.4** (1, 5)	1735	PSME
RT	30°33′	108°38′	**59.4** (26–90)	**2467** (2377–2735)	**2.0** (1, 3)	1770	PIDU
AB	30°32′	108°37′	**63.4** (49–73)	**2476** (2399–2617)	**3.2** (1, 5)	1766	...

Note: Mean values are in boldface; minimum and maximum are in parenthesis.
†Site abbreviations are: MP, Mesa Prieta; PS, Mesa Prieta Sur; RT, Rincón de las Tinajas; and AB, El Abeto.
‡ Establishment is that of the oldest dated tree (year A.D.).
§Indicator species from Indicator Species Analysis results (*$P < 0.05$). Abbreviations are: PIST, *Pinus strobiformis*; PSME, *Pseudotsuga menziesii*; PIDU, *Pinus durangensis*.

them individually. We grouped the remaining species into three categories: *Quercus* spp., Other Conifers (*Cupressus arizonica*, *Juniperus deppeana* and *Abies* sp.), and Other Broadleaved species (*Fraxinus velutina*, *Prunus* sp. and *Robinia neomexicana*). We relativized BA by plot in order to equalize weights for inter-plot analyses (McCune and Grace 2002). Information regarding snag density, an important component of old-growth and Thick-billed Parrot habitat, will be presented in a forthcoming paper.

Boxplots and scatterplots indicated that the BA data were not normally distributed, so we used methods amenable to non-normally distributed datasets to assess the composition of the overstory among the four sites. Non Metric Multidimensional Scaling (NMDS) is recommended for the analysis of non-normally distributed ecological community data (McCune and Grace 2002). It reduces the dimensions of a distance matrix and derives an optimal solution to the relationships of species distribution in plots. We produced an ordination with the NMDS function in PC-ORD (McCune and Mefford 2006), using the relativized BAs of the six groups and Sørensen similarity indexes to create a distance matrix based on three individual species and three multi-species groups ($N = 39$ plots, because one plot was eliminated from the analyses due to lack of tree cover). We used a second matrix with environmental variables (for example, number of fires at each site, elevation, fuel loads) to assess their correlations to the axis scores of the ordination. We rotated the graphic to make the displayed vector (correlation >0.45) parallel to the axis (McCune and Grace 2002). We conducted 250 runs with the real data and 250 Monte Carlo randomized runs to ensure that the axes extracted by the ordination were not a result of chance. We used random starting configurations, a maximum of 500 iterations per run and a stability criterion of 0.00001. Once a final solution was achieved, its stress value was compared to random solutions generated through Monte Carlo tests. Stress values for NMDS ordinations are considered acceptable at <20; and instability values are optimal at $<10^{-4}$ (McCune and Grace 2002).

To assess the significance of the differences in species composition among the four sites we used the PERMANOVA function in the vegan package (Oksanen et al. 2011) for R (R Development Core Team 2010). Permutational ANOVA (PERMANOVA) is a multivariate test analog to the univariate ANOVA. It can be used with non-normally distributed data since it makes no distributional assumptions (Anderson 2001). Its test statistic is a pseudo-*F*, calculated through permutations under an assumed H_0 that the data are not responding to a particular grouping effect, such as treatment or site (Anderson 2001). We conducted paired PERMANOVA tests to explore differences in composition among pairs of sites, since there were statistically significant differences in species composition among the four sites. We estimated *P*-values using 9999 permutations, which is well over the minimum of 5000 permutations recommended for $\alpha < 0.01$ (Anderson 2001).

To determine characteristic species for each site we used the Indicator Species Analysis (ISA) function in PC-ORD. We used a dataset that included all tree species with relative BA $> 2.5\%$. These were *Cupressus arizonica*, *Pinus durangensis*, *P. strobiformis*, *Prunus* sp., *Pseudotsuga menziesii*, *Quercus coccolobifolia*, *Q. gambelii* and *Q. mcvaughii*. We considered a species to be a strong indicator for a site when its indicator value was $>25\%$ and significant ($P < 0.05$) (Dufrene and Legendre 1997).

In order to understand regeneration dynamics and to create an age distribution for the four sites, we reconstructed age distributions from the collected cores. We mounted and sanded cores and sections with increasingly finer sandpaper grits until individual cells were visible with a microscope. We used a master tree-ring chronology for the area (Villanueva et al., *unpublished*) to crossdate each core or section. We used a pith locator to establish the number of rings to center for cores that missed the pith (Applequist 1958). Pith locators are transparent overlays of concentric circles with curvatures that vary as a function of the distance to the pith. Since we did not have enough dateable cores and sections to match the six species and groups used for the analyses described above, we grouped the cores into two broad categories (Conifers or Broadleaved) to analyze the age data.

We used the equations in Brown (1974) to calculate fuel loads from the planar transects. Since we were unable to find coefficients for

Table 2. Structural characteristics (number of trees and basal area by species and species groups)† of the overstory (all trees >1.3 m tall) by site at Mesa de las Guacamayas.

Site	Characteristic	PIDU	PIST	PSME	OTH CON	QUERCUS	OTH BL	Total
MP	TPH	**20**	**130**	**30**	**90**	**110**	...	**380**
		(0–50)	(0–400)	(0–100)	(0–900)	(0–450)	...	(0–900)
	BA	**3.7**	**11.3**	**7.8**	**0.9**	**3.1**	...	**26.8**
		(0–20.2)	(0–41.4)	(0–58.5)	(0–9.3)	(0–9.2)	...	(0–58.5)
PS	TPH	**60**	**55**	**150**	**70**	**360**	**25**	**720**
		(0–600)	(0–550)	(0–1500)	(0–700)	(0–3600)	(0–250)	(0–3600)
	BA	**10.1**	**1.4**	**29.9**	**0.5**	**1.7**	**0.01**	**43.6**
		(0–37.0)	(0–5.4)	(0–71.6)	(0–2.8)	(0–8.6)	(0–0.04)	(0–71.6)
RT	TPH	**250**	**5**	**25**	...	**125**	**50**	**455**
		(100–2500)	(0–50)	(0–250)	...	(0–1250)	(0–500)	(0–2500)
	BA	**26.9**	**0.0**	**1.85**	...	**0.5**	**0.4**	**29.7**
		(4.7–50.1)	(0–0.02)	(0–8.6)	...	(0–2.4)	(0–3.73)	(0–50.1)
AB	TPH	**25**	**90**	**120**	**75**	**295**	**590**	**1195**
		(0–250)	(0–900)	(0–1200)	(0–750)	(0–2950)	(0–5900)	(0–5900)
	BA	**6.4**	**4.2**	**17.8**	**3.1**	**2.8**	**0.6**	**34.9**
		(0–27.5)	(0–22.0)	(0–49.7)	(0–22.1)	(0–9.6)	(0–4.8)	(0–49.7)

Notes: Site codes are as in Table 1. Mean values are in boldface; minimum and maximum are in parenthesis. TPH is number of trees per hectare, BA is basal area (m^2 ha^{-1}).

†Species abbreviations are: PIDU, *Pinus durangensis*; PIST, *Pinus strobiformis*; PSME, *Pseudotsuga menziesii*; OTH CON, other conifers; QUERCUS, *Quercus* spp.; OTH BL, other broadleaved species.

specific gravity and average squared diameters of fine fuel particles for SMOc species, we used the coefficients for *Pinus ponderosa*, a species closely related to *P. durangensis* (Gernandt et al. 2009).

We used a dataset created by a companion study (Fulé et al. 2012) to model fire dates and fire-climate relations. A tree-ring based climatic reconstruction of the Palmer Drought Severity Index (PDSI) provided information to establish relationships between historical climatic patterns in the region, tree establishment and recruitment to the overstory, and fire histories. The Palmer Drought Severity Index is a hydroclimatic measure of the extent and intensity of drought at the regional scale (Alley 1984). We used a tree-ring based reconstruction of PDSI developed by Cook et al. (2004), which includes four grid points close to our research area (points 105, 106 and 120, 121). Grid point 121 is located in NW Chihuahua, but its PDSI reconstruction ends in 1990, so we used grid point 120, located in SW New Mexico, USA. Grid point 120 is the closest point to our research area with a record that extends into the 21st century, and is highly correlated (Pearson's $r = 0.94$) with grid point 121.

Results

Forest structure and composition

Pinus durangensis, *P. strobiformis* and *Pseudotsuga menziesii* had the highest basal areas in the four sites (Table 2). The species with the largest trees was *Pseudotsuga menziesii*, followed by *Pinus durangensis* and *P. strobiformis* (Fig. 3). The groups Other Conifers, *Quercus* spp. and Broadleaved had higher numbers in the smallest diameter classes and very few individuals >40 cm DBH. Tree density was highest in the AB site (1195 trees ha^{-1}), mostly due to the abundance of *Robinia neomexicana*; and lowest at MP (380 trees ha^{-1}). Basal area was lowest at site MP (26.8 m^2 ha^{-1}), and highest at PS (43.6 m^2 ha^{-1}), driven by the large *Pseudotsuga menziesii* trees found there.

The final NMDS ordination (Fig. 4) had three axes and was achieved with a final stress of 13.013 and 0.06 instability. The ordination explained 91.6% of the variability in BA and similarity (Axis 1 = 30.7%, Axis 2 = 38.6%, and Axis 3 = 22.5%). Correlations between species and the ordination axes showed that Axis 1 was driven by a transition in dominance from *Pinus strobiformis* to *Pseudotsuga menziesii* and Axis 2 by dominance of *Pinus durangensis*. The vector overlay suggested that Axis 2 was also influenced by the number of fires in the past 60 years, which was greater at site RT. Indicator Species Analysis results (all $P < 0.05$) showed that *Pinus durangensis* was a good indicator for RT (Indicator Value, IV = 57%), *Pinus strobiformis* for MP (IV = 47%) and *Pseudotsuga menziesii* for PS (IV = 42%). The ISA results supported plot groupings

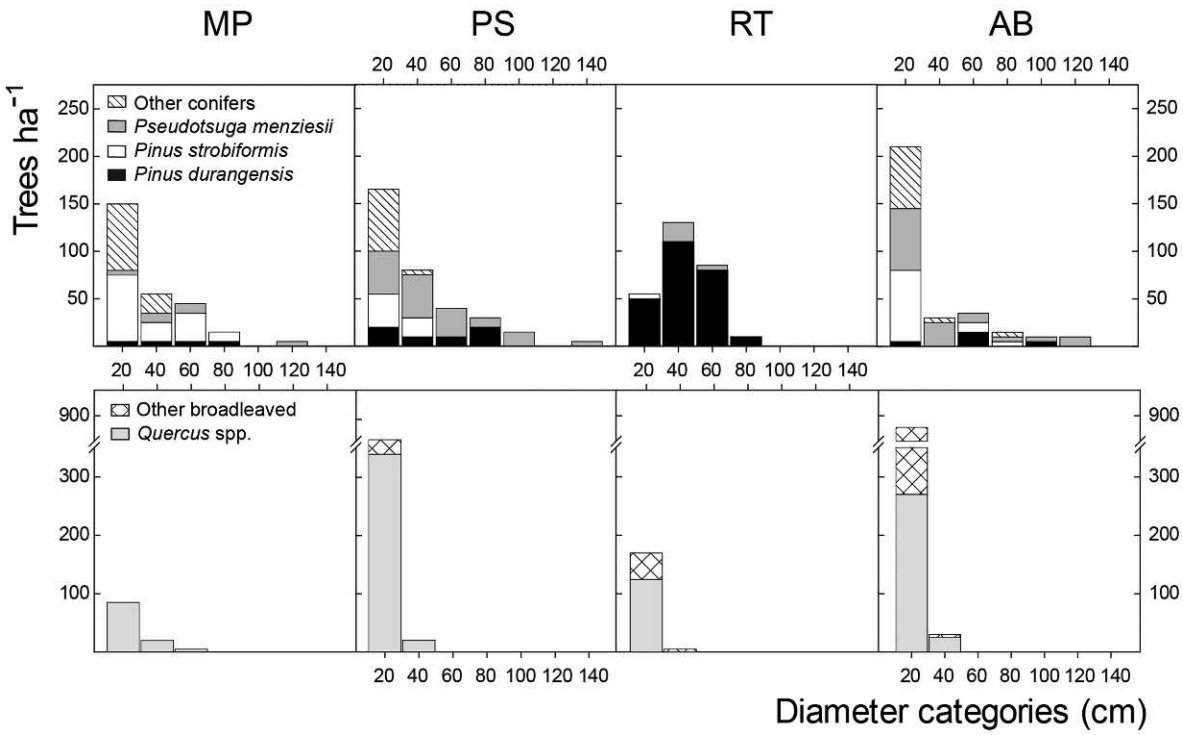

Fig. 3. Diameter distribution of live trees in the four study sites at Mesa de las Guacamayas. The *x*-axis indicates the upper end of each diameter category. The top panel shows the diameter distributions of all conifer species and the bottom panel shows those of *Quercus* spp. and other broadleaved species. Site labels are as in Fig. 1.

based on dominance and indicator values of those three species. The lack of indicator species for AB is due to high variation in the composition of the overstory in this site. The most diverse stratum at the four sites was the subcanopy, formed of *Quercus* spp. and other broadleaved species.

Paired PERMANOVA tests showed that the plant community at RT was statistically significantly different from all other sites (Bonferroni adjusted $\alpha = 0.008$; MP-RT pseudo-$F = 3.728$; PS-RT pseudo-$F = 4.781$ RT-AB pseudo-$F = 4.358$). *Pinus durangensis* comprised 90.7% of the total BA at RT. *Pinus strobiformis* and *Pseudotsuga menziesii* were dominant species at the other sites (MP, PS and AB), followed by *Quercus* spp. in MP and PS, and Other Conifers (*Cupressus arizonica* and *Juniperus deppeana*) in AB.

Tree age and demography, fuels, fire and climate

We were able to crossdate 63% of the total collected cores and sections, 69 from conifers and 18 from broadleaved species. The oldest trees in the PS, RT, and AB sites were from the species with highest basal area values: *Pinus durangensis, P. strobiformis*, and *Pseudotsuga menziesii* (Fig. 5). *Quercus* sp., included in the Broadleaved group, comprised the oldest age group at MP. However, by the end of the 18th century, *Pinus* and *Pseudotsuga* had established in all the sites. The oldest dateable trees established in the mid-18th century. Other trees established earlier than this date, but the cores could not be dated to pith and were excluded from the analyses. The excluded cores were collected from two *Pseudotsuga menziesii* in PS and one *Pinus durangensis* in AB, with inner ring dates of 1735, 1747, and 1766, showing that two study sites had older trees than those included in the age distribution. Establishment of conifers and broadleaved species in the early 20th century was observed at PS and RT, and all sites showed a pulse of recruitment starting at or after the 1950s. The age distribution

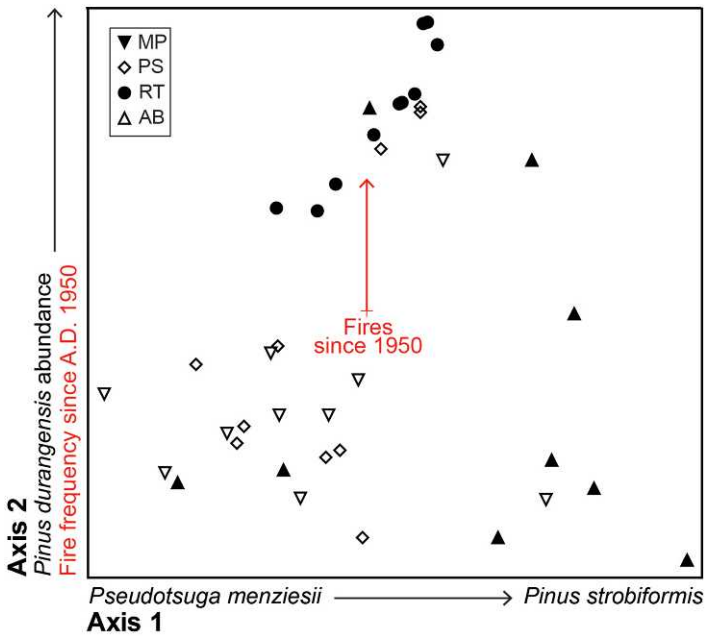

Fig. 4. Non-metric multidimensional scaling ordination (stress = 13.01, instability = 0.05) of study sites at Mesa de las Guacamayas based on relativized basal areas of overstory species. The ordination was rotated 20° to the right to make the vector parallel to Axis 2. Total variance explained by the three axes was 91.7% of the variation in the distance matrix. Axis 1 (30.7% of variation explained) is driven by a transition in abundance from *Pinus strobiformis* to *Pseudotsuga menziesii*. Axis 2 (38.6% of variation explained) and was driven by abundance of *Pinus durangensis* and fire frequency since 1950 A.D., as shown by the vector overlay. Site labels are as in Fig. 1.

showed that relatively few broadleaved trees, including *Quercus* spp., established between 1750 and 1900 A.D. A pulse of recruitment of broadleaved species was observed in the late 1990s and early 2000s.

The regeneration stratum was dominated by *Quercus* spp. at PS, RT, and AB (Fig. 6). *Pinus* spp. was abundant in the 0–40 cm class at MP. *Robinia neomexicana*, included in the Broadleaved group, was a major component of the >40–80 cm height class, but it dwindled dramatically in the next class.

Average litter depth was deepest at RT (3.1 cm) and shallowest in MP (1.5 cm). Average duff depth was deepest at MP (2.6 cm) and shallowest at PS (1.0 cm). Coarse woody debris loads were highest at AB (19.17 Mg ha^{-1}) and lowest at PS (13.18 Mg ha^{-1}) (Table 3). Average canopy cover values for the four sites ranged between 51.4% (RT) and 60.7% (PS and AB) (Table 4). *Pseudotsuga menziesii* had the highest average height of all trees in the canopy at MP, PS, and RT (MP: 22.9 m total, 5.1 m crown base, PS: 22.4 m total, 6.6 m crown base, RT: 17.5 m total, 6.6 m crown base) and *Pinus durangensis* at AB (25.0 m total height, 9.4 m crown base height).

Fires occurred frequently (mean fire intervals <10 yr) in the four sites before the mid-20th century (Fulé et al. 2012). The dates of fires that scarred ≥25% of the samples, a measure of relatively large fires, are shown in Fig. 5. Using this filter, 37 fires burned the four study sites between 1733 and 2008, while 68 fires were detected using all scarred trees for the same period (a measure of smaller fires) (Fulé et al. 2012). A fire-free period began in 1945 at MP and PS, and 1953 at AB, and ~50 years later, those sites burned at least once between 1989 and 2009. One site (RT) maintained an uninterrupted fire regime through the early summer of 2009 (Fulé et al. 2012).

Regional hydroclimatic patterns, expressed by PDSI, were related inconsistently to temporal patterns of tree ages and fire events in the last

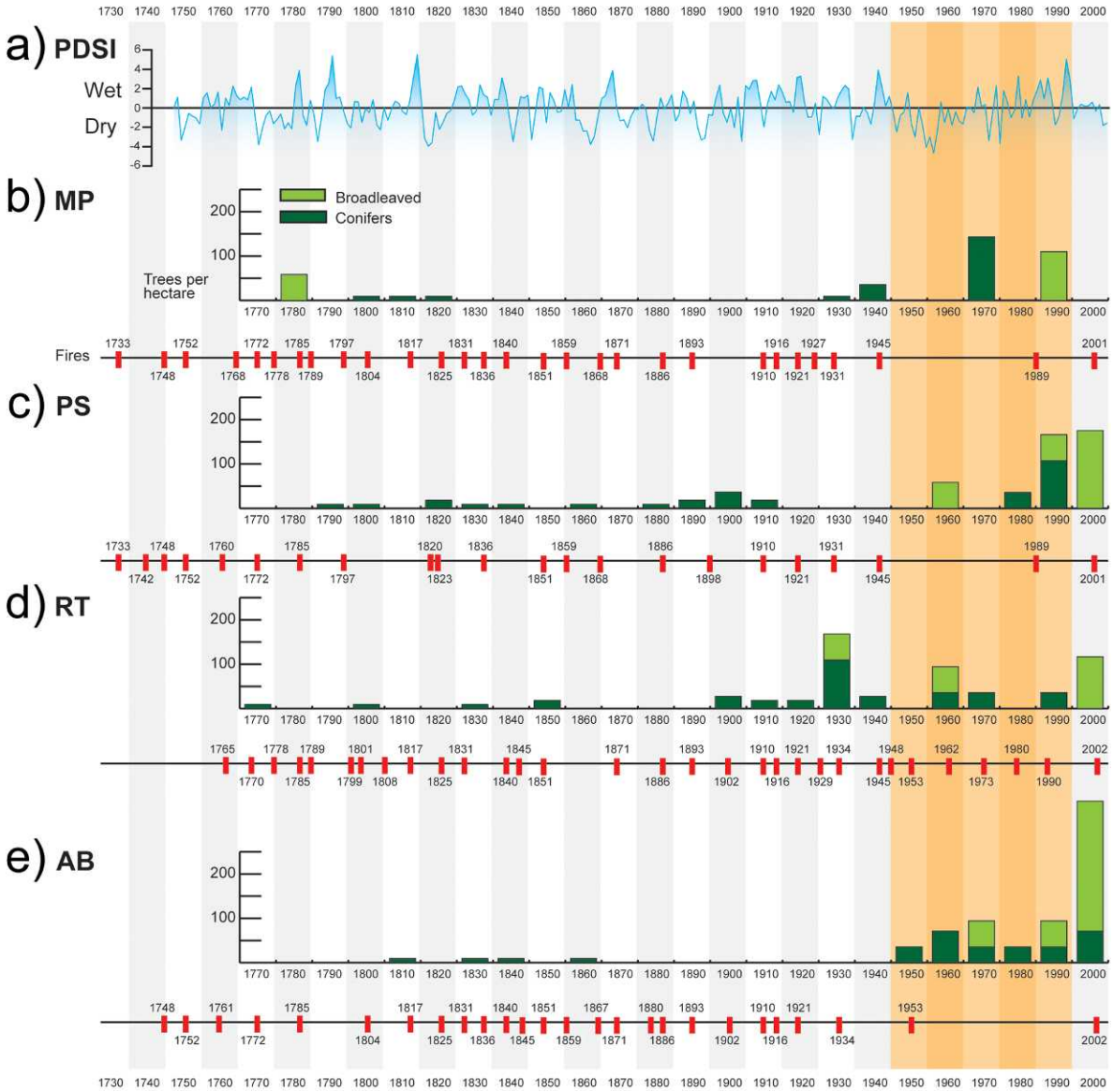

Fig. 5. Climatic reconstructions, years of establishment of conifer and broadleaved species, and fire histories at the four study sites in Mesa de las Guacamayas. (a) PDSI index reconstruction for point 120 in SW New Mexico (Cook et al. 2004). (b–e) Age distributions and fire histories for each site. Dates are shown for fires that scarred 25% or more of the samples collected at the study sites in a companion study (Fulé et al. 2012). Highlighted decades (1950–1990) show fire interruption in MP, PS and AB. Site labels are as in Fig. 1.

250 years (Fig. 5). A weak climate signal was observed in post 1950s recruitment trends in all sites; otherwise we did not visually detect strong associations between climate, fire frequency, and tree demography. There was an increase in broadleaved tree recruitment in the second half of the 20th century, following the fire-free period of 1950–1990 in PS and AB. A pulse of conifer establishment was observed in MP in the 1970s. This site had the lowest overall recruitment among the study sites. In RT we observed consistent conifer recruitment throughout the 20th century, with a pulse in the 1930s.

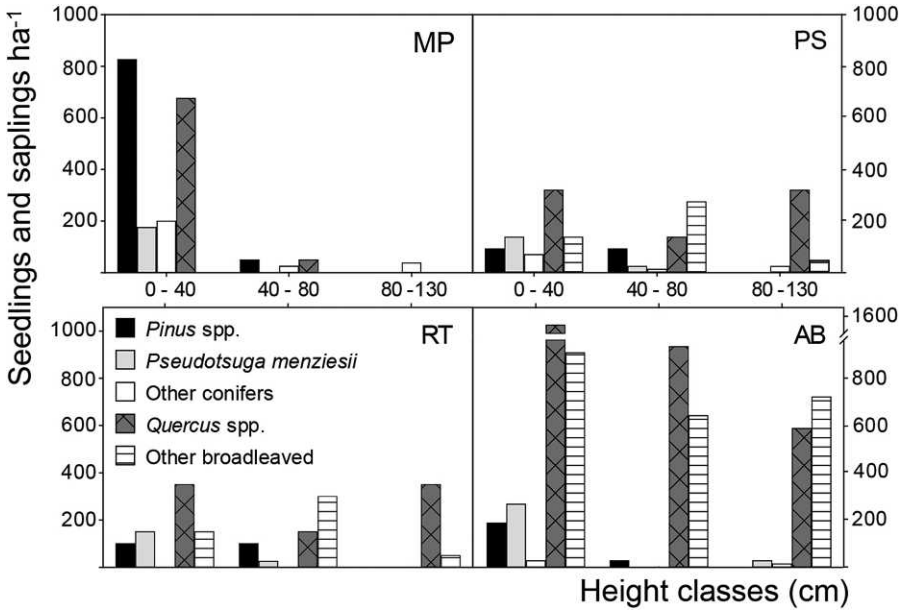

Fig. 6. Average density of seedlings and saplings in the regeneration stratum at the four study sites in Mesa de las Guacamayas. Site labels are as in Fig. 1.

Discussion

Until the 1950s, fire frequencies of the four sites at MDG resembled those of pre-European conditions of ponderosa pine forests in Arizona and New Mexico (Fulé et al. 1997, Swetnam and Baisan 2003) and other sites in northern México (Fulé and Covington 1997, Heyerdahl and Alvarado 2003, Fulé et al. 2005, Fulé et al. 2012). Fire records at the four study sites show high synchrony, except for a ~50 year fire interruption period in MP, PS, and AB. Fire return intervals were <10 years across the four sites until the 1940s. Three sites underwent a fire-free period that ended in the early 2000s. Only one site (RT) maintained a 6.2 year mean fire frequency into the 21st century, which makes it a rare example of a relatively continuous fire regime in southwestern North America.

Fire is still at work in the forests of Mesa de las Guacamayas, since fires were recorded at least once in all the sites since the late 1990s. Despite alterations to the historical fire regimes in the past 50 years, fuel loads in these sites remained relatively low. Average fuel loads were comparable to those of other unharvested sites in the

Table 3. Depth by site of forest floor fuels and woody debris loads by site at Mesa de las Guacamayas. Values are expressed in logarithmically increasing standard time lag classes based on the time of each fuel size to reach moisture equilibrium with ambient conditions.

Site	Litter (cm)	Duff (cm)	1 hr	10 hr	100 hr	1000 hr sound	1000 hr rotten	Total
MP	**1.5**	**2.6**	**0.29**	**1.02**	**5.86**	**6.25**	...	**13.43**
	(0.4–2.9)	(0–9.6)	(0–0.99)	(0.20–2.82)	(0–15.76)	(0–34.56)	...	(0–34.56)
PS	**1.9**	**1.0**	**0.47**	**1.99**	**5.94**	**4.77**	...	**13.18**
	(0.4–3.8)	(0.4–2.0)	(0.09–1.32)	(0.21–7.40)	(0–30.89)	(0–40.98)	...	(0–40.98)
RT	**3.1**	**2.6**	**0.17**	**1.60**	**2.47**	**8.12**	**5.35**	**17.73**
	(1.1–5.1)	(0.2–5.4)	(0–0.36)	(0.60–2.46)	(0–9.39)	(0–48.69)	(0–35.29)	(0–48.69)
AB	**1.7**	**2.0**	**0.62**	**1.39**	**3.63**	**12.09**	**1.45**	**19.17**
	(0.5–3.3)	(0.4–3.9)	(0.06–1.57)	(0.20–3.38)	(0–10.49)	(0–70.88)	(0–9.43)	(0–70.88)

Notes: Site codes are as in Table 2. Mean values are in boldface; minimum and maximum values are in parentheses. Time lag class values are expressed in megagrams per ha (Mg ha^{-1}).

Table 4. Canopy fuel characteristics (number of trees and tree height by species and species groups) by site and percent canopy cover by site at Mesa de las Guacamayas.

Site	Characteristic	PIDU	PIST	PSME	OTH CON	QUERCUS	OTH BL	Canopy cover (%)
MP	N	2	26	6	18	22	...	
	TH	**12.2**	**12.1**	**22.9**	**5.3**	**4.1**	...	
		(11.5, 12.8)	(1.4, 33.7)	(4.9, 38.9)	(1.6, 17.3)	(1.3, 16.3)	...	**54.0**
	CBH	**3.3**	**3.7**	**5.1**	**1.4**	**1.2**	...	(6.7, 93.3)
		(2.0, 4.6)	(0.1, 13.3)	(0, 12.1)	(0, 3.9)	(0.2, 3.6)	...	
	CBH:TH	27.0%	30.6%	22.3%	26.4%	29.3%	...	
PS	N	12	11	29	14	71	5	
	TH	**16.6**	**9.5**	**22.4**	**2.9**	**2.5**	**1.8**	
		(1.4, 33.7)	(3.1, 20.0)	(4.0, 48.3)	(1.4, 6.0)	(1.3, 11.0)	(1.6, 2.3)	**60.7**
	CBH	**7.8**	**4.1**	**6.6**	**0.4**	**0.8**	**0.4**	(0, 80.0)
		(0.3, 21.1)	(0, 11.6)	(0, 18.1)	(0, 1.9)	(0, 4.4)	(0.1, 1.3)	
	CBH:TH	47.0%	43.2%	29.5%	13.8%	32.0%	22.2%	
RT	N	43	1	5	...	24	10	
	TH	**16.6**	**2.3**	**17.5**	...	**3.1**	**2.6**	
		(1.6, 43.4)	(2.3, 2.3)	(6.7, 38.1)	...	(1.4, 10.4)	(1.3, 8.3)	**51.4**
	CBH	**9.5**	**0.9**	**6.6**	...	**1.0**	**1.1**	(6.7, 80.0)
		(0.5, 32.6)	(0.9, 0.9)	(1.9, 10.1)	...	(0, 3.7)	(0, 3.7)	
	CBH:TH	57.2%	39.1%	37.7%	...	32.3%	42.3%	
AB	N	3	18	22	16	59	118	
	TH	**25.0**	**6.4**	**12.5**	**6.4**	**3.5**	**2.1**	
		(2.4, 38.5)	(1.5, 33.2)	(1.4, 37.7)	(1.1, 22.0)	(1.3, 13.8)	(1.3, 16.3)	**60.7**
	CBH	**9.4**	**2.0**	**2.8**	**1.2**	**1.1**	**0.9**	(13.3, 100.0)
		(0.1, 17.0)	(0.1, 14.2)	(0, 13.3)	(0, 5.8)	(0, 4.4)	(0.2, 2.0)	
	CBH:TH	37.6%	31.3%	22.4%	18.8%	31.4%	42.9%	

Notes: Site and species codes are as in Table 2. Mean values are in boldface; minimum and maximum values are in parentheses. N is number of trees measured, TH is total height (m), CBH is crown base height (m).

SMOc (Fulé and Covington 1997, Stephens and Fulé 2005) and below the current average of 23.3 Mg ha^{-1} for pine and pine-oak forests in México (Rodríguez Trejo 2008). The dominant overstory trees, mostly in the Pinaceae, are tall and have relatively high total height to crown base height ratios. This could be induced by self-pruning, by the effect of frequent fires, or by both processes, which keep lower branches from reaching the forest floor and forming fuel ladders.

The tree-ring record of Mesa de las Guacamayas indicates that episodic drought has been part of the disturbance regime of these forests throughout the reconstructed period. The fire histories for the four sites show that fires tended to occur during or following drought episodes (Fulé et al. 2012), which are largely entrained by the El Niño oscillations. However, the high synchrony of fire occurrence at the four sites was interrupted abruptly in 1945 at MP and PS, and in 1953 at AB. The initiation of this fire-free period in those three sites coincided with the 1950s regional drought observed in tree-ring records of the U.S. Southwest and northern México (Villanueva et al. 2009, Swetnam and Brown 2010).

In contrast to pre-European settlement fire-free periods of the southwestern U.S., which coincided with wet periods (Swetnam and Brown 2010), fire interruption at MDG coincided with the 1950s drought. This was the driest period of the 20th century in the region (Grissino-Mayer and Swetnam 2000), suggesting that fire exclusion was not related to wet conditions. Instead, we hypothesize that the fire-free period may have been due in part to logging and road building driven by the holders of the concessions, and by the introduction of livestock grazing. However, despite the ~60 year absence of fire, all sites burned at least once in the 21st century and none showed evidence of widespread fire or pathogen infestations.

Diversity in species composition commonly translates to diversity in tree architecture, which confers structural heterogeneity to the overstory. This attribute has been associated with disturbance resistance of OGFs in northwestern México (Stephens et al. 2008) and the U.S. Southwest (Binkley et al. 2007). The overstory at the sampling sites was heterogeneous, and different species were dominant in each site. The species-rich subcanopy at the sample sites could play an

important role providing key habitat for wildlife, as has been shown in forests of southern Chihuahua (Miller and Chambers 2007).

Information regarding historical and current ignition sources is circumstantial at best. There is evidence that links the recent (~250 years) human history of the México-U.S. borderlands (Seklecki et al. 1996) and fire incidence. However, the lack of documentation or other evidence of the role of humans makes these assertions difficult to prove.

Given the lack of information about ignition sources, the uninterrupted fire regime of RT poses an intriguing question about the role of humans as agents of ecological processes. In our view, this site represents an example of how human history is linked inextricably to fire regimes as both a top-down and a bottom-up factor. The fire regime of MDG is comparable to that of Pino Gordo, a remote site in the SMOc that is managed as a multiple use landscape by Rarámuri people (Fulé et al. 2011). However, in contrast to Pino Gordo, decisions concerning the management of the landscape in MDG have been made by a succession of geographically distant stakeholders, including the federal government, timber concessionaires, foresters and even the *ejido* itself. Boundary conflicts between Ejido Cinco de Mayo and a neighboring landowner could be a partial cause of the site's uninterrupted fire history, maintained into the 21st century. This site was relatively closer to the valley and its human settlements, and thus nearer to lands where fire is used as a management tool for activities such as grass burning or agricultural plot clearing.

Management implications

The forests of MDG are important biodiversity reservoirs, providing habitat to endangered species such as Thick-billed Parrots, and highly diverse understory plant communities (Cortés Montaño 2011). These forests appear to maintain their structural characteristics and fuel loads through frequent fires. Consequently, they could be used to set reference conditions for management of similar ecosystems in the SMOc and the Sky Islands in Arizona and New Mexico.

The frequently burnt OGFs at Mesa de las Guacamayas may be more resistant to disturbances like severe fire and drought. The resistance of the forests at the study site could be derived from the fire histories and the heterogeneity of the landscape matrix in which they are found. This contrasts with the extensive catastrophic fires occurring currently in dense, fire-excluded forests of the western U.S. (Allen et al. 2010, Williams et al. 2010). The forests at MDG are a potential source of organisms that are better adapted to face the systemic changes expected from climate change in the region (Williams et al. 2010).

For almost one month in the late spring of 2012 an estimated 13,500 ha of oak, pine-oak and mixed conifer forests burned in the MDG range. Satellite imagery and MODIS data points showed that some of our sites may have been affected by the fires. If this is confirmed and new studies are carried out, the information presented in this paper represents a baseline that sets the context to understand forest dynamics in this region, including the effects of disturbances like fire.

The old-growth heritage of the SMOc urgently needs to be incorporated into México's conservation agenda. Their future is threatened by human activities and lack of protection in a situation that parallels the early 1990s old-growth controversy of the Pacific Northwest in the U.S. and British Columbia in Canada (Johnson and Swanson 2009). Uncertainty derived from climate change also adds to the threats faced by these systems. Conservation of these forests should include fire management that incorporates frequent surface fires, while structural and compositional complexity should be maintained in order to ensure habitat quality for old-growth dependent species.

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