THE TREASURE OF THE SIERRA MADRE:
ECOLOGY OF OLD-GROWTH FORESTS IN CHIHUAHUA, MÉXICO

By Citlali Cortés-Montaño

A dissertation

Submitted in Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

in Forest Science

Northern Arizona University

December 2011

Approved:

Peter Z. Fulé, Ph.D., Chair

Ernesto Alvarado-Celestino, Ph.D.

Tina J. Ayers, Ph.D.

Margaret M. Moore, Ph.D.

José Villanueva-Díaz, Ph.D.

Abstract

THE TREASURE OF THE SIERRA MADRE:
ECOLOGY OF OLD-GROWTH FORESTS IN CHIHUAHUA, MÉXICO

By Citlali Cortés-Montaño

Old-growth forests are valuable but declining worldwide. 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. These forests provide habitat for Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*: Psittacidae; “guacamaya”), a CITES-listed endangered species. We studied four old-growth remnants in Mesa de las Guacamayas, a site in the Sierra Madre Occidental in Chihuahua, México, to assess the composition, structure, and age characteristics of the overstory, relating it to fire histories and continental and regional climatic data. We linked our findings to the habitat needs of Thick-billed Parrots reported by the literature, and we studied the β-diversity of the understory plant communities at these sites and related them to the composition, cover, density and fire regimes of the overstory.

We found that frequent disturbance by surface fires appears to have contributed to maintaining open, diverse, and productive forests for at least 250 years. While climate was a historical driver of the fire regimes in this mountain range, humans appear to have played a role in the fire regime interruptions of the second half of the 20th century. We found large live trees (>60 cm DBH) in the four sampling sites. We also found densities of five or more large snags per ha^{-1} in two of the sampling sites, which are considered good nesting habitat conditions for Thick-billed Parrots. *Pinus strobiformis*, an important food source for the parrots, was common in three of the four sites. We also detected close interactions between understory, overstory and fire regimes in the sampled old-growth forests. We did not encounter non-native plant species, which suggests that β-diversity of the plant communities and maintenance of the ecological process of fire could play a “shielding” role in preventing invasions.

We also collected data about overstory age and structure, and understory cover and composition in temperate pine-oak forests inside Parque Nacional Cascada de Basaseachi, and outside the park, in a logged forest. Both of these sites are located in central Chihuahua, in the Sierra Madre Occidental range. We used these datasets to evaluate the effectiveness of the park at conserving plant species richness and diversity. We concluded that the forest plant communities inside the park are more species rich and diverse than outside the park. We proposed a source-sink model in which regional biodiversity conservation goals could be achieved or magnified by combining alternative approaches, such as community-based management with traditional models, such as protected areas.

Acknowledgments

I am here because of the encouragement and support of my family. Our early adventures in the mountains of Jalisco, my home state in México, made me fall in love with trees, rocks, flowers and animals. My parents allowed me to explore that love with absolute freedom. They also taught me to ask questions until I found a satisfying answer, and to look for answers through observation, reading, and conversation. My mom and all the other fantastic women in my family have been a life-long source for inspiration, especially when the going gets tough. My dad taught me, among many other things, how to ride a bike. He always motivated me to stay active and practice sports, which have been key to my sanity during these years of graduate school.

I wouldn't be here without the help, support and love of my non-biological family throughout the years, my sisters: Heather (dearest Doctora, ¡many many thanks desde lo más profundo de mi corazón!), Miss B-Bee, Jen and Cindy. Andrea, Kikis, Ana (Chicotito), Jenny (Zapatiux) and Moma are my dear hermanas that never let me quit, always sending love and good vibes from the south. Many friends in town, including Hill-Mili, Tab, Karin, Jessica and Cerissa, were a most excellent source of good times during my stay in Flagstaff, and a great loving network when times weren't so fun. BMan was always ready to show me the way to the mountains in search for the perfect single-track trail. Tina, Randy and Alec have opened their house, their fridge and their hearts to me, I will never be able to express how thankful I am for all the cariño and support and the delicious chocolate cake.

Enrique Jardel always motivated me and pushed me to go further, I wouldn't be here if it wasn't for him and Manantlán, those beautiful mountains. Héctor Arias encouraged me to go ahead with this process, and has been very supportive throughout. Jim Brooks and Nick Smith have been excellent friends all along, on this side and the other, exploring the endless Sierras.

Pete allowed me to take ownership of this project and turn it into something meaningful and of great interest to me, ¡muchas gracias! My committee has been fantastic all along. ¡Muchas gracias, matétera-ba! Many thanks as well to Chris McGlone, who was especially helpful in the analyses, preparation and multiple reviews of Chapter 4. Don Falk has been great to work with, especially during this last year of thinking and writing, and I want to express my gratitude for his help, hard questions and willingness to guide my search for answers. Jherime Kellermann provided excellent ideas on how to use our information and relate it to Thick-billed Parrots, and was very helpful with the preparation of Chapter 3. Tony DeLuz from the Bilby Research Center designed Figure 2.4.

The fire ecology lab group has been a source of critical and insightful reviews in manuscript preparation and methodological approaches. I especially want to thank Katie Ireland and Amanda Stan for their help. The graduate students at the School of Forestry and the Environmental Sciences and Policy program have been phenomenal sources of support throughout my stay at NAU. Muchas gracias.

Don Tomás in Tres Tumbas provided valuable help and insights as field guide in Mesa de las Guacamayas. Don Teodoro Campos in Janos facilitated obtaining permission from the ejido, and Ejido 5 de Mayo kindly let us work in their forests. Pablo Domínguez and María Elena Rodarte from the CONANP Regional Office in Chihuahua helped us contact communities and protected area managers in Janos and Basasaeachi. Ejido Basaseachi kindly allowed us to work in their forests. Nélida Barajas

Acosta and José Luis García Loya from The Nature Conservancy-Rancho El Uno helped with logistics and field work. Tina Ayers, Isaac Bickford, Edgar Bustillos Daniel, Peter Brown, Julián Cerano Paredes, Walker Chancellor, Marco Córdoba Castillo, Vicenta Constante García, Nancy Duarte, Don Falk, Christen Irby, Marissa Joe, Fernando Morales, Margarita Moreno Hinojos, Melissa McNell, Alec and Randy Scott, Mike Stoddard, Cindy Tolle and José Villanueva helped with field work.

Marissa Joe (ASC), Tina Ayers (ASC) and Socorro González (CIIDIR) helped with the organization and determination of the botanical specimens. Marissa Joe processed and organized the collections, sent specimens to experts and entered data into the database. Susan Nyoka helped to sort and decipher the mysteries of uglies and vegetative specimens. Experts that assisted with determinations at other herbaria were Mark Egger (WTU), Socorro González (CIIDIR), Phil Jenkins (ARIZ), Guy Nesom (TEX), Andrew Salywon (DES), Randy Scott (ASC), Richard Spellenberg (NM), Billie L. Turner (TEX), Tom van Devender and Tom Wendt (TEX).

The staff at ERI have been welcoming and very helpful, I especially want to thank Don Normandin, Joe Crouse and Karen Gilbreath for their support throughout this process. Many ERI undergraduate students were the workforce behind the endless hours of core dating and data entering, I’m very grateful for their help. April DeMars Sandoval at the School of Forestry has gone way beyond the call of duty in order to provide help and support, mostly in the form of kind words, tissue and chocolate. ¡Gracias!

NSF grant DEB-0640351 CONACYT and the NAU IGERT program provided financial support during my doctoral studies.

Table of Contents

Abstract ii

Acknowledgments v

Table of Contents viii

List of Tables x

List of Figures xii

Dedication xiv

Preface xv

Chapter 1: Introduction 1

- References 5

Chapter 2: Linking old-growth forest composition and structure to fire history, climate and land-use in northwestern México 9

- Abstract 9
- Introduction 11
- Methods 14
- Results 20
- Discussion 22
- References 27

Chapter 3: Assessing Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*: Psittacidae) old-growth forest habitat in northwestern México 44

- Abstract 44
- Introduction 45
- Methods 47
- Results 49
- Discussion 51
- References 55

Chapter 4: High β-diversity in the understory vegetation of remnant old-growth forests in northwestern México 63

- Abstract 63
- Nomenclature 65
- Introduction 66

Methods 69
Results 75
Discussion 77
References 81
Chapter 5: Forests of the past, present and future: assessing overstory and understory plant communities in pine-oak forests in a national park and its surroundings in northwestern México..99
Abstract 99
Introduction 100
Methods 103
Results 108
Discussion 111
References 115
Chapter 6: Management Recommendations 126
Appendix 1: Coordinates (UTM) of sampling sites at Mesa de las Guacamayas and Basaseachi. 126
Appendix 2: List of flowering plant collections for Parque Nacional Cascada de Basaseachi and Ejido Basaseachi..126

List of Tables

Table 2.1. Physical and biological characteristics at the four sampling sites: MP (Mesa Prieta), PS (Mesa Prieta Sur), RT (Rincón de las Tinajas) and AB (El Abeto). Mean values are bolded, minimum and maximum are in parenthesis. Indicator species from ISA results, species codes are: PIDU-Pinus durangensis, PIST-Pinus strobiformis, PSME-Pseudotsuga menziesii.. 35

Table 2.2. Structural characteristics of the overstory by site. Mean values are bolded, minimum and maximum are in parenthesis. Site codes as in Table 2.1, species and group codes are: PIDU-Pinus durangensis, PIST-Pinus strobiformis, PSME-Pseudotsuga menziesii, OTH CON-Other conifers, QUERCUS-Quercus spp., OTH BL-Other broadleaved species. TPH are trees per hectare, BA is basal area (m2 ha-1)...... 36

Table 2.3. Depth of forest floor fuels and woody debris loads by site. Mean values are in bold text, minimum and maximum are in parentheses. 37

Table 2.4. Canopy fuel characteristics by species and site, and % canopy cover by site. Mean values are in bold text; minimum and maximum are in parentheses. Species codes are as in Table 2.1. CBH: Crown base height (m), TH: Total height (m), N: Number of trees measured.. 38

Table 3.1. Summary of factors quantified in studies of Thick-billed Parrot nesting habitat in Northern Mexico. Average values bolded, ranges in parentheses. *Pinus strobiformis* Engelm. is synonymous with *P. ayacahuite* var. *brachyptera* Shaw. 58

Table 3.2. Snag and tree density (number of snags or trees ha-1) per DBH class with suitable characteristics (>60 cm DBH and >15 m height) for Thick-billed Parrot nesting by site. Site names are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB). Species names and codes are *Pinus durangensis* (PIDU), *Pinus strobiformis* (PIST), *Pseudotsuga menziesii* (PSME)... 59

Table 4.1. Physical and biological characteristics of the study sites: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB). Mean values are bolded, minimum and maximum are in parentheses. 25% and 10% filters indicate % of samples scarred at each site... 88

Table 4.2. Names and growth habit for species with highest Pearson's *r* correlation coefficients to axes 1 and 3 of the NMDS ordinations based on species richness and aerial cover.. 89

Table 4.3. Families and number of species per family in the four sites (MP, PS, RT and AB) at MDG. Numbers in parentheses indicate number of species in the family exclusive to the site. Total indicates number of species in each family at the four sites. 90

Table 4.4. Species richness (S) of flowering plants in 39 plots (1 plot = 200 m^2), 95% confidence intervals for $\widehat{N}$ estimated with Abundance-based Coverage Estimator. H' is Shannon's Diversity Index and is expressed as effective number of species, $e^{H'}$, 95% confidence intervals for $e^{\widehat{H'}}$ calculated with Chao & Shen's estimator. Average values in bold, standard error in parentheses. Statistical significance of paired PERMANOVA (Bonferroni-corrected $\alpha = 0.008$) marked with *. 91

Table 4.5. Regression models for species richness, diversity (H') and aerial cover. Site names as in Table 4.1. Statistical significance at $p<0.05$ indicated with *. 92

Appendix 4.1. Preliminary flowering plant list for MDG. Scientific names and authorities follow the International Plant Names Index (http://www.ipni.org). Synonyms and alternative families obtained from Van Devender et al. (2010). * indicates that a species is considered rare. Numbers in the Site column indicate presence (1) or absence (0) from a site. 95

Table 5.1. Physical and biological characteristics at the three sampling sites: AE (Arroyo El Estacado), CP (Cañón El Pájaro) and AZ (Arroyo La Zorra). Mean values are bolded, minimum and maximum are in parentheses. 120

Table 5.2. Species richness and diversity of the overstory (O) and understory (U) of the sampling sites. Shannon's Diversity Index is H'. Site labels as in Table 5.1. 121

Table 5.3. Overstory species present at each site. Site labels as in Table 5.1. Scientific names and authorities follow the International Plant Names Index (http://www.ipni.org). 122

Table 6.1. Proposed national standard components (NOM, Norma Oficial Mexicana) for old-growth temperate forests in the SMOc.. 132

List of Figures

Figure 2.1. Location of the study area in the state of Chihuahua, México. Sampling sites: MP (Mesa Prieta), PS (Mesa Prieta Sur), RT (Rincón de las Tinajas) and AB (El Abeto)........ 39

Figure 2.2. Diameter distribution of live trees in the four sites. Site labels as in Figure 2.1. The x-axis lists 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........ 40

Figure 2.3. Non Metric Multidimensional Scaling ordination (stress=13.01, instability=0.05) of study sites at Mesa de las Guacamayas based on relativized basal areas. Site labels as in Figure 2.1. 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 explained 30.7% of the variation and we interpret it as driven by a transition in dominance from *Pinus strobiformis* to *Pseudotsuga menziesii*. Axis 2 explained 38.6% of the variation and was driven by fire frequency, as shown by the vector overlay........ 41

Figure 2.4. Climatic reconstructions, age distributions of conifer and broadleaved species, and fire histories of the four sites in Mesa de las Guacamayas. Site labels as in Figure 2.1. a) PDSI index reconstruction for point 120 in SW New Mexico (Cook et al. 2004). b), c), d), 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. In review). Highlighted decades (1950-1990) show fire interruption in MP, PS and AB........ 42

Figure 2.5. Average density of seedlings and saplings in the regeneration stratum at the four sites. Site labels as in Figure 2.1........ 43

Figure 3.1 Location of the study area in the state of Chihuahua, México. Site names are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB)........ 60

Figure 3.2. Tree basal area (m2 ha-1) and tree density (trees ha-1) per site. Species codes are Pinus durangensis (PIDU), Pinus strobiformis (PIST), Pseudotsuga menziesii (PSME), other conifer species (OTH CON), Quercus spp. (QUERCUS), and other broadleaved species (OTH BL). Site names as in Figure 3.1........ 61

Figure 3.3. Number of fires that scarred >25% of samples during five 50-year periods at four sites in Mesa de las Guacamayas, México. Site names as in Figure 3.1........ 62

Figure 4.1. Study site location in the state of Chihuahua, México. Site names are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB)..... 93

Figure 4.2. Top panel shows NMDS ordination of study sites at MDG based on presence-absence data. Site labels as in Figure 4.1. Axes 1 and 3 explained 60.8% of the variation in the distance matrix, total variation explained by the three axes was 82.2% (stress = 16.88, instability 0.004). Vector overlay showed that total number of fires with the 10% and 25% filters had the highest correlation with Axis 3. Axis 1 was not explained by our data. Bottom panel shows NMDS ordination based on cover data. Axes 1 and 3 explained 50.7% of the variation in the distance matrix, total variation explained by the three axes was 63.3% (stress = 16.58, instability = 0.0001). Vector overlay was similar as in the presence-absence ordination, but also showed density of *Pinus durangensis*. Axis 1 was not explained by our data... 94

Figure 5.1. Location of the sampling sites in the state of Chihuahua, México........... 123

Figure 5.2. Age and diameter distributions of trees and number of saplings in three height classes in the three sites: Arroyo El Estacado (AE), Cañón El Pájaro (CP) and Arroyo La Zorra (AZ). Species groups are *Pinus* spp., *Quercus* spp., Other Conifers (*Juniperus deppeana*. *Cupressus lusitanica* and *Pseudotsuga menziesii*), and Other Broadleaved (*Arbutus* spp., *Fraxinus* velutina, *Ilex* spp., *Osmanthus americanus*). ... 124

Figure 5.3. Ordinations (NMDS) of overstory based on relativized basal area (a), understory based on species presence-absence (b), and % aerial cover (c) in the three sites. Site labels are as in Figure 5.2. All ordinations had three axes, total variance explained by these was 83.1% in a), 72.9% in (b) and 50.8% in (c). Axis 1 explained 29.6% of the variation in (a), 34.8% in (b) and 16.6% in (c). Axis 2 explained 30.8% of the variation in (a), 23.0 in (b) and 17.4 in (c). The ordination based on presence-absence (b) showed that elevation was one of the drivers of Axis 1 (Pearson's *r*>0.35). 125

Dedication

I dedicate this dissertation to Esperanza Amaya Coronado, my grandmother, my dear manina, on her 95th birthday. Born in the heart of my beloved Sierra, she lived through Apache raids, a civil war (la Revolución), and many changes in a society that is still struggling to define itself and in which women continue to fight the centuries-old legacy of machismo.

She was unstoppable when women in México were bound by many obstacles and rules.

I wouldn’t be here if it wasn’t for her example:
Gracias manina, te quiero mucho.

Preface

Chapters 2, 3, 4 and 5 of this dissertation were written in journal manuscript format. There is unavoidable redundancy, particularly in the Methods and References sections, since these chapters are intended for publication with co-authors, which is also why I retained third person pronouns throughout. The second chapter is formatted for submission to *Ecological Applications*, the third chapter for *Conservation Biology*, the fourth chapter for the *Journal of Vegetation Science,* and the fifth chapter for *Biological Conservation*. Appendix 1 includes a list of the UTM coordinates for all the plots at both sampling sites (Mesa de las Guacamayas and Basaseachi). Appendix 2 includes a list of plants collected at Basaseachi.

Chapter 1
Introduction

México is considered a megadiverse country that is only surpassed by few others in terms of its biological and ecological heritage. This natural richness comes with many responsibilities, as the conservation and management of these vast resources poses many technical, social and economic challenges. While the country has strengthened its protected area system since the 1990s, important biotic resources are still at risk. Some of the proximate and ultimate drivers of forest degradation and loss in México are land-use change and fragmentation, illegal logging, poverty and demographic growth. Lack of inventories and basic information concerning the natural history of the elements of forest communities is another important challenge to their conservation (Challenger 1998, Challenger et al. 2009).

The Sierra Madre Occidental (SMOc) is the longest mountain range in México, spanning >1200 km from the international border with the U.S. in a southeast direction (Ferrari et al. 2007). Ecosystems in these mountains range from subtropical deciduous forest to mixed conifer forests in its highest altitudes, and they also provide habitat or act as corridors for rare and endangered species, such as the Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*: Psittacidae) (Challenger 1998). Its temperate forests host a large number of the known species in *Pinus* and *Quercus* (Nixon 1993, Styles 1993). Examples of highly diversified genera in the understory are *Castilleja* (Scrophulariaceae), *Eryngium* (Apiaceae), *Muhlenbergia* (Poaceae), *Sedum* (Crassulaceae), *Stevia* (Asteraceae) and *Salvia* (Lamiaceae) (Challenger 1998).

Historically, fire has been an important disturbance in the temperate forests of this mountain range (Fulé and Covington 1999, Heyerdahl and Alvarado 2003, Fulé et al. 2005, Stephens and Fulé 2005, Rodríguez Trejo 2008, Fulé et al. 2011) and has helped create and maintain old-growth characteristics (Fulé et al. 2005, Fulé et al. 2011). These forests are dominated by tree species that tend to be adapted to frequent surface fires (Rodríguez Trejo and Fulé 2003, Manson et al. 2009), with fire regimes characterized by short fire return intervals and low burning intensities (Fulé and Covington 1997, Heyerdahl and Alvarado 2003, Fulé et al. 2005, Manson et al. 2009).

Even though México has had fire suppression policies in place since the early 20th century (Rodríguez Trejo 1999), loose enforcement has allowed historical fire regimes to continue up to the present in some forests in remote mountains in the country's northwest (Heyerdahl and Alvarado 2003, Stephens et al. 2008, Fulé et al. 2011). Previous studies in the SMOc suggest that there is a strong relationship between large-scale climatic patterns and fire occurrence. Fire years coincide with dry years and are preceded by wet years that allow accumulation of fine fuels (Heyerdahl and Alvarado 2003, Fulé et al. 2005, Cerano Paredes et al. 2010).

The forests in the mountains of the SMOc in Chihuahua are closely associated with centuries of continuous human use and management (Richardson and Rundel 1998). Prior to the arrival of Europeans in the 16th and 17th centuries, these forests were part of the territories of different indigenous groups (Lartigue 1983, Challenger 1998). Upon the arrival of the Spanish, the imperial expansion created tensions between them and the indigenous groups that lived in the fertile and mild-weathered valleys. The mountains became a refuge for groups of Indians that wanted to avoid the white invaders (Lartigue 1983). Thus, throughout the colonial period, the mountains and their forests staged skirmishes between Apache guerrillas and the Spanish army, which continued after México's Independence and into the 20th century (Biggers 2007). They also provided shelter and hiding places for groups involved in the Mexican Revolution, in the early 1900s (Biggers 2007).

Commercial forestry has been the most important agent of change in the temperate forests of the SMOc since the onset of the 20th century (Challenger et al. 2009). In 1902, Carl Lumholtz noted that trees of "100 feet [30 m] of average height and more than 15 ft girth [4.6 m circumference]" were frequently observed in these mountains (Lumholtz 1902).

Nearly 50 years later, Brand (1937) described forests similar to those described by Lumholtz, where large trees were still abundant. He also ascertained that the impacts of lumbering in the mountains of Chihuahua were only visible around larger human settlements. Aldo Leopold visited the mountains of northern Chihuahua in the 1930s, and was impressed by the healthy conditions of the watersheds and the well-maintained fire regimes that prevailed in the forests (Leopold 1937). However, a decade later, Starker Leopold reported that the sites visited by his father had been seriously degraded following logging (Fleming and Forbes 2006), the fate of most of the forests in the SMOc. By the end of the 20th century, researchers estimated that <1% remained of the original area covered by temperate old-growth forests in the SMOc (Escalante 1996, Lammertink et al. 1998).

Despite the biological, ecological and economic importance of the temperate forests of the SMOc, there are large knowledge gaps of their basic biology and ecological dynamics. In this context, the overall goal of this dissertation was to generate information about ecological and biological features of these systems. We studied two old-growth sites in the state of Chihuahua from a comprehensive historical and ecological perspective, and expect that our data will help guide conservation efforts in the region.

Our first study site was Mesa de las Guacamayas, a remote mountain in northwestern Chihuahua that hosts temperate old-growth forest remnants. Chapter 2 examined the possible relations among the current forest structure and composition with fire and long-term climatic fluctuations over a timeline of approximately 250 years in a site located in northwestern Chihuahua, nearly 100 km south of the México-U.S. border. Chapter 3 examined the overstory structure and fire histories of the same site from a wildlife management perspective, since the northernmost known nesting site of Thick-billed Parrots is found at this location. Chapter 4 analyzed the understory component of the old-growth remnants at Mesa de las Guacamayas from a community perspective that looked at α and β diversity and the interactions of the understory with the overstory and the site-level fire regimes.

Parque Nacional Cascada de Basaseachi is one of the few protected areas in the SMOc, it was established in 1981 with the objective of protecting temperate forests and landscape features of the land surrounding the tallest perennial waterfall in México. Chapter 5 presents the results of a study conducted at this site, comparing the diversity of forest plant communities inside the park to a managed forest outside the park.

Chapter 6 presents ideas and conclusions derived from the studies conducted for this dissertation in the form of management recommendations. I sincerely hope that the work that I have carried out throughout these four years becomes a useful contribution to the conservation of the true treasure of the Sierra Madre.

References

Biggers, J. 2007. In the Sierra Madre. The University of Chicago Press, Urbana and Chicago, Illinois.

Brand, D. D. 1937. The natural landscape of northwestern Chihuahua. The University of New Mexico, Albuquerque, NM.

Cerano Paredes, J., J. Villanueva Díaz, and P. Z. Fulé. 2010. Reconstrucción de incendios y su relación con el clima para la reserva Cerro El Mohinora, Chihuahua. Revista Mexicana de Ciencias Forestales **1**:89-103.

Challenger, A. 1998. Utilización y Conservación de los Ecosistemas Terrestres de México. Pasado, Presente y Futuro. CONABIO, Instituto de Biología-UNAM, Agrupación Sierra Madre, S.C., México, D.F.

Challenger, A., R. Dirzo, J. C. López Acosta, E. Mendoza, R. Dirzo, A. Lira-Noriega, and I. Cruz. 2009. Factores de Cambio y Estado de la Biodiversidad. Pages 37-73 Capital Natural de México Vol. II: Estado de Conservación y Tendencias de Cambio. CONABIO, México, D.F.

Escalante, P. 1996. Informe final del proyecto G028. La situación del carpintero imperial (*Campephilus imperialis*) y de los bosques de coníferas maduros de la Sierra Madre Occidental, México. CONABIO, México, D.F.

Ferrari, L., M. Valencia-Moreno, and S. Bryan. 2007. Magmatism and tectonics of the Sierra Madre Occidental and its relation with the evolution of the western margin of North America. Geology of México: Celebrating the Centenary of the Geological Society of México: Geological Society of America Special Paper 422:1-39.

Fleming, W., and W. Forbes. 2006. Following in Leopold's footsteps: revisiting and restoring the Rio Gavilan watershed. Ecological Restoration **24**:25-31.

Fulé, P. Z., and W. W. Covington. 1997. Fire regimes and forest structure in the Sierra Madre Occidental, Durango, México. Acta Botanica Mexicana **41**:43-70.

Fulé, P. Z., and W. W. Covington. 1999. Fire regime changes in La Michilía Biosphere Reserve, Durango, Mexico. Conservation Biology **13**:640-652.

Fulé, P. Z., M. A. Ramos Gómez, C. Cortés Montaño, and A. M. Miller. 2011. Fire regime in a Mexican forest under indigenous resource management. Ecological Applications **21**:764–775.

Fulé, P. Z., J. Villanueva-Díaz, and M. Ramos-Gómez. 2005. Fire regime in a conservation reserve in Chihuahua, Mexico. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:320-330.

Heyerdahl, E. K., and E. Alvarado. 2003. Influence of Climate and Land Use on Historical Surface Fires in Pine-Oak Forests, Sierra Madre Occidental, Mexico. Pages 196-217 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. Fire and Climatic Change in Temperate Ecosystems of the Western Americas.

Lammertink, J. M., J. A. Rojas-Tome, F. M. Casillas-Orona, and R. L. Otto. 1998. Situación y conservación de los bosques antiguos de pino-encino de la Sierra Madre Occidental y sus aves endémicas. Consejo Internacional para la Preservación de las Aves, Sección Mexicana, México, D.F.

Lartigue, F. 1983. Indios y bosques. Políticas forestales y comunales en la Sierra Tarahumara. Ediciones de la Casa Chata, México, D.F.

Leopold, A. 1937. Conservationist in Mexico. American Forests **43**:118-120.

Lumholtz, K. S. 1902. Unknown Mexico; a record of five years' exploration among the tribes of the western Sierra Madre; in the Tierra Caliente of Tepic and Jalisco, and among the Tarascos of Michoacan. The Rio Grande Press, Inc., Glorieta, NM.

Manson, R. H., E. J. Jardel Peláez, M. Jiménez E., and C. A. Escalante S. 2009. Perturbaciones y Desastres Naturales: Impactos sobre las Ecorregiones, la Biodiversidad y el Bienestar Socioeconómico. Pages 131-184 Capital Natural de México Vol. II: Estado de Conservación y Tendencias de Cambio. CONABIO, México, D.F.

Nixon, K. C. 1993. The genus *Quercus* in Mexico. Pages 447-458 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, editors. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, NY and Oxford, UK.

Richardson, D. M., and P. W. Rundel. 1998. Ecology and biogeography of Pinus: an introduction. Pages 3-46 *in* D. M. Richardson, editor. Ecology and biogeography of Pinus. Cambridge University Press, Cambridge, United Kingdom.

Rodríguez Trejo, D. A. 1999. A look at wildland fires in México. Fire Management Notes **59**:15-23.

Rodríguez Trejo, D. A. 2008. Fire regimes, fire ecology, and fire management in Mexico. AMBIO: A Journal of the Human Environment **37**:548-556.

Rodríguez Trejo, D. A., and P. Z. Fulé. 2003. Fire ecology of Mexican pines and a fire management proposal. International Journal of Wildland Fire **12**:23-37.

Stephens, S. L., D. L. Fry, and E. Franco-Vizcaino. 2008. Wildfire and spatial patterns in forests in Northwestern Mexico: the United States wishes it had similar fire problems. Ecology and Society **13**.

Stephens, S. L., and P. Z. Fulé. 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. Journal of Forestry **103**:357-362.

Styles, B. T. 1993. Genus *Pinus*: a Mexican purview. Pages 397-420 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, editors. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, NY and Oxford, UK.

Chapter 2

Linking old-growth forest composition and structure to fire history, climate and land-use in northwestern México

Abstract

Old-growth forests are valuable but declining worldwide. 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. 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. The lack of vertical fuel continuity 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 appears to have contributed to maintaining open, diverse, and healthy forests for at least 250 years. While historically climate was a driver of fire regimes in this mountain range, humans played a role in the fire regime interruptions of 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 the ones that we sampled are becoming increasingly rare in the SMOc. 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.

Introduction

Old-growth forests (OGFs) differ in a broad range of ecological and biological characteristics from secondary forests (Wirth et al. 2009). For example, they 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). They 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). However, since the advent of industrialization in the 1850s, the area covered by OGFs has decreased dramatically worldwide (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). Its forests have a plant endemism rate of 70%, the highest identified for all vegetation types in México (Felger et al. 1997).

Fire suppression policies have been in place in México since the early 20th century (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). Forests with uninterrupted fire regimes are more resilient to severe fire and are more heterogeneous than those in which fires have been suppressed (Stephens and Fulé 2005). Previous studies in the SMOc suggest a strong relationship between large-scale climatic patterns, such as El Niño Southern Oscillation, and fire occurrence. Fire years coincide with dry years and are preceded by wet years that allow 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 17thcenturies, these forests were part of the territories of different 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). Commercial forestry has been the most important agent of human-induced change in the SMOc since the last century (Challenger et al. 2009), and Chihuahua remains one of the most important timber-producing states in the country (CONAFOR 2009).

Changes in forest age and structural characteristics in forests of the SMOc by the end of the 20th century were so dramatic that two different studies (Escalante 1996, Lammertink et al. 1998) estimated that only ~1% of OGFs remained. The Imperial

Woodpecker, Mexican Grizzly and Mexican Wolf were extirpated from the SMOc in the 20th 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 in the SMOc, and they are considered endangered by México's legislation (SEMARNAT 2010). They favor old-growth habitat for nesting and breeding (Monterrubio-Rico and Enkerlin-Hoeflich 2004). Thus, they are especially susceptible to changes in forest structure, and 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 the interactions among forest development, fire and large-scale climatic processes in OGFs that are a biodiversity hotspot. We studied four OGF sites at Mesa de las Guacamayas, in northwestern México. We measured 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, to answer the following questions:

1. Are the structure and floristic composition of the overstory of each site associated with fire histories and regional climatic oscillations across a ~250 year timeline?
2. What are the possible interactions among inter-site heterogeneity of the overstory composition, fire histories, and the known record of recent human-induced land-use changes?

Methods

Study area

Mesa de las Guacamayas is a mountain range located at the northern end of the SMOc in northwestern Chihuahua, México (Figure 2.1). It is part of Ejido 5 de Mayo, a communal holding created through the allocation of federal land by presidential decree executed in 1972 (RAN 2010). The ejido covers ~25,000 ha of forests and grasslands. 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 Mesa de las Guacamayas were included in these. In the 1960s, at least one sawmill was established in the area, operating until the ejido formation in the 1970s. The ejido continued to log its more accessible forests as recently as the late 1990s (Campos, pers. comm.). Only one family lives there 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 and Pinaceae. Species in the Cupressaceae were *Juniperus deppeana* Steud. and *Cupressus arizonica* Greene. Species in the Pinaceae were *Abies* sp., *Pinus durangensis* Martínez, *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.).

Field methods

We searched the study area on foot, looking for forest stands with no signs of harvesting, dominated by *Pinus* spp. and *Pseudotsuga menziesii*. We identified four sites: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB) (Figure 2.1). At each study site we established ten plots on a 100 x 100 m sampling grid (N=40 plots). The sites were on steep, north-facing slopes (Table 2.1). MP and PS were only accessible 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 permanently marked each plot center and recorded elevation, slope and aspect.

We identified tree species in the field using 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 only record 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; >40-80 cm, >80-130 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. 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-meter planar transects in a random direction from each plot center (N=40). We tallied all fuels in the first 5 m of the transect using the following classes: 1-hour timelag fuels (0 to 0.62 cm diameter), 10-hour timelag fuels (0.63 to 2.53 cm diameter) and 100-hour timelag fuels (2.54 cm to 7.61 cm). We measured all dead and live 1000-hour timelag fuels (≥7.62 cm at the narrowest point) and the depth in cm of the organic (duff and litter) layers every 5 meters. 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. In review).

Laboratory methods and data analysis

Botanists at ASC determined the botanical specimens. In some cases specimens were sent 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 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).

Boxplots and scatterplots clearly indicated that the 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 the recommended method for the analysis of non-normally distributed ecological community data (McCune and Grace 2002). It reduces the dimensions of a distance matrix and produces a graphic that depicts 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 (three individual species and three multi-species groups, N=39 plots). We eliminated one plot from the analyses since it lacked 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.

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 Core Development 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. This is 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 detect indicator 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 was 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 all the cores and sections with increasingly finer sandpaper grits until all 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 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*.

We used a dataset created by a companion study (Fulé et al. In review) 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. This index is a hydroclimatic measure of the extent and intensity of drought at the regional scale (Alley 1984). We used the 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. Grid point 120 is the closest point to our research area with a record that extends into the 21st century, and it 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 2.2). The species with the largest trees was *Pseudotsuga menziesii*, followed by *Pinus durangensis* and *P. strobiformis* (Figure 2.2). The Other Conifers, *Quercus* spp. and Broadleaved groups 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}). The site with the lowest basal area was MP (26.8 m^{2} ha^{-1}), and PS had the highest basal area (43.6 m^{2} ha^{-1}), driven by the large *Pseudotsuga menziesii* trees found there.

The final NMDS ordination (Figure 2.3) had three axes and was achieved with a final stress of 13.01 and 0.05 instability. The ordination explained 91.6% of the variability in the dataset (Axis 1=30.7%, Axis 2=38.0% and Axis 3=22.9%). Correlations between species and the ordination axes showed that Axis 1 was driven by a transition in dominance from *Pinus strobiformis* to *Pseudotsuga menziesii*. The vector overlay showed that Axis 2 was influenced by the number of fires in the past 60 years at each site. ISA results showed that *Pinus durangensis* was a good indicator for RT (Indicator Value, IV=57%, $p<0.05$), *Pinus strobiformis* for MP (IV=47%, p 0.05) and *Pseudotsuga menziesii* for PS (IV=42%, $p<0.05$). The ISA results did not identify indicator species for AB.

Paired PERMANOVA tests showed that 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 four sites were from the species with highest basal area values: *Pinus durangensis, P. strobiformis* and *Pseudotsuga menziesii* (Figure 2.4). 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 trees older than the dateable trees. Mesa Prieta Sur was the only site with continuous and relatively even tree establishment in the 19th century (Figure 2.4). 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 showed that 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 *Pinus* spp. in the 0-40 cm height class, but their abundance decreased dramatically in the taller height classes (Figure 2.5). *Pinus* spp. dominated the 0-40 cm class in MP. *Quercus* spp. dominated all the regeneration height classes in PS, RT and AB. *Robinia neomexicana* was a major component of the >40-80 cm height class, but it dwindled dramatically in the next class.

The deepest average litter depth was measured at RT (3.1 cm) and the shallowest in MP (1.5 cm). The deepest average duff depth was at MP (2.6 cm) and the shallowest was 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 2.3). Average canopy cover values for the four sites ranged between 51.4% (RT) and 60.7% (PS and AB) (Table 2.4). *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).

The relations of regional hydroclimatic patterns, expressed by PDSI, with temporal patterns of tree ages and fire events in the last 250 years are shown in Figure 2.4. A weak climate signal was observed in post 1950s recruitment trends in all sites. Otherwise we did not visually detect other relations 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. Consistent conifer recruitment throughout the 20th century, with a pulse in the 1930s, was observed in RT.

Discussion

Fire frequencies of the four sites at Mesa de las Guacamayas resemble those of pre-European conditions of ponderosa pine forests in Arizona (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). Fires occurred frequently (mean fire intervals <10 years) in the four sites before the mid-20th century (Fulé et al. In review). This is shown by the dates of fires that scarred >25% samples, a measure of relatively large fires (Figure 2.4). A total of 55 fires burnt the four study sites between 1733 and 2009 (Fulé et al. In review). Of these, 9% burnt the four sites, 22% burnt three sites, 25% burnt two sites, and 44% burnt one site only. A fire-free period began in 1945 at MP and PS, and 1953 at AB. After an extended fire-free period of ~50 years those sites burnt at least once between 1989 and 2009. One site (RT) maintained an uninterrupted fire regime up to 2009 (Fulé et al. In review).

Fire records at the four 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, when fires were recorded at all the sites. The 6.2 year mean fire frequency observed at RT into the 21st century makes it a rare example of a site with a maintained fire regime in southwestern North America.

Low fuel loading was associated with recurring surface fire in the forests of Mesa de las Guacamayas. Average fuel loads were comparable to those of other unharvested sites in the SMOc (Fulé and Covington 1997). These are 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. Thus, they keep lower branches from reaching the forest floor and forming fuel ladders. Despite alterations to the historical fire regimes in the past 50 years, fuel loads in these sites remained relatively low. They are consistent with those of other reference sites in northwestern México and the southwestern U.S. where frequent fires continue to burn through the landscape (Stephens and Fulé 2005).

The tree-ring record of Mesa de las Guacamayas indicates that episodic drought has been part of the disturbance regime of these forests since at least the late 17th century. The fire histories for the four sites show that fires tend to occur during or following drought episodes, which are largely entrained by the El Niño/Southern Oscillation (Fulé et al. In review). The high synchronicity of fire occurrence at the four sites was interrupted abruptly in 1945 at MP and PS, and in 1953 at AB. The initiation of the fire-free period in MP, PS and AB coincided with the 1950s regional drought observed in tree-ring records of the U.S. Southwest (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 the study sites coincides with the 1950s regional drought. This was the driest period of the 20th century in the region (Grissino-Mayer and Swetnam 2000). We hypothesize that this fire-free period may have been due to the onset of logging and road building, and by the introduction of livestock grazing. However, despite the ~60 year absence of fire, the sites burnt at least once in the 21st century and none showed evidence of widespread fire-caused mortality or pathogen infestations.

Diversity in species composition translates commonly to diversity in tree architecture, which confers structural heterogeneity to the overstory. This attribute has been associated with resilience 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 dominated each site, as shown by the spread in the NMDS ordination and the ISA results. ISA results supported grouping the plots for which *Pinus strobiformis* and *Pseudotsuga menziesii* were strong indicators along Axis 1. The separation of RT along Axis 2 was also supported by ISA results. We did not identify indicator species for AB due to the variation in the composition of the overstory in this site. This can be observed in the scattered distribution of plots along the ordination axes. The most diverse stratum at the four sites was the subcanopy, formed of *Quercus* spp. and other broadleaved species. This stratum provides key habitat for wildlife, as has been shown in forests of southern Chihuahua (Miller and Chambers 2007).

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 uninterrupted fire regime of this site 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 Mesa de las Guacamayas 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 5 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 spatially closer to lands where fire is used as a management tool (for example in activities such as grass burning or agricultural plot clearing).

Management implications

The forests of Mesa de las Guacamayas are important biodiversity reservoirs, providing habitat to endangered species such as Thick-billed Parrots. 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, such as 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, pathogens, and drought. This contrasts with the extensive, catastrophic fires reported in dense, fire-excluded forests of the western U.S. (Allen et al. 2010, Williams et al. 2010). The resilience of the forests at the study site could be derived from the heterogeneity and the fire histories of the landscape matrix in which they are found. These forests also have potential to become valuable sources for biodiversity genotypes that are more resistant to the systemic changes expected from climate change in the region (Williams et al. 2010).

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 incorporate integrated fire management, while structural and compositional complexity should be maintained in order to ensure habitat quality for old-growth dependent species.

References

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.-H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management **259**:660-684.

Alley, W. M. 1984. The Palmer Drought Severity Index: Limitations and assumptions. Journal of Climate and Applied Meteorology **23**:1100-1109.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**:32-46.

Applequist, M. B. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry **56**:141.

Binkley, D., T. Sisk, C. L. Chambers, J. D. Springer, and W. Block. 2007. The role of old-growth forests in frequent-fire landscapes. Ecology and Society **12**.

Boucher, Y., D. Arseneault, L. Sirois, and L. Blais. 2009. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. Landscape Ecology **24**:171-184.

Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT 16, 1974. Intermountain Forest & Range Experiment Station, Ogden, Utah.

Burrascano, S., L. Rosati, and C. Blasi. 2009. Plant species diversity in Mediterranean old-growth forests: A case study from central Italy. Plant Biosystems **143**:190-200.

Carey, E. V., A. Sala, R. Keane, and R. M. Callaway. 2001. Are old forests underestimated as global carbon sinks? Global Change Biology **7**:339-344.

Cerano Paredes, J., J. Villanueva Díaz, and P. Z. Fulé. 2010. Reconstrucción de incendios y su relación con el clima para la reserva Cerro El Mohinora, Chihuahua. Revista Mexicana de Ciencias Forestales **1**:89-103.

CONAFOR. 2009. Producción forestal maderable (http://148.223.105.188:2222/snif_portal/secciones/demas/compendio2006/Reportes/D3_FORESTAL/D3_RFORESTA04/D3_RFORESTA04_01.htm).

Cook, E. R., D. M. Meko, D. W. Stahle, and M. K. Cleaveland. 2004. North American Summer PDSI Reconstructions. IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series # 2004-045. NOAA/NGDC Paleoclimatology Program. Boulder CO, USA.

CSM. N.A. Estaciones climatológicas del sistema CLICOM. Comisión Nacional del Agua, Subdirección General Técnica, Coordinación del Servicio Meteorológico.

Challenger, A. 1998. Utilización y Conservación de los Ecosistemas Terrestres de México. Pasado, Presente y Futuro. CONABIO, Instituto de Biología-UNAM, Agrupación Sierra Madre, S.C., México, D.F.

Challenger, A., R. Dirzo, J. C. López Acosta, E. Mendoza, R. Dirzo, A. Lira-Noriega, and I. Cruz. 2009. Factores de Cambio y Estado de la Biodiversidad. Pages 37-73 Capital Natural de México Vol. II: Estado de Conservación y Tendencias de Cambio. CONABIO, México, D.F.

Challenger, A., and J. Soberón. 2008. Los Ecosistemas Terrestres. Capital Natural de México Vol. I: Conocimiento Actual de la Biodiversidad. CONABIO, México, D.F.

D'Amato, A. W., D. A. Orwig, and D. R. Foster. 2009. Understory vegetation in old-growth and second-growth *Tsuga canadensis* forests in western Massachusetts. Forest Ecology and Management **257**:1043-1052.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Escalante, P. 1996. Informe final del proyecto G028. La situación del carpintero imperial (*Campephilus imperialis*) y de los bosques de coníferas maduros de la Sierra Madre Occidental, México. CONABIO, México, D.F.

Farjon, A., J. A. Pérez de la Rosa, and B. T. Styles. 2000. Field guide to the pines of Mexico and Central America. Kew Botanical Gardens, Kew, U.K.

Felger, R. S., G. P. Nabhan, and R. Bye. 1997. Apachian/Madrean Region of Southwestern North America, Mexico and USA. Mexico and USA: CPD site MA11. Pages 172-180 *in* S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, editors. Centres of Plant Diversity, Volume 3: The Americas. WWF, IUCN, National Museum of Natural History-Smithsonian Institution, European Community, ODA, Cambridge, U.K.

Felger, R. S., and M. F. Wilson. 1994. Northern Sierra Madre Occidental and Its Apachian Outliers: A Neglected Center of Biodiversity. Pages 36-59 *in* Biodiversity and the management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. U.S.F.S. General Technical Report RM-GTR-264, Tucson, AZ.

Ferrari, L., M. Valencia-Moreno, and S. Bryan. 2007. Magmatism and tectonics of the Sierra Madre Occidental and its relation with the evolution of the western margin of North America. Geology of México: Celebrating the Centenary of the

Geological Society of México: Geological Society of America Special Paper 422:1-39.

Fulé, P. Z., and W. W. Covington. 1997. Fire regimes and forest structure in the Sierra Madre Occidental, Durango, México. Acta Botanica Mexicana **41**:43-70.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of Southwestern ponderosa pine forests. Ecological Applications **7**:895-908.

Fulé, P. Z., M. A. Ramos Gómez, C. Cortés Montaño, and A. M. Miller. 2011. Fire regime in a Mexican forest under indigenous resource management. Ecological Applications **21**:764–775.

Fulé, P. Z., J. Villanueva-Díaz, and M. Ramos-Gómez. 2005. Fire regime in a conservation reserve in Chihuahua, Mexico. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:320-330.

Fulé, P. Z., L. L. Yocom, C. Cortés Montaño, D. A. Falk, J. Cerano Paredes, and J. Villanueva Díaz. In review. Testing a pyroclimatic hypothesis on the México-U.S. border.

Grissino-Mayer, H. D., and T. W. Swetnam. 2000. Century-scale climate forcing of fire regimes in the American Southwest. Holocene **10**:213-220.

Herold, L. C. 1965. Trincheras and physical environment along the Río Gavilán, Chihuahua, México. Department of Geography, University of Denver, Denver, CO.

Heyerdahl, E. K., and E. Alvarado. 2003. Influence of Climate and Land Use on Historical Surface Fires in Pine-Oak Forests, Sierra Madre Occidental, Mexico. Pages 196-217 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W.

Swetnam, editors. Fire and Climatic Change in Temperate Ecosystems of the Western Americas.

Howard, W. A., and T. M. Griffiths. 1966. Trinchera distribution in the Sierra Madre Occidental, México. Department of Geography, University of Denver, Denver, CO.

Johnson, K. N., and F. J. Swanson. 2009. Historical Context of Old-Growth Forests in the Pacific Northwest-Policy, Practices and Competing Worldviews. Pages 12-28 *in* T. A. Spies and S. L. Duncan, editors. Old Growth in a New World. A Pacific Northwest Icon Reexamined. Island Press, Washington, D.C.

Keeton, W. S., M. Chernyavskyy, G. Gratzer, M. Main-Knorn, M. Shpylchak, and Y. Bihun. 2010. Structural characteristics and aboveground biomass of old-growth spruce-fir stands in the eastern Carpathian mountains, Ukraine. Plant Biosystems **144**:148-159.

Lammertink, J. M., J. A. Rojas-Tome, F. M. Casillas-Orona, and R. L. Otto. 1998. Situación y conservación de los bosques antiguos de pino-encino de la Sierra Madre Occidental y sus aves endémicas. Consejo Internacional para la Preservación de las Aves, Sección Mexicana, México, D.F.

Lartigue, F. 1983. Indios y bosques. Políticas forestales y comunales en la Sierra Tarahumara. Ediciones de la Casa Chata, México, D.F.

Luyssaert, S., E. D. Schulze, A. Borner, A. Knohl, D. Hessenmoller, B. E. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. Nature **455**:213(213).

McCune, B., and J. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and M. J. Mefford. 2006. PC-ORD. Multivariate analysis of ecological data. MjM Software, Gleneden Beach, Oregon.

Miller, A. M., and C. L. Chambers. 2007. Birds of harvested and unharvested pine-oak forests, Chihuahua, Mexico. Southwestern Naturalist **52**:271-283.

Monterrubio-Rico, T., and E. Enkerlin-Hoeflich. 2004. Present Use and Characteristics of Thick-Billed Parrot Nest Sites in Northwestern Mexico. Journal of Field Ornithology **75**:96-103.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package.

Palomares Peña, N. G. 1991. Propietarios Norteamericanos y Reforma Agraria en Chihuahua, 1917-1942. Universidad Autónoma de Ciudad Juárez, Cd. Juárez, Chihuahua, México.

R Core Development Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAN. 2010. Padrón Histórico de Núcleos Agrarios (http://app.ran.gob.mx/phina/).

Rodríguez Trejo, D. A. 1999. A look at wildland fires in México. Fire Management Notes **59**:15-23.

Rodríguez Trejo, D. A. 2008. Fire regimes, fire ecology, and fire management in Mexico. AMBIO: A Journal of the Human Environment **37**:548-556.

Sánchez Colón, S., A. Flores Martínez, I. A. Cruz-Leyva, and A. Velázquez. 2009. Estado y Transformación de los Ecosistemas Terrestres por Causas Humanas. Pages 75-129 Capital Natural de México, Vol. II: Estado de Conservación y Tendencias de Cambio. CONABIO, México, D.F.

SEMARNAT. 2010. Norma Oficial Mexicana NOM-059-SEMARNAT-2010 Protección ambiental - Especies nativas de México de flora y fauna silvestres - Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio - Lista de especies en riesgo.*in* SEMARNAT, editor. NOM-059-SEMARNAT-2010, Diario Oficial de la Federación, 30 de diciembre del 2010.

Spellenberg, R. 2001. Oaks of La Frontera. Pages 176-211 *in* G. L. Webster and C. J. Bahre, editors. Changing Plant Life of La Frontera. The University of New Mexico Press.

Stephens, S. L., D. L. Fry, and E. Franco-Vizcaino. 2008. Wildfire and spatial patterns in forests in Northwestern Mexico: the United States wishes it had similar fire problems. Ecology and Society **13**.

Stephens, S. L., and P. Z. Fulé. 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. Journal of Forestry **103**:357-362.

Swetnam, T. W., and C. H. Baisan. 2003. Tree-Ring Reconstructions of Fire and Climate History in the Sierra Nevada and Southwestern United States.*in* T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. Fire and Climatic Change in Temperate Ecosystems of the Western Americas. Springer, New York.

Swetnam, T. W., and P. M. Brown. 2010. Climatic Inferences from Dendroecological Reconstructions. Pages 263-295 *in* M. K. Hughes, T. W. Swetnam, and H. F. Diaz, editors. Dendroclimatology. Progress and Prospects. Springer.

Thomas, J. W. 1979. Wildlife habitats in managed forests the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553. Forest Service, U.S. Department of Agriculture.

Unidad Forestal Casas Grandes-Babícora, A. C. 1999. Programa de manejo forestal para aprovechamiento de recursos forestales maderables persistente, ejido 5 de Mayo, municipio de Janos, Chihuahua. Chihuahua, Chih.

Williams, A. P., C. D. Allen, C. I. Millar, T. W. Swetnam, J. Michaelsen, C. J. Still, and S. W. Leavitt. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. Proceedings of the National Academy of Sciences **107**:21289-21294.

Wirth, C., H. Gleixner, and M. Heimann. 2009. Old-growth Forests: Function, Fate and Value -An Overview. Pages 1-10 *in* C. Wirth, H. Gleixner, and M. Heimann, editors. Old-growth Forests: Function, Fate and Value. Springer-Verlag.

Table 2.1. Physical and biological characteristics at the four sampling sites: MP (Mesa Prieta), PS (Mesa Prieta Sur), RT (Rincón de las Tinajas) and AB (El Abeto). Mean values are bolded, minimum and maximum are in parenthesis. Indicator species from ISA results, species codes are: PIDU-*Pinus durangensis*, PIST-*Pinus strobiformis*, PSME-*Pseudotsuga menziesii*.

Site	**Latitude (N)**	**Longitude (W)**	**Slope (%)**	**Elevation (masl)**	**Tree species richness**	**Oldest dated tree**	**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**	--

Table 2.2. Structural characteristics of the overstory by site. Mean values are bolded, minimum and maximum are in parenthesis. Site codes as in Table 2.1, species and group codes are: PIDU-*Pinus durangensis*, PIST-*Pinus strobiformis*, PSME-*Pseudotsuga menziesii*, OTH CON-Other conifers, QUERCUS-*Quercus* spp., OTH BL-Other broadleaved species. TPH are trees per hectare, BA is basal area ($m^2\ ha^{-1}$).

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

Table 2.3. Depth of forest floor fuels and woody debris loads by site. Mean values are in bold text, minimum and maximum are in parentheses.

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

Table 2.4. Canopy fuel characteristics by species and site, and % canopy cover by site. Mean values are in bold text; minimum and maximum are in parentheses. Species codes are as in Table 2.1. CBH: Crown base height (m), TH: Total height (m), N: Number of trees measured.

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

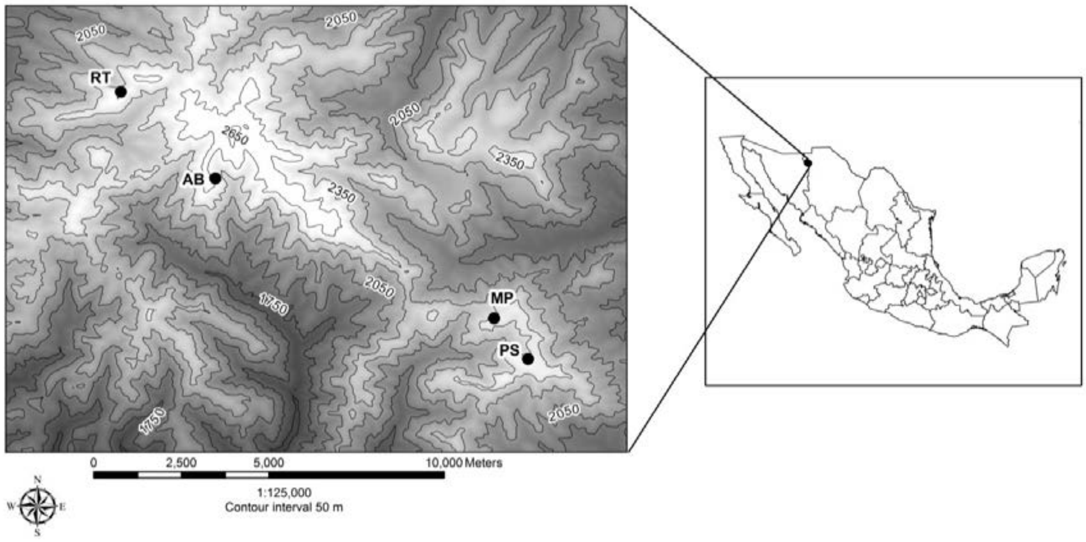

Figure 2.1. Location of the study area in the state of Chihuahua, México. Sampling site codes and names are: MP (Mesa Prieta), PS (Mesa Prieta Sur), RT (Rincón de las Tinajas) and AB (El Abeto).

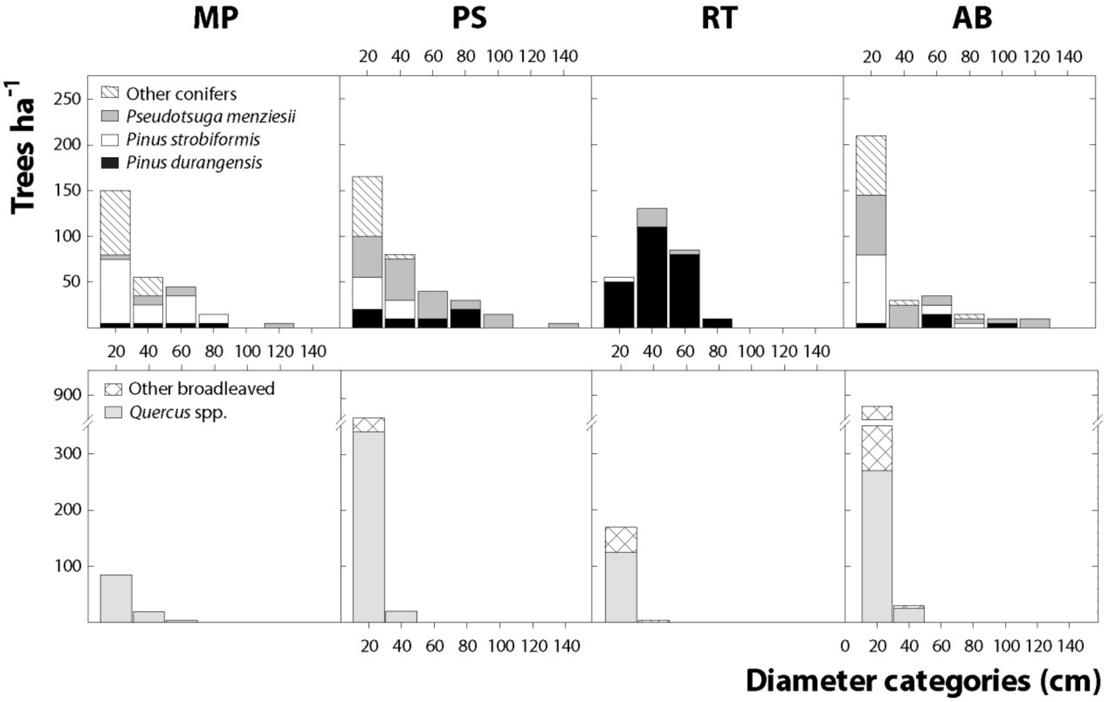

Figure 2.2. Diameter distribution of live trees in the four sites. Site labels as in Figure 2.1. The x-axis lists the upper end of each diameter category. The top panel shows the diameter distributions of all conifer species and the bottom panel shows those of *Quercus* spp. and other broadleaved species.

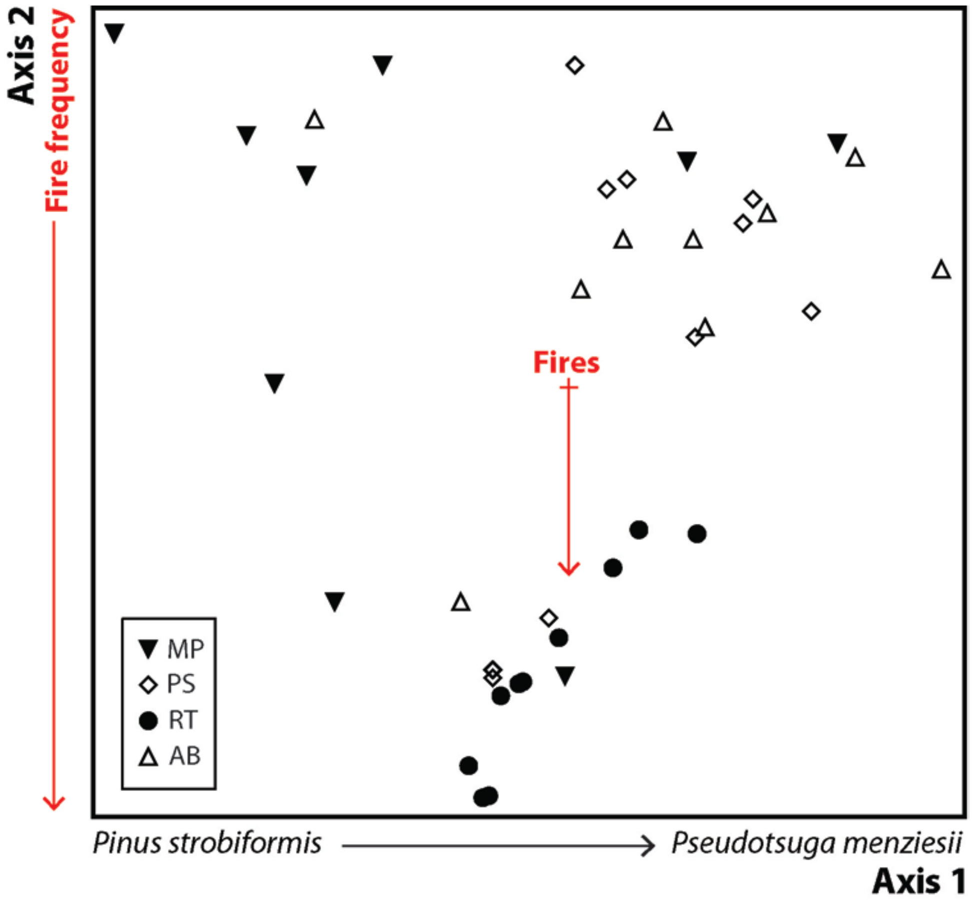

Figure 2.3. Non Metric Multidimensional Scaling ordination (stress = 13.01, instability = 0.05) of study sites at Mesa de las Guacamayas based on relativized basal areas. Site labels as in Figure 2.1. The ordination was rotated 20° to the right to make the vector parallel to Axis 2. Total variance explained by the three axes was 91.7% of the variation in the distance matrix. Axis 1 explained 30.7% of the variation and we interpret it as driven by a transition in dominance from *Pinus strobiformis* to *Pseudotsuga menziesii*. Axis 2 explained 38.6% of the variation and was driven by fire frequency, as shown by the vector overlay.

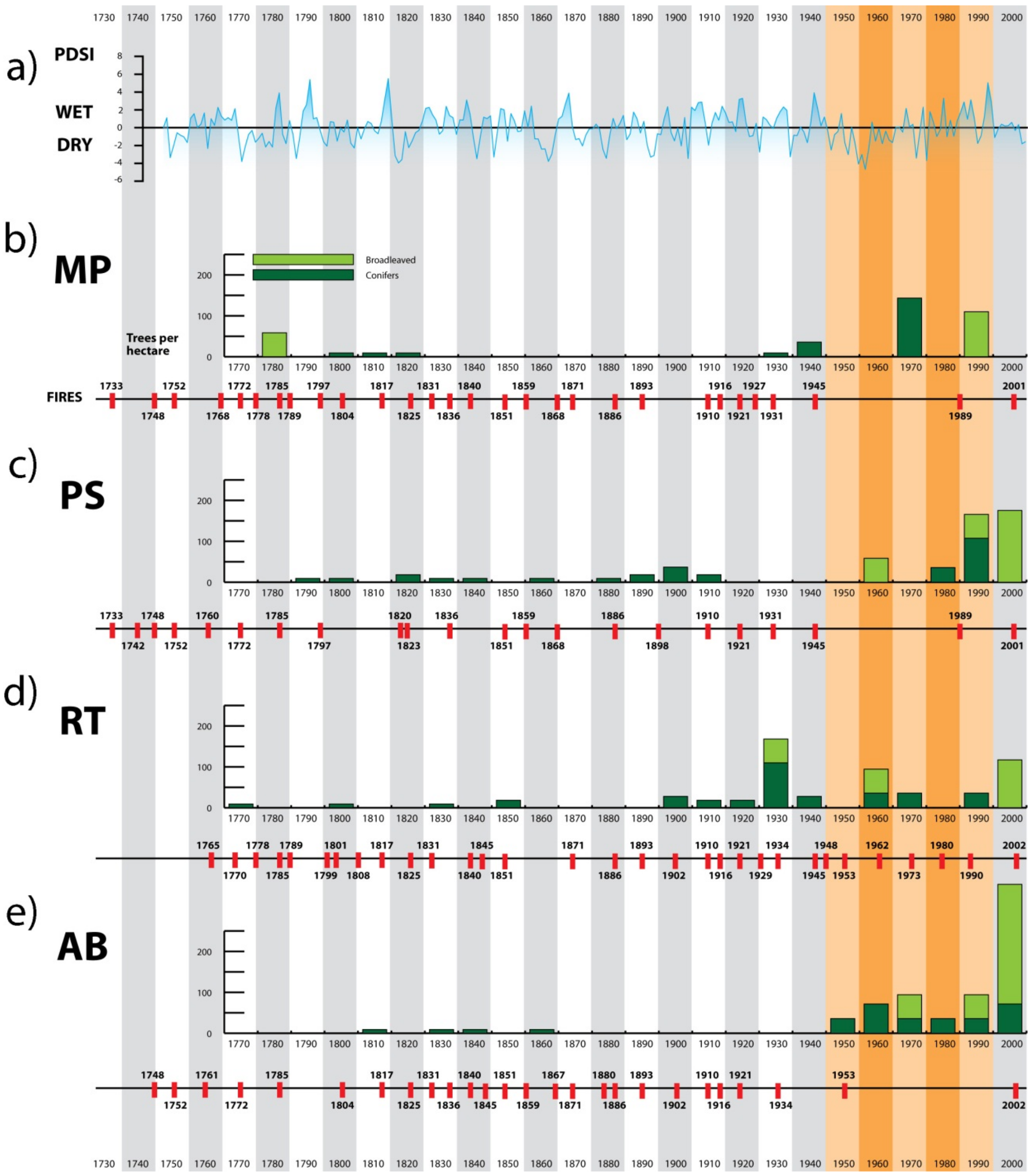

Figure 2.4. Climatic reconstructions, age distributions of conifer and broadleaved species, and fire histories of the four sites in Mesa de las Guacamayas. Site labels as in Figure 2.1. a) PDSI index reconstruction for point 120 in SW New Mexico (Cook et al. 2004). b), c), d), e) Age distributions and 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. In review). Highlighted decades (1950-1990) show fire interruption in MP, PS and AB.

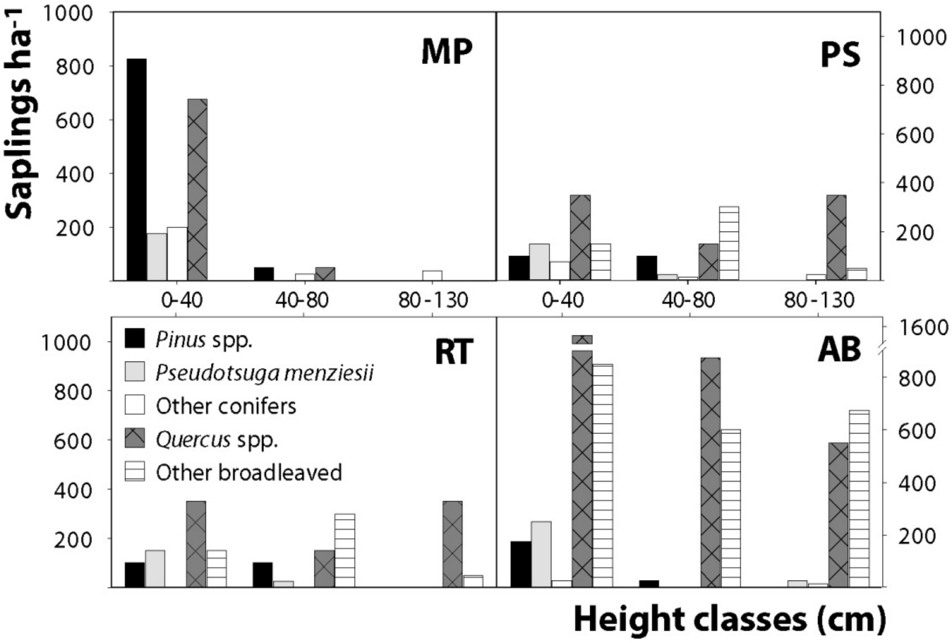

Figure 2.5. Average density of seedlings and saplings in the regeneration stratum at the four sites. Site labels as in Figure 2.1.

Chapter 3

Assessing Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*: Psittacidae) old-growth forest habitat in northwestern México

Abstract

In northern Chihuahua, old-growth forests provide habitat for Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*: Psittacidae; “guacamaya”), a CITES-listed endangered species. We examined the structure, composition, age and fire regimes of old-growth forests in Mesa de las Guacamayas, the northernmost known nesting site for this species. In this study we link those findings to the habitat needs of these parrots reported by the literature. We found large live trees (>60 cm DBH) in the four sampling sites. We found snag densities >5 large snags (>60 cm DBH) per ha, considered good nesting habitat conditions for Thick-billed Parrots, at two of the sampling sites. *Pinus strobiformis*, an important food source for the parrots, was common in three of the four sites. Fire frequencies at the four sites were <10 years until the 1950s, when fire-free periods were recorded at three of the sampling sites. We need a better understanding of the temporal and spatial dynamics of the preferred parrot habitat, as well as it relationships to ecological processes like vegetation phenology, annual bird movements. We also need to better understand the role of current and historical anthropogenic and natural disturbance regimes in these forests, including fire frequencies and land management practices.

Introduction

The Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*), guacamaya or cotorra serrana in México, is one of few parrot species that nests in temperate forests (Monterrubio-Rico and Enkerlin-Hoeflich 2004a). It is a symbol of the challenges faced by conservationists in the México-U.S. Borderlands region, identified by Aldo Leopold as a species susceptible to human-induced change (1937).

In the U.S., their historical range included southeastern Arizona and southwestern New Mexico. Their historical range in México were the mountains of the Sierra Madre Occidental (SMOc), extending into southern Jalisco and Michoacán (Monterrubio-Rico and Enkerlin-Hoeflich 2004b), and possibly as far east as Veracruz (Lanning and Shiflett 1983). Their breeding range has been reduced to the northern end of the SMOc, in eastern Sonora, western Chihuahua, and western Durango (Snyder et al. 2011). Mesa de las Guacamayas in northern Chihuahua is the northernmost known nesting and breeding site for the species (Monterrubio-Rico and Enkerlin-Hoeflich 2004a, Monterrubio-Rico and Enkerlin-Hoeflich 2004b).

The Thick-billed Parrot is considered endangered under Mexican and U.S. laws, and is included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2011). In the late 1980s, a reintroduction program was attempted in southeastern Arizona with captive-bred or rescued birds from the illegal pet trade. However, despite some successful nesting attempts, no self-sustaining population established (Snyder et al. 1994).

The Mexican and U.S. governments are in the process of designing and implementing recovery actions, and the Mexican government published a recovery plan in January 2010 (Cruz Romo et al. 2010). The U.S. Fish and Wildlife Service signed an agreement to draft a recovery plan for the species in December of the same year, following multiple lawsuits from conservation groups. The two governments plan to collaborate in recovery efforts in the U.S., which would be largely dependent on wild parrot populations found in México. The population of Thick-billed Parrots in Mesa de las Guacamayas could play a pivotal role, considering its geographical proximity to the former range of the species in the U.S. Understanding the factors that drive structure and composition of key Thick-billed Parrot habitat features will be useful in selecting and managing future conservation areas.

A literature review indicated that two critical habitat requirements of Thick-billed Parrots are suitable nest substrates and ample food sources (Table 3.1). Thick-billed Parrots are obligate cavity nesters that utilize snags and live trees with a minimum height of 15 m and >60 cm diameter at breast height (DBH), which are large enough to allow sufficiently large cavities (Table 3.1). Their preferred food sources include conifer seeds of *Pinus arizonica*, *P*. *durangensis* and *P*. *strobiformis* (Lanning and Shiflett 1983), and occasionally acorns (Wetmore 1935, Snyder et al. 1994).

Thick-billed Parrots are a gregarious and potentially “eruptive” species which practices synchronized foraging and can travel long distances in search of food (Wetmore 1935, Snyder et al. 1994, Monterrubio-Rico and Escalante-Pliego 2006). This behavior is similar to that of other species that track temporal and spatial variation in cone crop productivity (Bock and Lepthien 1976). Contiguous stands of high-elevation conifer forests capable of sustaining viable parrot populations are increasingly rare in the SMOc, due to regional logging practices. Habitat needs of the species include large trees and snags that are geographically extensive enough to provide predictable and consistent seed crops (Lammertink et al. 1998, Monterrubio-Rico and Enkerlin-Hoeflich 2004a).

Immature forest structures that follow logging provide inadequate nesting habitat and food resources for the parrots (Monterrubio et al. 2002).

Our goal was to understand how information about forest attributes and fire regimes can be applied to management for conservation and restoration of old-growth nesting habitat for Thick-billed Parrots. We reviewed the components of Thick-billed Parrot nesting and breeding habitat reported in the primary literature (Table 3.1). We then contacted conservation organizations working in the SMOc in order to identify old-growth habitat remnants used by Thick-billed Parrots in Mesa de las Guacamayas. Lastly, we examined the ecological factors that can create the forest attributes necessary for suitable Thick-billed Parrot habitat, including forest composition, structure, and fire history.

Methods

Study area

Mesa de las Guacamayas is a mountain range at the northern end of the Sierra Madre Occidental, in northwestern Chihuahua, México (Figure 3.1). The Mesa is part of Ejido 5 de Mayo, a ~25,000 ha communal holding created from federal land by a presidential decree executed in 1972. Large concessions were granted to lumbering operations in the first half of the 20th century (Palomares Peña 1991), but we were unable to confirm if the forests of Mesa de las Guacamayas were included in them. At least one sawmill was established in the site in the 1960s, operating until ejido formation in the 1970s. As recently as the late 1990s, the ejido logged the more accessible forests (Campos, pers. comm.). Currently the ejido is used mostly for light cattle and equine grazing, and only one family maintains permanent year-round residence.

The Mesa is located at the northern end of the SMOc and its parent material is of volcanic origin, formed mostly of rhyolitic ignimbrites (Ferrari et al. 2007). Predominant soils in the region are Phaeozems and Regosols, with Lithosols present in small pockets (Unidad Forestal Casas Grandes-Babícora 1999). The weather record for the area is incomplete, the closest weather station is Guapoca, located ~90 km to the SE. For the period 1961-1998, mean annual precipitation was 584.6 mm and mean annual temperature was 15.9°C at Guapoca (CSM N.A.).

We searched the study region on foot for unharvested forests, dominated by *Pinus* spp. and *Pseudotsuga menziesii* that had Thick-billed Parrots present. We identified four sites that matched our criteria: Mesa Prieta (MP, 30º30’1”, 108 º32’56”), Mesa Prieta Sur (PS, 30º29’21”, 108 º32’25”), Rincón de las Tinajas (RT, 30º33’28”, 108 º38’41”) and El Abeto (AB, 30º32’9”, 108 º37’16”) (Figure 3.1). At each study site we established ten permanent plots on a 100 x 100 m sampling grid (N=40 plots) where we sampled tree density, height, basal area, DBH, and species richness. All the sites were on steep north-facing slopes with complex topography. Average slope was 57.2 % (range 4-90 %) and elevation was 2375-2476 meters. Two sites (MP and PS) were inaccessible by road, AB was at the end of a logging road. Rincón de las Tinajas (RT) was along a secondary road but at the time of sampling it had not been logged, apparently due to boundary conflicts with neighboring landowners.

Conifer species that form the overstory in the sampled sites are in the Cupressaceae and Pinaceae. Species in the Cupressaceae were *Juniperus deppeana* Steud. and *Cupressus arizonica* Greene. Species in the Pinaceae were *Abies* sp., *Pinus durangensis* Martínez, *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).

Field methods

We used circular fixed-area plots located at each grid point to obtain data about the structure, composition and age of the overstory. Plots for overstory measurements were 200 m^2 (7.98 m radius). We recorded the species of each tree or snag (for some decaying snags we could only record the genus), and DBH of all live and dead trees and snags >1.3 m tall in each plot. We counted *Robinia neomexicana* as a tree since it reached tree height and was part of the subcanopy. We used increment borers to core all trees >30 cm DBH and a 10% subsample of randomly selected smaller trees in each plot. 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. In review). Two companion studies detail the methods used for the collection of forest structure (Cortés Montaño et al. in review) and fire history data (Fulé et al. In review).

Results

Based on the literature, Thick-billed Parrot nest cavities have been identified primarily in *Pinus arizonica, P. strobiformis, Pseudotsuga menziesii,* and *Populus tremuloides*. The parrots prefer trees >22 m in height and >60 cm DBH (Table 3.1). At least 50% of nests were in snags of these species. One study assessed cavity formation, and found that these were created mostly by woodpeckers. Disturbance factors identified at nesting sites included fire and anthropogenic factors, especially logging (Table 3.1). One study specified a minimum density of snags >60 cm DBH and 15 m height.

The overstory composition of the sampling sites was dominated by *Pinus durangensis*, *P. strobiformis* and *Pseudotsuga menziesii*, which had the highest basal areas. The site with the lowest basal area was MP (26.8 m^2 ha^{-1}), and PS had the highest basal area (43.6 m^2 ha^{-1}), driven by the large *Pseudotsuga menziesii* trees found there (Figure 3.2). The largest trees recorded were *Pseudotsuga menziesii*, followed by *Pinus durangensis* and *P. strobiformis*. Two sites had Pinaceae snags >60 cm DBH: MP (5 snags ha^{-1}) and AB (10 snags ha^{-1}), which are above the recommended minimum of 5 snags ha^{-1} (Table 3.2). The four sites had live *Pinus* spp. and *Pseudotsuga menziesii* >60 cm DBH. 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 AB (1195 trees ha^{-1}), mostly due to the abundance of *Robinia neomexicana*; and lowest at MP (380 trees ha^{-1}).

The oldest trees that we found in the four sites belonged to the three dominant species: *Pinus durangensis, P. strobiformis* and *Pseudotsuga menziesii*. The oldest dateable trees in the sites established in the mid-18th century. However, other trees established even earlier than this date, as shown by three cores that we excluded from the analyses since they could not be dated to pith. These cores belong to two *Pseudotsuga menziesii* (from PS) and one *Pinus durangensis* (from AB), with the following inner ring dates: 1735, 1747 and 1766. Mesa Prieta Sur (MP) was the only site that showed continuous and even recruitment in the 19th century. Recruitment in the early 20th century occurred in PS and RT, and all sites showed a pulse of recruitment starting at or after the 1950s. Few broadleaved trees established in the period 1750-1900

A.D., but they showed a pulse of recruitment in the late 1990s and early 2000s (Cortés Montaño et al. in review).

Reconstructed fire histories showed similar patterns across the four sites before the mid-20th century (Figure 3.3). In this period, fires were frequent with mean fire intervals <10 years (Fulé et al. In review). After an extended fire-free period of ~50 years, in the 20th century, all sites burnt at least once from 1989 to the present. The period from 1950-2000 had statistically significantly fewer fires than the other periods (t=3.33, d.f.=19, p<0.01). Only RT experienced a relatively consistent fire frequency up to the present (Fulé et al. In review).

Discussion

Detailed knowledge of Thick-billed Parrot habitat requirements throughout their annual cycle is required for conservation of existing populations. Information is also needed to guide reintroduction efforts and successful establishment of viable populations within their former range. This parrot species requires sufficiently large-diameter trees for nest cavities and reliable conifer seed crops. Our forest attribute data can be used to inform management for conservation and restoration of old-growth nesting habitat for Thick-billed Parrots.

Snag density in two of the four study sites in Mesa de las Guacamayas was below the recommended levels of 5 snags >60 cm DBH and 15 m height ha^{-1} (Monterrubio-Rico and Enkerlin-Hoeflich 2004a). Snags with these characteristics were found only at MP and AB. However, all sites had densities of live trees >60 cm DBH and 15 m height ranging between 10 and 55 trees ha^{-1}. These represent a potential source for future large snag recruitment. Large trees are preferentially targeted for harvest in the region, and thus the combination of large living and dead trees that support Thick-billed Parrots at these study sites is uncommon. The forests of Mesa de las Guacamayas play an important role as habitat for this endangered species, and host a potential source population for translocation efforts. However, the effects of human activities have decreased their potential use for nesting and breeding.

Monterrubio-Rico and Enkerlin-Hoeflich (2004a) noted that during their study the use of *Pinus* spp. and snags for nesting had decreased significantly as compared to historical records. They attributed this to the effects of industrial logging practices that target those species and remove snags. Therefore, the use of snags of *Pseudotsuga menziesii* and *Populus tremuloides* by Thick-billed Parrots (Monterrubio-Rico et al. 2006) may be opportunistic. This could be due to higher abundances of large fast-growing *Pseudotsuga menziesii* following logging of *Pinus* spp. However, use of *Populus tremuloides* for nest cavities, sometimes at high densities (Monterrubio-Rico et al. 2006), could be more limited in modern times. This could be a result of altered fire regimes, drought, and impacts by ungulate populations that have limited aspen regeneration in other areas of North America (Ripple and Larsen 2001, Hessl and Graumlich 2002).

Thick-billed Parrots have fairly broad behavioral plasticity for selection of nest tree species, as long as the tree has a diameter adequately broad for a nest cavity and is tall enough for the preferred entrance height. This is shown by the diversity of tree species used for nesting, as well as the fluctuation of nest establishment as the available habitat changes. Since species such as aspen do not provide a food source, aspen stands must be located within or near forests that provide seed crops. Future research should determine maximum foraging distances between nest sites and food sources.

Thick-billed Parrots certainly rely on *Pinus* and occasionally *Quercus* species for food. Synchronized foraging requires low seasonal variation in crop food supply. However, it remains unclear how they contend with phenological variation in the annual supply of these crops and what is the most beneficial habitat composition of these species. Other bird species have developed adaptive strategies for coping with the extreme spatial and temporal variation in food resources driven by conifer phenology (Bock and Lepthien 1976). Eruptive migration allows large groups of birds to track cone crops across great geographic expanses (Koenig and Knops 2001). Cone abundance modulates the onset of breeding activity rather than photoperiod in opportunistic breeding (Hahn 1998).

The landscape of Mesa de las Guacamayas should be protected by a suite of legal instruments that restrict logging and foster sound forest management practices. Forests should be allowed to achieve the structural characteristics needed by Thick-billed Parrots. Old-growth stands should be protected and large live tree and snag densities in core use areas should be maintained through active management practices.

Management should also incorporate maintenance of frequent surface fires. Three of the sampled sites experienced a 25-50% decline in fire frequency between the 19th and 20th centuries, while only one maintained it. Maintenance or restoration of a high-frequency, low-severity fire regime should be part of local and regional forest management plans and strategies to foster nesting and foraging habitat for Thick-billed Parrot populations. A landscape-level analysis should be undertaken to identify sites that should be preserved in their current state as well as sites that could be set aside as reserves that over time would be allowed to acquire old-growth characteristics. The Thick-billed Parrots could become a flagship species to convey the message of the importance of integrated landscape and fire management and the importance of maintaining old-growth forests in northwestern México.

References

Bock, C. E., and L. W. Lepthien. 1976. Geographical Ecology of the Common Species of Buteo and Parabuteo Wintering in North America. The Condor **78**:554-557.

CITES. 2011. CITES species database.

Cortés Montaño, C., P. Z. Fulé, D. A. Falk, J. Villanueva-Díaz, and L. L. Yocom. in review. Linking old-growth forest composition and structure to fire history and climate in northwestern México.

Cruz Romo, J. L., I. Cruz Molina, and M. Prado Lallande. 2010. Programa de acción para la conservación de las especies. Cotorras Serranas (*Rhynchopsitta* spp.).*in* CONANP, editor. SEMARNAT, México, D.F.

CSM. N.A. Estaciones climatológicas del sistema CLICOM. Comisión Nacional del Agua, Subdirección General Técnica, Coordinación del Servicio Meteorológico.

Ferrari, L., M. Valencia-Moreno, and S. Bryan. 2007. Magmatism and tectonics of the Sierra Madre Occidental and its relation with the evolution of the western margin of North America. Geology of México: Celebrating the Centenary of the Geological Society of México: Geological Society of America Special Paper 422:1-39.

Fulé, P. Z., L. L. Yocom, C. Cortés Montaño, D. A. Falk, J. Cerano Paredes, and J. Villanueva Díaz. In review. Testing a pyroclimatic hypothesis on the México-U.S. border.

Hahn, T. P. 1998. Reproductive seasonality in an opportunistic breeder, the red crossbill, *Loxia curvirostra*. Ecology **79**:2365-2375.

Hessl, A. E., and L. J. Graumlich. 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (Populus tremuloides) age structures in western Wyoming. Journal of Biogeography **29**:889-902.

Lammertink, J. M., J. A. Rojas-Tome, F. M. Casillas-Orona, and R. L. Otto. 1998. Situación y conservación de los bosques antiguos de pino-encino de la Sierra Madre Occidental y sus aves endémicas. Consejo Internacional para la Preservación de las Aves, Sección Mexicana, México, D.F.

Lanning, D. V., and J. T. Shiflett. 1983. Nesting Ecology of Thick-Billed Parrots. The Condor **85**:66-73.

Leopold, A. 1937. The Thick-Billed Parrot in Chihuahua. The Condor **39**:9-10.

Monterrubio-Rico, T., and E. Enkerlin-Hoeflich. 2004a. Present Use and Characteristics of Thick-Billed Parrot Nest Sites in Northwestern Mexico. Journal of Field Ornithology **75**:96-103.

Monterrubio-Rico, T. C., J. Cruz-Nieto, E. Enkerlin-Hoeflich, D. Venegas-Holguin, L. Tellez-Garcia, and C. Marin-Togo. 2006. Gregarious nesting behavior of Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) in aspen stands. The Wilson Journal of Ornithology **118**:237-243.

Monterrubio-Rico, T. C., and E. Enkerlin-Hoeflich. 2004b. Variación anual en la actividad de anidación y productividad de la cotorra serrana occidental (*Rhynchopsitta pachyrhyncha*). Anales del Instituto de Biología. Universidad Nacional Autónoma de México. Serie Zoología **75**:341-354.

Monterrubio-Rico, T. C., and P. Escalante-Pliego. 2006. Richness, distribution and conservation status of cavity nesting birds in Mexico. Biological Conservation **128**:67-78.

Monterrubio, T., E. Enkerlin-Hoeflich, and R. B. Hamilton. 2002. Productivity and nesting success of Thick-billed Parrots. Condor **104**:788-794.

Palomares Peña, N. G. 1991. Propietarios Norteamericanos y Reforma Agraria en Chihuahua, 1917-1942. Universidad Autónoma de Ciudad Juárez, Cd. Juárez, Chihuahua, México.

Ripple, W. J., and E. J. Larsen. 2001. The Role of Postfire Coarse Woody Debris in Aspen Regeneration. Western Journal of Applied Forestry **16**:61-64.

Snyder, N. F. R., E. Enkerlin-Hoeflich, and M. A. Cruz Nieto. 2011. Birds of North America online - Thick-billed Parrot (Issue no. 406).

Snyder, N. F. R., W. D. Koenig, and T. B. Johnson. 1994. Ecological relationships of the Thick-billed Parrots with the pine forests of southeastern Arizona. Pages 288-293 *in* Biodiversity and the management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. U.S.F.S. General Technical Report RM-GTR-264, Tucson, AZ.

Unidad Forestal Casas Grandes-Babícora, A. C. 1999. Programa de manejo forestal para aprovechamiento de recursos forestales maderables persistente, ejido 5 de Mayo, municipio de Janos, Chihuahua. Chihuahua, Chih.

Wetmore, A. 1935. The Thick-Billed Parrot in Southern Arizona. The Condor **37**:18-21.

Table 3.1. Summary of factors quantified in studies of Thick-billed Parrot nesting habitat in Northern Mexico. Average values bolded, ranges in parentheses. *Pinus strobiformis* Engelm. is synonymous with *P. ayacahuite* var. *brachyptera* Shaw.

				Authors					
	Lanning and Shiftlett (1983)			**Monterrubio-Rico and Enkerlin-Hoeflich (2004)**			**Monterrubio-Rico et al. (2006)**		
Study sites	17 sites in Chihuahua and Durango	Lat N	Long W		Lat N	Long W		Lat N	Long W
		30° 20’	108° 30’	Mesa de las Guacamayas	30°33’	108°36’	Madera	29°19’	108°11’
		20° 0’	105° 30’	Madera	29°19’	108°11’			
				Cebadillas de Yahuirachi	28°37’	108°14’			
				Piceas	28°37’	108°13’			
				Vallecillo	28°30’	108°04’			
				San Juanito	28°07’	107°57’			
Total nests	55			187			147		
Nest tree species (%)	76.3	*Pinus arizonica* and *P. strobiformis*		32.6	*Pseudotsuga menziesii*		97.6	*Populus tremuloides*	
	16.4	*Populus tremuloides*		21.9	*P. strobiformis*		2.4	*Pinus strobiformis*	
	7.3	*Pseudotsuga menziesii*		18.7	*Populus tremuloides*				
Nests in snags (%)	63.6			58.8			49.7		
Nests in live trees (%)	36.4			41.2			51.3		
Snags with no bark (%)	NA			NA			25		
Nest tree height (m)	**22.1** (12-35)			22.8 (10-38)			26.3 ± 6		
Nest entrance height (m)	**17.1** (8-28)			18.2 (8-30)			(6.5-31)		
Site disturbance	Fire			Fire, logging, human residence			NA		
Nest tree DBH (cm)	**69.5** (43-115)			**75.2** (30-143)			**57** ± 12		
Nest cavity creation	NA			NA			86% Woodpecker holes 14% natural cavities		
Snag density				5 ha^{-1}					

Table 3.2. Snag and tree density (number of snags or trees ha^{-1}) per DBH class with suitable characteristics (>60 cm DBH and >15 m height) for Thick-billed Parrot nesting by site. Site names are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB). Species names and codes are *Pinus durangensis* (PIDU), *Pinus strobiformis* (PIST), *Pseudotsuga menziesii* (PSME).

		DBH class (cm)			
Site		**60-70**	**70-80**	**>80**	**Total**
MP	Snags	0	0	5	5
	PIDU	5	0	5	10
	PIST	25	10	0	35
	PSME	10	0	5	15
PS	Snags	0	0	0	0
	PIDU	5	10	10	25
	PIST	0	0	0	0
	PSME	25	10	20	55
RT	Snags	0	0	0	0
	PIDU	30	5	5	40
	PIST	0	0	0	0
	PSME	0	0	0	0
AB	Snags	5	5	0	10
	PIDU	15	0	5	20
	PIST	0	0	5	5
	PSME	5	0	20	25

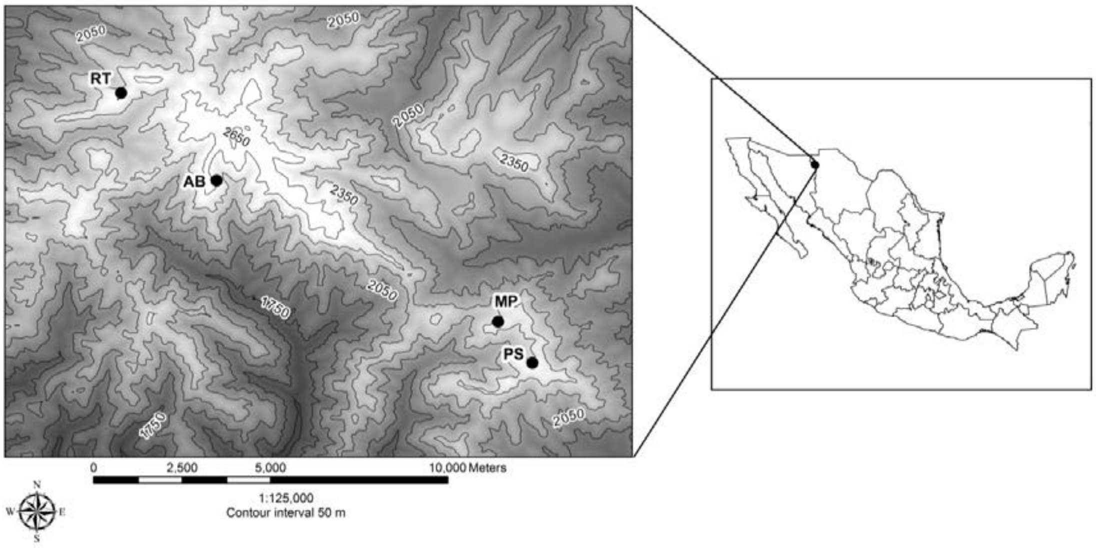

Figure 3.1 Location of the study area in the state of Chihuahua, México. Site names are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB).

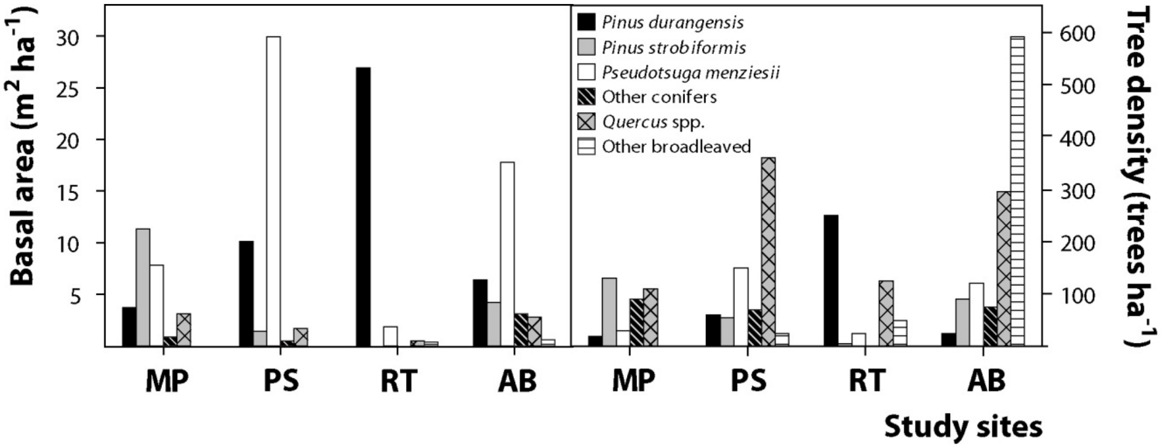

Figure 3.2. Tree basal area (m^2 ha^{-1}) and tree density (trees ha^{-1}) per site. Site names as in Figure 3.1. Species codes are *Pinus durangensis* (PIDU), *Pinus strobiformis* (PIST), *Pseudotsuga menziesii* (PSME), other conifer species (OTH CON), *Quercus* spp. (QUERCUS), and other broadleaved species (OTH BL).

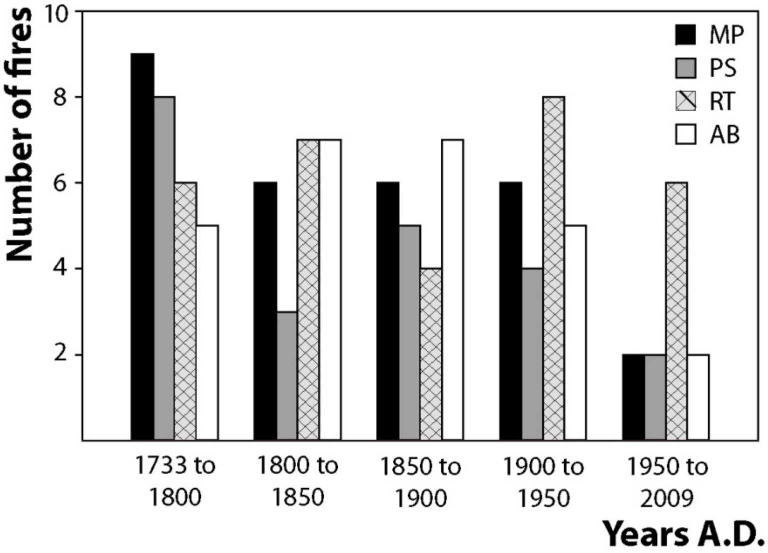

Figure 3.3. Number of fires that scarred >25% of samples during five 50-year periods at four sites in Mesa de las Guacamayas, México. Site names as in Figure 3.1.

Chapter 4

High β-diversity in the understory vegetation of remnant old-growth forests in northwestern México

Abstract

The Sierra Madre Occidental contains México's largest area of temperate forests. These include old-growth relicts in which frequent fire is a driver of ecological processes. We identified four old-growth relicts and studied their composition and the relationships with the overstory and fire histories.

Questions

1. Is there high β-diversity across four old-growth sites with similar geographic settings?
2. What are the effects of the composition, cover and density of the overstory, as well as the fire histories at each site, on the understory plant communities?

Location

Mesa de las Guacamayas, Chihuahua, México.

Methods

We collected understory composition and aerial cover data in previously established permanent plots in four old-growth sites. Companion studies document overstory composition and structure data, as well as fire histories at the same location. We calculated species richness and diversity at the plot and site level, and used non metric multidimensional scaling to assess patterns in understory community composition. We tested for differences among the understory communities at all sites

and between pairs of sites with permutational analysis of variance. We fitted regression models to assess relationships between understory, overstory, and site variables.

Results

We compiled a preliminary flowering plant list that included 102 species in 39 families. Asteraceae (25), Fabaceae (12), Poaceae (8) and Lamiaceae (5) had the highest number of species. Five families had three species and eight families had two species; 59% had one species. A new species of *Erigeron* (Asteraceae) was described from our collections. The understory of each site formed distinct groups in the ordinations, and the ordination axes were highly correlated to fire histories. β-diversity was different for most pairs of sites and regression models showed negative effects of fire frequency on richness and diversity, tree density was an important predictor of aerial cover.

Conclusions

We generated the first dataset of understory composition in old-growth sites with relatively well-preserved fire regimes in four sites in northwestern México. We showed that there are close interactions between understory and overstory and fire regimes in these old-growth forests, and that their effects appeared to change depending on the level of analysis (plot or site). The composition of the understory at these sites did not include non-native species, even after a >50 year fire interruption in three sites. This suggests that β-diversity and frequent fires, maintained over at least 250 years, could play a shielding role in preventing invasions.

Nomenclature

Species names follow the nomenclature and authorship listed in The International Plant Names Index (http://www.ipni.org).

Introduction

Old-growth forests are declining worldwide (Wirth 2009), despite efforts that document their biological and ecological importance from multiple perspectives. Two recent books (Spies and Duncan 2009, Wirth et al. 2009) provide summaries of regional and global status of scientific research and policy issues involving these systems. For example, old-growth forests are valuable sources of information about long-term ecological dynamics (Foster et al. 1996). Thus, they can be used as references to evaluate the effects of management or disturbance (D'Amato et al. 2009, Wyatt and Silman 2010), or to set management, restoration and conservation goals (Burrascano et al. 2009).

Old-growth forests are among the most threatened ecosystems by human-induced changes in northwestern México (Lammertink et al. 1998). However, some remnants can still be found in remote sites of the Sierra Madre Occidental (SMOc), the longest mountain range in México (Ferrari et al. 2007). These mountains span ~1200 km in a NW-SE direction from the international border with the U.S. Their width varies from 200 to 400 km (Ferrari et al. 2007), and are considered a biodiversity hotspot that supports numerous ecosystems (Felger et al. 1997). However, challenging work conditions, such as poor access, rugged terrain, insecurity, drug cultivation and trafficking, have historically deterred their exploration and study.

Given the broad variation in the use of the term understory, in this paper we use it to refer to the group of vascular plants formed of forbs, grasses, sedges and shrubs that don’t reach the subcanopy. The highest concentration of species in a forest usually resides in the understory (Gilliam 2007), a stratum that is remarkably rich in montane forests of México (Challenger 1998). Highly diversified genera in these forests include

Castilleja and *Eryngium* (50 species each), *Muhlenbergia* (52 species), *Sedum* (60 species), *Stevia* (90 species) and *Salvia* (312 species) (Challenger 1998). These numbers are likely to increase with botanical explorations.

The temperate forests of the SMOc have the highest rate of vascular plant endemism (70%) of all vegetation types in México (Felger et al. 1997). While it is known that plant richness and diversity is concentrated in the understory of these forests (Challenger 1998), information about the floristics and ecology of this stratum is especially limited. Vegetation studies in temperate forests of the SMOc have focused on overstory dynamics (for example, Fulé and Covington 1998, Fulé et al. 2005, Fulé et al. 2011), or the taxonomy and distribution of tree species (for example, Márquez-Linares and González-Elizondo 1998, González-Elizondo et al. 2011, Gugger et al. 2011).

Historical evidence has shown that fire plays an important role in these forests (Heyerdahl and Alvarado 2003, Fulé et al. 2005, Fulé et al. 2011). In some sites of the SMOc, fire frequencies have maintained historical patterns (Fulé et al. 2011, Fulé et al. In review). This is of high ecological relevance, since it has been documented for few dry temperate forests in North America, mostly due to the successful implementation of fire-suppression policies, extensive grazing and logging (Stephens and Fulé 2005). Despite the relevance of fire as an ecological driver across this mountain range, there are no published studies that document the relations between fire histories, understory species composition, diversity, and cover.

The diversity of plant species in the understory of old-growth forests has been studied from different perspectives. Many studies in the U.S. Southwest emphasize the differences in understory communities of temperate forests following restoration treatments. These consist mostly of thinning and burning following >100 years of regional-level fire supression (for example, Huisinga et al. 2005, Laughlin et al. 2008, Stoddard et al. 2011). One study reported the effect of fire on the understory in old-growth remnants with maintained fire regimes (Laughlin and Grace 2006). It appears that frequent fires in these dry temperate systems are a driver of understory species richness (Laughlin et al. 2005, Laughlin and Grace 2006). Frequent fires also appear negatively related to ponderosa pine basal area and positively related to oak basal area (Laughlin et al. 2005, Laughlin and Grace 2006).

Species diversity implies relationships between richness and frequencies. Two communities with the same number of species but unequal frequencies will have different diversity values. Diversity is commonly measured as the number of incidences of a species' occurrence across the set of plots that comprise the sampled community (Magurran 2004). The spatial distribution of species diversity is commonly expressed through three scales. α–diversity is a measure of similarity within a basic spatial unit, such as a plot or sampling point, β-diversity indicates the heterogeneity among those basic units, and γ-diversity indicates diversity at the landscape level (Whittaker 1972, Jost et al. 2010).

Ecologists have developed different indices to measure diversity, but Shannon's Diversity Index (H') is recommended to make comparisons among communities (Jost et al. 2010). Through a simple mathematical transformation, this Index can be expressed as an “effective number of species” that has a linear relation to species richness. This number represents the species richness found in a perfectly even community—where richness = abundance—with the same diversity index as that of the original community (Jost et al. 2010).

The role of species diversity in a community or an ecosystem is still debated among ecologists (e.g. Walker et al. 1999, Tilman 2004, Boeken and Shachak 2006). However, information about species presence and abundance in a given area is a valuable input for conservation planning (Kessler et al. 2009, Jost et al. 2010) or to assess the performance of established protected areas (Shackleton 2000).

The study of old-growth sites with fire frequencies that maintain historical patterns in the SMOc can provide useful information to managers of forests that have undergone fire cessation (Stephens and Fulé 2005). We present the results of a study conducted in Mesa de las Guacamayas (MDG), a mountain with several remnant old-growth forests located at the northern end of the SMOc.

The goal of this study was to examine the variability in the composition of the understory plant communities in four old-growth remnants, their interactions with the overstory, and the role of fire frequency as a regulator of understory plant communities through the following questions:

1. Is there high β-diversity across four old-growth sites with similar geographic settings?
2. What are the effects of the composition, cover and density of the overstory, as well as the fire histories at each site, on the understory plant communities?

Methods

Location

The study sites were in Mesa de las Guacamayas (MDG), a mountain range at the northern end of the SMOc, in the communal holdings of Ejido 5 de Mayo, in northwestern Chihuahua, México (Figure 4.1). Due to the remoteness of the site, only one family lives there year round. Records of logging in the study area are scarce, but at least one sawmill was established and operated in the area in the 1960s and until ejido formation in 1972 (Campos pers. comm.). Following this event, commercial logging continued as recently as the late 1990s. Currently, the most prevalent land use in the mountain is light grazing by cattle and equines. There are no records for grazing in the area, but visual assessment suggests that current impacts from this disturbance are light.

The regional geology of the study site is predominantly formed of rhyolitic ignimbrites (Ferrari et al. 2007). Phaeozems and Regosols are the dominant soil types, with Lithosols present in small pockets (Unidad Forestal Casas Grandes-Babícora 1999). Weather information for the region is incomplete; the closest weather station is in Guapoca, ~90 km SE of the site at an altitude of 1260 m. The Guapoca station records show that annual precipitation in the period 1961-1998 was on average 704.91 mm. Mean annual temperature was 15.9°C, with a mean minimum of 6.3°C and a mean maximum of 25.6°C (CSM N.A.).

Field methods

In June 2009 we established a grid of 40 permanent plots in old-growth stands of at least 12 ha dominated by pines (*Pinus* spp.) and Douglas-firs (*Pseudotsuga menziesii* (Franco). The four sites were: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB) (Figure 4.1). At each study site we established ten plots on a 100 x 100 m sampling grid (N=40 plots). The sites were located on steep, north-facing slopes with similar elevations (Table 4.1). We used circular fixed-area plots of 200 m^2 (7.98 m radius) to characterize the overstory, used planar transects to measure fuels, and recorded understory species presence. Each plot center was permanently marked. Two companion studies detail the methods used for the collection of forest structure (Cortés Montaño et al. in review) and fire history data (Fulé et al. In review).

The overstory at RT was mostly formed by *Pinus durangensis* (Martínez). The dominant species at MP, PS and AB were *P strobiformis* (Engelm.) and *Pseudotsuga menziesii* (Franco). The subcanopy was formed of seven *Quercus* species and three broadleaved species at the four sites, with *Cupressus arizonica* (Greene) at MP and AB, and *Juniperus deppeana* (Steud.) at PS. Appendix 4.1 presents a preliminary plant list of the overstory and understory species for MDG, based on our collections from these study sites. The fire histories show fires occurring at intervals of <10 years for at least 250 years until the 1950s at the four sampling sites. A fire-free period then started at MP, PS and AB , but subsequent fires burnt the four sites in the late 1990s and in this century (Fulé et al. In review).

To assess aerial understory cover, we established four 1 m^2 subplots (0.5 x 2 m) at the end of radial lines of the overstory plots (at 7.98 m) in each cardinal direction. We were unable to locate one of the overstory plots, so for the understory datasets N=39. We collected the overstory data in June 2009 and the understory data in early September 2009, in order to capture the most species with summer flowering/fructification. We collected specimens for all flowering and cone-bearing plants in the four sites and deposited a full set of our collections (M. L. Joe and C. Cortés 2009) at ASC, the Deaver Herbarium of Northern Arizona University.

Most collections were identified at ASC, but specimens from challenging taxa (such as Asteraceae, Cyperaceae, Ericaceae, Fabaceae, Poaceae and *Castilleja* (Scrophulariaceae)) were sent to other herbaria for identification or verification. When identification at the species level was not possible we grouped specimens by morphotype. We used a checklist of plants for the state of Sonora (Van Devender et al. 2010) and the USDA Plants website (http://plants.usda.gov/java/) to identify exotic or invasive species.

Species richness and β-diversity

Since the sampling sites were spatially separated, we treated each as a different community in the β-diversity calculations. Henceforth, we will use the word community to refer to a study site. In order to assess the species richness and diversity for each community, we calculated total species number and Shannon's Diversity Index (H') (Magurran 2004). We converted all H' into effective species numbers with the formula $e^{H'}$ (Jost et al. 2010). To assess the statistical significance of differences in H' for community pairs we used Hutcheson's *t*-test for H' (Hutcheson 1970). Since we estimated H' for each community, this was effectively a comparison of the statistical significance of β-diversity indices between pairs of communities.

Sampling incompleteness can be a problem in areas with high biodiversity (Kessler et al. 2009). In order to assess sample coverage at each site, and to generate estimators for species richness (ACE, Abundance-based Coverage Estimator) and H' (Chao & Shen estimator), we used the program SPADE (Chao and Shen 2010). These estimators assume that rare species were missed at the time of sampling. We compared calculated richness and diversity to the estimators generated for each sampling site.

To assess the differences in communities expressed by species richness and cover we used two datasets (presence-absence and % aerial cover) for community analyses. We used methods robust to non-normally distributed multivariate datasets since both datasets clearly showed non-normal distributions. We deleted species occurring in <5%

of all the overstory plots (N=39). Total species in the datasets were 89 for the presence-absence dataset and 67 for the % aerial cover dataset.

In order to create a visual description of the spread of plots in species space we used Non Metric Multidimensional Scaling (NMDS). This is the primary method recommended for analysis of non-normal ecological multivariate community datasets (McCune and Grace 2002). We created a distance matrix using Sørensen similarity indices, and used the NMDS function in PC-ORD (McCune and Mefford 2006) to produce ordinations with the presence-absence and aerial cover datasets. The seed number was 1972, and we carried-out 250 runs with the real data and 250 Monte Carlo randomized runs to ensure that the axes extracted by the ordinations were not a result of chance.

To associate the NMDS ordinations to environmental variables, we used a second matrix with physical variables (elevation, slope, and heat loads) and overstory information (basal area, tree density, number of fires in the past 60 years with 25% and 10% filters, fine fuel and coarse woody debris loads). When there are strong correlations (>0.45) between the ordinations and the data included in the second matrix, a vector overlay shows in the ordination graphic.

We converted the azimuth values into heat loads using Equation 2 described by McCune and Keon (2002). We separated cover and density of trees by dominant overstory species, since these have been shown to have different relations to the understory in dry pine forests of the U.S. Southwest (Laughlin and Grace 2006). We used the 60 year cutoff since all sites had similar fire frequencies until MP, PS and RT showed a gap starting >50 years ago and ending in the early 2000s. Since fire intensity can have different effects at the site-level and thus affect the understory in different forms, we used two filters for fire frequency (10% and 25%), which represent more, smaller fires and fewer, larger fires, respectively. We calculated fine fuel and coarse woody debris loads in Mg ha^{-1}for 1, 10, 100 and 1000-hr timelags. We used the species with highest Pearson's *r* correlation coefficients to analyze the relations among species and the ordination axes (Table 4.2).

Since the NMDS graphics displayed group segregation (Figure 4.2), we used permutational ANOVA (PERMANOVA, Anderson 2001) to test for significance in differences in the composition of the understory among all sites with both the presence-absence and aerial cover datasets. We used the PERMANOVA function in the vegan package (Oksanen et al. 2011) for R (R Core Development Team 2010). This multivariate test is analog to univariate ANOVA but it is robust to datasets with non-normal distributions. Its test statistic is a pseudo-F calculated through permutations. The pseudo-F is used as a test statistic under an H_0 that the data do not respond to a particular grouping effect, such as treatment or site (Anderson 2001). We estimated *p*-values using 9999 permutations, which is above the minimum 5000 recommended for $\alpha < 0.01$ (Anderson 2001). The overall PERMANOVA showed statistically significant differences in species composition among the four sites. Hence, we conducted paired PERMANOVA tests to assess the significance on differences in composition between all site pairs.

Assessing overstory and understory relationships

We looked in the literature for relevant regression models produced for similar forests in the U.S. Southwest (Laughlin et al. 2005, Laughlin et al. 2008). Then, we identified variables in our dataset that had been shown as significant predictors of understory diversity and richness. We used scatterplots to examine the associations between dependent and independent variables in our dataset. We used three dependent variables: species richness, diversity (expressed by site H' values) and aerial cover to create simple and multiple regression models. If the independent variables were correlated (>0.5 Pearson's *r*) we retained only one to reduce collinearity issues. We selected the best model for each dependent variable based on the statistical significance of the adjusted R^2 coefficient with $p<0.05$.

Results

Species richness and β-diversity

We recorded 102 flowering plant species (90 species and 12 morphotypes) distributed in 39 families. Our collections did not include exotic species. Families with the highest number of species were Asteraceae (25), Fabaceae (12), Poaceae (8) and Lamiaceae (5) (Table 4.3). There were five families with three species and eight families with two species, 59% of families had one species. Eight families were exclusive to one sampling site (Anacardiaceae, Asclepiadaceae, Caprifoliaceae, Celastraceae, Cucurbitaceae, Orchidaceae, Polemoniaceae and Saxifragaceae). *Erigeron nitens* (Asteraceae), an endemic with a narrow distribution, was described from our collections (Nesom 2010). A preliminary plant list for MDG is included as Appendix 4.1.

Sampling coverage was estimated at ~90% for all sites. Species richness was highest at AB, followed by PS, MP and RT. Highest diversity, expressed by H' was at PS and AB, followed by RT and MP (Table 4.4). Paired comparisons of H' showed that β-diversity was statistically significant for most site pairs ($p<0.05$), except for RT-MP and AB-PS. Values of H' obtained with the data were close to or at the lower limit of the

95% confidence intervals for the richness and diversity estimators obtained with SPADE (Table 4.4).

The final configuration of the NMDS ordination based on the frequency (presence-absence) data was achieved with final stress=16.884 and instability=0.004. It had three axes that explained 82.2% of the total variation (Axis 1=35.7%, Axis 2=21.6% and Axis 3=24.9%) (Figure 4.2). The vector overlay showed all variables with a Pearson's *r* correlation >|0.45|. Axis 3 was correlated with the number of fires in the past 60 years with both the 10% and the 25% filters. We rotated the ordination 3° to the right to align the vectors to Axis 3.

The NMDS ordination based on aerial cover had three axes that explained 63.3% of the total variation (Axis 1=21.3%, Axis 2=11.5% and Axis 3=30.5%) (Figure 4.2). The final stress was 16.581 and the instability was 0. The vector overlay for the cover ordination showed that Axis 3 had Pearson's *r* correlation >|0.45| to fires in the past 60 years based on both the 10% and 25% filters. Neither ordination showed correlations between Axis 1 and the variables included in the secondary matrix. Highest correlation values of species to the ordination axes are included in Table 4.2. Results of all paired PERMANOVA tests for both datasets showed that the understory communities in the four sites were significantly different (Table 4.4).

Relationships between understory and overstory

The regression model that was statistically significant and had the highest explanatory power (adjusted $R^2 = 0.37$, $p<0.005$) for species richness included elevation and all fires recorded with the 25 % filter (Table 4.5). Scatterplots showed negative associations among these independent variables and the dependent variable. The model for species diversity (H') with highest explanatory power (adjusted $R^2=0.19$, $p<0.005$)

incorporated the number of fires in the past 60 years with the 10% filter, showing a negative association between these two variables. We did not use *Pinus durangensis* cover and density in our regression models to avoid collinearity with the fire regime. Variability in cover was best explained by a model that included the density of *Pinus durangensis*, *Pseudotsuga menziesii*, and *Quercus* spp. (adjusted $R^2=0.28$, $p<0.005$).

Discussion

Is there high β-diversity across four old-growth sites with similar geographic settings?

Our results showed that site-level understory species richness and β-diversity patterns at the four old-growth sites in MDG were high. All sites had statistically significantly different understory plant communities despite having relatively homogenous environmental conditions (elevation, orientation, slope, fire histories and overstory composition). β-diversity was statistically significantly different among most pairs of sites, despite their relative proximity, which further shows that the understory communities had different species composition.

The combination of families of tropical and temperate affinities at MDG is typical of montane forests in the SMOc, which is a key factor explaining their rich biodiversity (Felger et al. 1997). The species richness values for the four sampling sites were all below or near the lower end of the confidence intervals generated for the richness and diversity estimators. This indicates that increasing the number of sampling sites, sampling throughout the growing season and including non-flowering vascular plants in MDG would likely result in added species to the preliminary list compiled through this study. The ordinations showed that RT and AB were the most divergent communities, which in the case of RT could be associated with its different overstory composition and ongoing fire regime.

The understory species richness of the forests of MDG was higher than other temperate forests in North America, especially considering that we sampled only four communities totaling 48 ha. A study conducted at a larger scale in twelve 14 ha sites in ponderosa pine forests of northern Arizona documented 203 understory plant species. These included non-flowering vascular plants and a substantial nonnative component (Stoddard et al. 2011). In old-growth forests of the central Appalachians, 103 species were found in ~30 ha, including woody plants, shrubs, forbs, forbs, grasses and non-flowering plants (McEwan and Muller 2011). Lastly, researchers found 47 plant species, including non-flowering plants, in old-growth forests of Western Massachusetts (D'Amato et al. 2009).

Our collections did not include plants identified as invasive or exotic, suggesting that these are infrequent in the sampling sites. A study conducted in Grand Canyon National Park suggests that absence of roads and logging is key in explaining the absence of exotics following an intense fire (Huisinga et al. 2005), which is likely related to propagule sources and dispersal. Distance to roads and propagule sources and vectors could be a partial explanation to the absence of exotics in the understory plant communities of MDG, as well as niche saturation by the native flora (Tilman 2004). Other factors could be the existence of a pool of native species that could potentially replace extirpated species (Walker et al. 1999) and facilitate recruitment of dominant species (Boeken and Shachak 2006).

There is a strong relation between invasion and intensity of human activities (Qian and Ricklefs 2006), and high species diversity could play an important role in deterring invasions in plant communities (Kennedy et al. 2002). The continuity of ecological processes, such as historically recurrent frequent fires, can also be an important factor in deterring invasions (Laughlin et al. 2008). We hypothesize that multiple factors contribute to the maintained resilience and ecological integrity of the forests of MDG. Among these are the heterogeneity of the richness and diversity of their plant overstory and understory communities, the lack of intensive human activities and their relatively undisturbed fire frequency.

What are the effects of the composition, cover and density of the overstory, as well as the fire histories at each site, on the understory plant communities?

The NMDS graphics for both understory datasets showed similar patterns of plot groupings. The strongest correlation with the vector overlays showed that the number of fires in the past ~60 years were an important driver of the axes of the ordinations. Scatterplots and regression models showed that understory plant richness was negatively correlated with fire, similar to a model proposed for ponderosa pine systems of northern Arizona (Laughlin and Grace 2006). The regression model created with the 25% filter for all fires at the four sites showed that long-term fire histories and elevation had negative associations with species richness at the plot level. The MDG sites show a decrease in species richness as altitude increases, a pattern documented by previous ecological studies (Murphy et al. 2011).

The apparently deleterious effects of fire frequency at the MDG sites need to be examined carefully. Fires appeared to affect species richness and diversity at the plot level, and overall β-diversity values were similar at the site level ($e^{H'}$ values ranged from 49 to 57 species). However, the composition of the sites was different, as shown by the

NMDS graphic and the Hutcheson's *t*-tests for site pairs. Lower $e^{H'}$ values were observed in a site that had an uninterrupted fire regime (RT) and a site that had fire interruption in the past ~60 years (MP). Since the composition of the overstory was very different at RT, it is likely that lower understory diversity reflects different site characteristics not addressed by this study (i.e. nutrient and moisture availability).

Understory species aerial cover was best predicted by the density of *Pinus durangensis*, *Pseudotsuga menziesii* and *Quercus* spp. in the regression models. Fire frequency the ordination graphic showed a fire. Tree density and understory aerial cover were negatively associated. This could reflect competition for resources between the understory and the regeneration and subcanopy strata, which has been identified in dry ponderosa pine forests of northern Arizona (Stoddard et al. 2011).

As far as we know, this is the first report that addresses ecological characteristics and floristics of old-growth forests in the SMOc. It is important to underline the absence of non-native or exotic species in our collections, which could be used as an indicator of the ecological integrity of our sampling sites. At MDG, there appear to be close interactions between the understory, overstory characteristics, and the fire histories of the sampled old-growth relicts. This suggests that plant diversity and fire frequencies maintained over at least 250 years could play a shielding role in preventing invasions, even following a recent >50 year interruption of fire frequencies in three of our sampling sites.

References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**:32-46.

Boeken, B., and M. Shachak. 2006. Linking Community and Ecosystem Processes: The Role of Minor Species. Ecosystems **9**:119-127.

Burrascano, S., L. Rosati, and C. Blasi. 2009. Plant species diversity in Mediterranean old-growth forests: A case study from central Italy. Plant Biosystems **143**:190-200.

Cortés Montaño, C., P. Z. Fulé, D. A. Falk, J. Villanueva-Díaz, and L. L. Yocom. in review. Linking old-growth forest composition and structure to fire history and climate in northwestern México.

CSM. N.A. Estaciones climatológicas del sistema CLICOM. Comisión Nacional del Agua, Subdirección General Técnica, Coordinación del Servicio Meteorológico.

Challenger, A. 1998. Utilización y Conservación de los Ecosistemas Terrestres de México. Pasado, Presente y Futuro. CONABIO, Instituto de Biología-UNAM, Agrupación Sierra Madre, S.C., México, D.F.

Chao, A., and T. J. Shen. 2010. Program SPADE (Species Prediction And Diversity Estimation).

D'Amato, A. W., D. A. Orwig, and D. R. Foster. 2009. Understory vegetation in old-growth and second-growth *Tsuga canadensis* forests in western Massachusetts. Forest Ecology and Management **257**:1043-1052.

Felger, R. S., G. P. Nabhan, and R. Bye. 1997. Apachian/Madrean Region of Southwestern North America, Mexico and USA. Mexico and USA: CPD site MA11. Pages 172-180 *in* S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J.

Villa-Lobos, and A. C. Hamilton, editors. Centres of Plant Diversity, Volume 3: The Americas. WWF, IUCN, National Museum of Natural History-Smithsonian Institution, European Community, ODA, Cambridge, U.K.

Ferrari, L., M. Valencia-Moreno, and S. Bryan. 2007. Magmatism and tectonics of the Sierra Madre Occidental and its relation with the evolution of the western margin of North America. Geology of México: Celebrating the Centenary of the Geological Society of México: Geological Society of America Special Paper 422:1-39.

Foster, D. R., D. A. Orwlg, and J. S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends in ecology & evolution (Personal edition) **11**:419-424.

Fulé, P. Z., and W. W. Covington. 1998. Spatial patterns of Mexican pine-oak forests under different recent fire regimes. Plant Ecology **134**:197-209.

Fulé, P. Z., M. A. Ramos Gómez, C. Cortés Montaño, and A. M. Miller. 2011. Fire regime in a Mexican forest under indigenous resource management. Ecological Applications **21**:764–775.

Fulé, P. Z., J. Villanueva-Díaz, and M. Ramos-Gómez. 2005. Fire regime in a conservation reserve in Chihuahua, Mexico. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:320-330.

Fulé, P. Z., L. L. Yocom, C. Cortés Montaño, D. A. Falk, J. Cerano Paredes, and J. Villanueva Díaz. In review. Testing a pyroclimatic hypothesis on the México-U.S. border.

Gilliam, F. S. 2007. The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. Bioscience **57**:845-858.

González-Elizondo, M., M. S. González-Elizondo, L. Ruacho-González, and M. Molina-Olvera. 2011. *Pinus maximartinezii* Rzed. (Pinaceae), primer registro para Durango, segunda localidad para la especie. Acta Botanica Mexicana **96**:33-48.

Gugger, P. F., A. González-Rodríguez, H. Rodríguez-Correa, S. Sugita, and J. Cavender-Bares. 2011. Southward Pleistocene migration of Douglas-fir into Mexico: phylogeography, ecological niche modeling, and conservation of 'rear edge' populations. New Phytologist **189**:1185-1199.

Heyerdahl, E. K., and E. Alvarado. 2003. Influence of Climate and Land Use on Historical Surface Fires in Pine-Oak Forests, Sierra Madre Occidental, Mexico. Pages 196-217 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. Fire and Climatic Change in Temperate Ecosystems of the Western Americas.

Huisinga, K. D., D. C. Laughlin, P. Z. Fulé, J. D. Springer, and C. M. McGlone. 2005. Effects of an Intense Prescribed Fire on Understory Vegetation in a Mixed Conifer Forest. Journal of the Torrey Botanical Society **132**:590-601.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology **29**:151-154.

Jost, L., P. DeVries, T. Walla, H. Greeney, A. Chao, and C. Ricotta. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions **16**:65-76.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature **417**:636-638.

Kessler, M., S. Abrahamczyk, M. Bos, D. Buchori, D. D. Putra, S. R. Gradstein, P. Höhn, J. Kluge, F. Orend, R. Pitopang, S. Saleh, C. H. Schulze, S. G. Sporn, I. Steffan-Dewenter, S. S. Tjitrosoedirdjo, and T. Tscharntke. 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. Ecological Applications **19**:2142-2156.

Lammertink, J. M., J. A. Rojas-Tome, F. M. Casillas-Orona, and R. L. Otto. 1998. Situación y conservación de los bosques antiguos de pino-encino de la Sierra Madre Occidental y sus aves endémicas. Consejo Internacional para la Preservación de las Aves, Sección Mexicana, México, D.F.

Laughlin, D., J. Bakker, M. Daniels, M. Moore, C. Casey, and J. Springer. 2008. Restoring plant species diversity and community composition in a ponderosa pine-bunchgrass ecosystem. Plant Ecology **197**:139-151.

Laughlin, D. C., J. D. Bakker, and P. Z. Fulé. 2005. Understorey plant community structure in lower montane and subalpine forests, Grand Canyon National Park, USA. Journal of Biogeography **32**:2083-2102.

Laughlin, D. C., and J. B. Grace. 2006. A multivariate model of plant species richness in forested systems: old-growth montane forests with a long history of fire. Oikos **114**:60-70.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford, U.K.

Márquez-Linares, M. A., and M. S. González-Elizondo. 1998. Composición y estructura del estrato arbóreo de un bosque de pino-encino en Durango, México. Agrociencia **32**:413-419.

McCune, B., and J. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science **13**:603-606.

McCune, B., and M. J. Mefford. 2006. PC-ORD. Multivariate analysis of ecological data. MjM Software, Gleneden Beach, Oregon.

McEwan, R., and R. Muller. 2011. Dynamics, diversity, and resource gradient relationships in the herbaceous layer of an old-growth Appalachian forest. Plant Ecology **212**:1179-1191.

Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2011. One, two and three-dimensional geometric constraints and climatic correlates of North American tree species richness. Ecography **34**:267-275.

Nesom, G. L. 2010. A new species of Erigeron (Asteraceae: Astereae) from northwestern Chihuahua, Mexico. Phytoneuron **28**:1-6.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package.

Qian, H., and R. E. Ricklefs. 2006. The role of exotic species in homogenizing the North American flora. Ecology Letters **9**:1293-1298.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Shackleton, C. M. 2000. Comparison of plant diversity in protected and communal lands in the Bushbuckridge lowveld savanna, South Africa. Biological Conservation **94**:273-285.

Spies, T. A., and S. L. Duncan, editors. 2009. Old growth in a new world. A Pacific Northwest icon reexamined. Island Press, Washington, D.C.

Stephens, S. L., and P. Z. Fulé. 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. Journal of Forestry **103**:357-362.

Stoddard, M. T., C. M. McGlone, P. Z. Fulé, D. C. Laughlin, and M. L. Daniels. 2011. Native Plants Dominate Understory Vegetation Following Ponderosa Pine Forest Restoration Treatments. Western North American Naturalist **71**:206-214.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America **101**:10854-10861.

Unidad Forestal Casas Grandes-Babícora, A. C. 1999. Programa de manejo forestal para aprovechamiento de recursos forestales maderables persistente, ejido 5 de Mayo, municipio de Janos, Chihuahua. Chihuahua, Chih.

Van Devender, T. R., R. S. Felger, M. Fishbein, F. E. Molina-Freaner, J. Sánchez-Escalante, and A. L. Reina-Guerrero. 2010. Biodiversidad de las plantas vasculares. Pages 229-262 *in* F. E. Molina Freaner and T. R. Van Devender, editors. Diversidad Biológica de Sonora. UNAM-CONABIO.

Walker, B., A. Kinzig, and J. Langridge. 1999. Plant Attribute Diversity, Resilience, and Ecosystem Function: The Nature and Significance of Dominant and Minor Species. Ecosystems **2**:95-113.

Whittaker, R. H. 1972. Evolution and Measurement of Species Diversity. Taxon **21**:213-251.

Wirth, C., H. Gleixner, and M. Heimann, editors. 2009. Old growth forests. Function, fate and value. Springer Verlag.

Wyatt, J. L., and M. R. Silman. 2010. Centuries-old logging legacy on spatial and temporal patterns in understory herb communities. Forest Ecology and Management **260**:116-124.

Table 4.1. Physical and biological characteristics of the study sites: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB). Mean values are bolded, minimum and maximum are in parentheses. 25% and 10% filters indicate % of samples scarred at each site.

Site	**Lat. (N)**	**Long. (W)**	**Slope (%)**	**Elevation (masl)**	**Fires since 1950 (25% filter)**	**Fires since 1950 (10% filter)**	**Total fires (25% filter)**	**Total fires (10% filter)**
MP	30° 30’	108° 32’	**59.8** (20-72)	**2375** (2250-2550)	2	2	29	35
PS	30° 29’	108° 32’	**46.2** (4-76)	**2409** (2350-2447)	2	2	22	29
RT	30° 33’	108° 38’	**59.4** (26-90)	**2467** (2377-2735)	6	6	31	34
AB	30° 32’’	108° 37’	**63.4** (49-73)	**2476** (2399-2617)	2	3	26	30

Table 4.2. Names and growth habit for species with highest Pearson's *r* correlation coefficients to axes 1 and 3 of the NMDS ordinations based on species richness and aerial cover.

NMDS presence-absence ordination			**NMDS aerial cover ordination**		
Species	**Pearson's *r***	**Growth form**	**Species**	**Pearson's *r***	**Growth form**
		Axis 1 (+ correlations)			
Stevia plummerae var. *plummerae*	0.563	Forb	*Oxalis alpina*	0.486	Forb
Muhlenbergia sp. 4	0.557	Graminoid	*Solidago wrightii* var. *adenophora*	0.477	Forb
Fabaceae sp. 1	0.555	Forb	*Lupinus aschenbornii*	0.421	Forb
Erigeron neomexicanus	0.487	Forb	*Chenopodium graveolens*	0.360	Forb
Viguiera linearis	0.468	Forb	*Vicia pulchella*	0.354	Forb
		Axis 1 (– correlations)			
Thalictrum pinnatum	-0.599	Forb	*Phacelia platycarpa*	-0.314	Forb
Oxalis alpina	-0.487	Forb	*Gentiana microcalyx*	-0.302	Forb
Cyclanthera minima	-0.464	Forb	*Muhlenbergia* sp. 4	-0.279	Graminoid
Panicum bulbosum	-0.417	Graminoid	*Cyperus fendlerianus*	-0.232	Sedge
Baccharis thesioides	-0.408	Forb	*Brickellia grandiflora*	-0.191	Forb
		Axis 3 (+ correlations)			
Bromus anomalus	0.741	Graminoid	*Chimaphila maculata*	0.568	Forb
Chenopodium graveolens	0.638	Forb	*Lupinus aschenbornii*	0.426	Forb
Galinsoga parviflora var. *semicalva*	0.606	Forb	*Roldana pennellii*	0.282	Forb
Verbesina sp. 2	0.527	Forb	*Muhlenbergia* sp. 4	0.237	Graminoid
Artemisia dracunculus	0.519	Shrub	*Viguiera linearis*	0.186	Forb
		Axis 3 (– correlations)			
Chimaphila maculata	-0.623	Forb	*Oxalis alpina*	-0.558	Forb
Castilleja patriotica	-0.605	Forb	*Bromus anomalus*	-0.507	Forb
Galium microphylla	-0.547	Forb	*Lopezia gracilis*	-0.499	Forb
Roldana pennelli	-0.537	Forb	*Solidago wrightii* var. *adenophora*	-0.437	Forb
Stachys coccinea	-0.445	Forb	*Pseudognaphalium macounii*	-0.423	Graminoid

Table 4.3. Families and number of species per family in the four sites (MP, PS, RT and AB) at MDG. Numbers in parentheses indicate number of species in the family exclusive to the site. Total indicates number of species in each family at the four sites.

Family	**MP**	**PS**	**RT**	**AB**	**Total**
Dicotyledons					
Amaranthaceae	1	1	0	0	1
Anacardiaceae	1 (1)	0	0	0	1
Apiaceae	1	1	1	1	1
Asclepiadaceae	0	0	0	1 (1)	1
Asteraceae	16	19	19 (3)	19	25
Boraginaceae	0	0	1	2 (1)	2
Brassicaceae	3	3	1	1	3
Caprifoliaceae	0	0	1 (1)	0	1
Caryophyllaceae	2	2	2	2	2
Celastraceae	0	1 (1)	0	0	1
Chenopodiaceae	1	1	0	1	1
Crassulaceae	1	0	1	1	1
Cucurbitaceae	0	0	0	1 (1)	1
Fabaceae	8	11 (1)	7	8	12
Gentianaceae	1	2	2	2	2
Geraniaceae	1	1	1	1	1
Hydrophyllaceae	1	1	1	1	1
Lamiaceae	4	4	3	5	5
Linaceae	1	1	0	0	1
Onagraceae	2	1	2	2 (1)	3
Oxalidaceae	2	2	1	2	2
Polemoniaceae	0	1 (1)	0	0	1
Polygonaceae	1	1	1	1	1
Pyrolaceae	0	0	1 (1)	0	1
Ranunculaceae	2 (1)	2 (1)	1	1	3
Rhamnaceae	1 (1)	1 (1)	0	3	3
Rosaceae	1	1	1	2 (1)	2
Rubiaceae	2	2	2 (1)	1	3
Saxifragaceae	0	0	1 (1)	0	1
Scrophulariaceae	1	0	2 (1)	1	2
Solanaceae	1	1	1	1	1
Valerianaceae	1	0	0	1	1
Verbenaceae	0	0	0	1 (1)	1
Violaceae	0	0	0	1 (1)	1
Monocotyledons					
Agavaceae	0	0	0	2 (2)	2
Commelinaceae	1	1	1	1	1
Cyperaceae	1	1	1	1	1
Orchidaceae	0	0	1 (1)	0	1
Poaceae	5	8 (2)	6	5	8
Total	63	70	62	72	102

Table 4.4. Species richness (S) of flowering plants in 39 plots (1 plot = 200 m^2), 95% confidence intervals for $\widehat{N}$ estimated with Abundance-based Coverage Estimator. H' is Shannon's Diversity Index and is expressed as effective number of species, $e^{H'}$, 95% confidence intervals for $e^{\widehat{H'}}$ calculated with Chao & Shen's estimator. Average values in bold, standard error in parentheses. Statistical significance of paired PERMANOVA (Bonferroni-corrected α = 0.008) marked with *.

Site	Understory cover (%)	Sample coverage	S	$\hat{S}$	$e^{H'}$	$e^{\widehat{H'}}$	PERMANOVA pseudo-F values		
								Presence-absence	Aerial cover
MP	**5.9** (0.3-18.9)	94%	64	68-92	49	48-60	MP-PS*	3.2	3.9
PS	**11.9** (6-17.8)	95%	71	74-91	57	58-69	MP-RT*	8.4	2.0
RT	**3.8** (1.2-7.8)	89%	63	69-98	50	54-70	MP-AB*	4.6	2.8
AB	**3.5** (0.1-7.9)	90%	73	81-114	57	59-76	PS-RT*	6.4	4.3
							PS-AB*	3.6	6.6
							RT-AB*	3.6	2.3

.

Table 4.5. Regression models for species richness, diversity (H') and aerial cover. Site names as in Table 4.1. Statistical significance at *p*<0.05 indicated with *.

Dataset	**Variables**	**Adjusted R^2**	**F ratio for model**
Richness	All fires with 25 % filter* + Elevation*	0.37	12.1*
Diversity	Fires in the past 60 years with 10% filter*	0.21	10.0*
Aerial Cover	*Pinus durangensis* trees ha^{-1}* + *Pseudotsuga menziesii* trees ha^{-1}* + *Quercus* spp. trees ha^{-1}*	0.28	6.0*

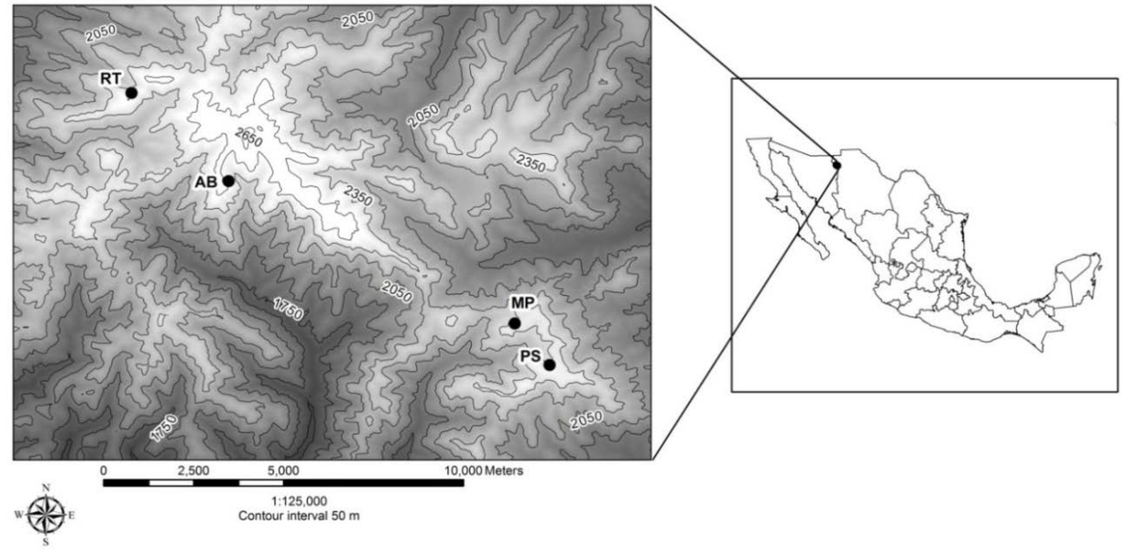

Figure 4.1. Study site location in the state of Chihuahua, México. Site names are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT) and El Abeto (AB).

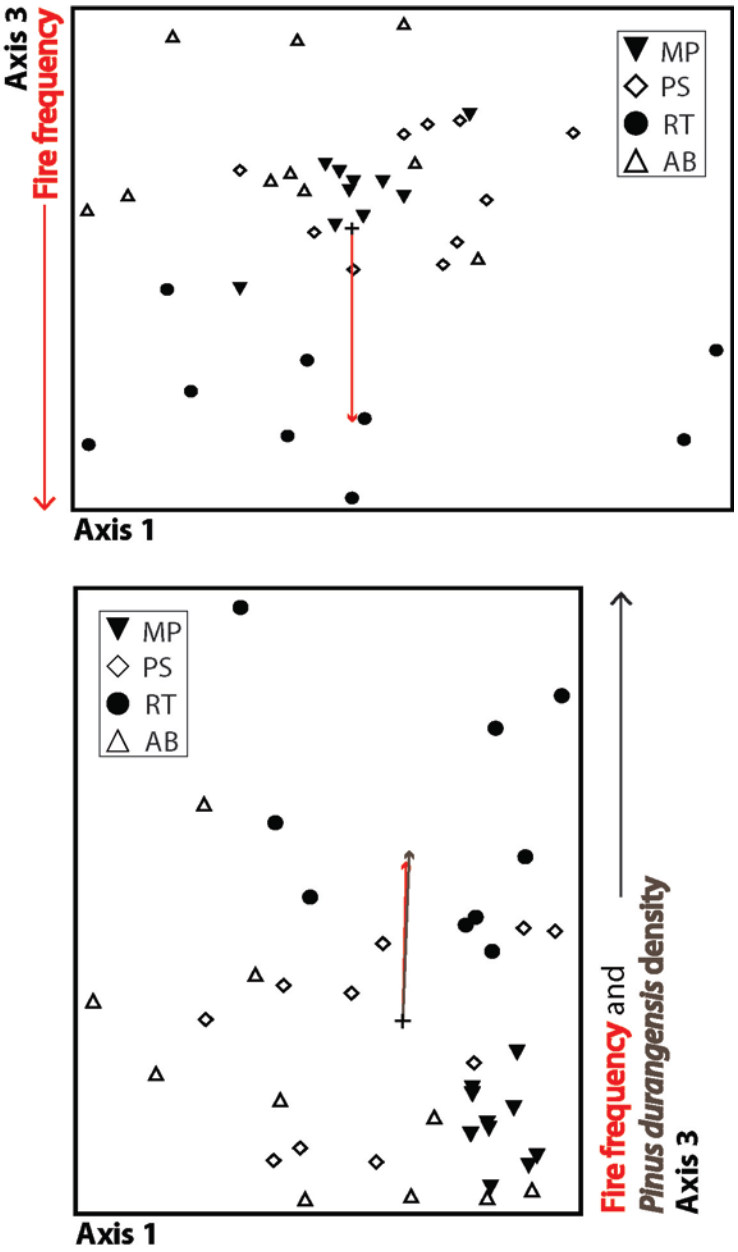

Figure 4.2. Top panel shows NMDS ordination of study sites at MDG based on presence-absence data. Site labels as in Figure 4.1. Axes 1 and 3 explained 60.8% of the variation in the distance matrix, total variation explained by the three axes was 82.2% (stress = 16.88, instability 0.004). Vector overlay showed that total number of fires with the 10% and 25% filters had the highest correlation with Axis 3. Axis 1 was not explained by our data. Bottom panel shows NMDS ordination based on cover data. Axes 1 and 3 explained 50.7% of the variation in the distance matrix, total variation explained by the three axes was 63.3% (stress = 16.58, instability = 0.0001). Vector overlay was similar as in the presence-absence ordination, but also showed density of *Pinus durangensis*. Axis 1 was not explained by our data.

Appendix 4.1. Preliminary flowering plant list for MDG. Scientific names and authorities follow the International Plant Names Index (http://www.ipni.org). Synonyms and alternative families obtained from Van Devender et al. (2010). * indicates that a species is considered rare. Numbers in the Site column indicate presence (1) or absence (0) from a site.

Scientific name (Synonym)	**Author**	**Family (Alternative family)**	**Growth form**	**Site**			
				MP	**PS**	**RT**	**AB**
		Overstory					
Coniferopsida							
Cupressus arizonica (*Callitropsis arizonica*)	Greene	Cupressaceae	Tree	1	1	0	1
Juniperus deppeana	Steud.	Cupressaceae	Tree	0	1	0	0
Abies sp.		Pinaceae	Tree	0	0	0	0
Pinus durangensis	Martínez	Pinaceae	Tree	1	1	1	1
Pinus strobiformis (*P. ayacahuite* var. *brachyptera*)	Engelm.	Pinaceae	Tree	1	1	1	1
Pseudotsuga menziesii	(Mirb.) Franco	Pinaceae	Tree	1	1	1	1
Magnoliopsida							
Robinia neomexicana	A. Gray	Fabaceae	Tree	0	1	1	1
Quercus coccolobifolia (*Quercus jonesi* Trel.)	Trel.	Fagaceae	Tree	1	1	1	1
Quercus durifolia	Seemen	Fagaceae	Tree	0	0	0	1
Quercus gambelii	Nutt.	Fagaceae	Tree	1	1	0	1
Quercus grisea	Liebm.	Fagaceae	Tree	0	1	0	0
Quercus mcvaughii	Spellenb.	Fagaceae	Tree	0	0	1	1
Quercus sideroxyla	Hum. & Bonpl.	Fagaceae	Tree	0	0	0	1
Quercus viminea	Trel.	Fagaceae	Tree	1	0	0	0
Fraxinus velutina	Torr.	Oleaceae	Tree	0	1	1	0
Prunus sp.		Rosaceae	Tree	0	0	1	1
		Understory					
Magnoliopsida							
Amaranthus powellii	S. Watson	Amaranthaceae	Forb	1	1	0	0
Rhus sp.		Anacardiaceae	Shrub	1	0	0	0
Pseudocymopterus montanus	(Greene) Kartesz	Apiaceae	Forb	1	1	1	1
Asclepias sp.		Asclepiadaceae (Apocynaceae)	Forb	0	0	0	1
Ageratina lemmonii	(B.L.Rob.) R.M.King & H.Rob.	Asteraceae	Forb	0	0	1	0
Ageratina stricta	(A. Gray) R.M. King & H. Rob.	Asteraceae	Forb	1	1	1	1
Artemisia dracunculus	L.	Asteraceae	Forb	1	1	0	1
Artemisia ludoviciana	Nutt.	Asteraceae	Forb	1	1	0	1
Baccharis thesioides	Kunth	Asteraceae	Forb	0	0	1	1
Bidens ferulifolia	(Jacq.) Sweet	Asteraceae	Forb	1	1	1	0
Brickellia grandiflora	(Hook.) Nutt.	Asteraceae	Forb	1	1	1	1
Carphochaete pringlei	(S.Watson) Grashoff ex B.L.Turner	Asteraceae	Forb	0	0	1	0
Cosmos parviflorus	Pers.	Asteraceae	Forb	1	1	0	1
*Erigeron nitens**	A. Gray	Asteraceae	Forb	0	1	1	1
Erigeron neomexicanus	Torr. in Sitgr.	Asteraceae	Forb	0	1	0	0
Galinsoga parviflora var. *semicalva*		Asteraceae	Forb	1	1	0	1
Gutierrezia wrightii	A. Gray	Asteraceae	Forb	1	1	1	1
Hieracium fendleri	Schp. Bip.	Asteraceae	Forb	0	0	1	1

Scientific name (Synonym)	Author	Family (Alternative family)	Growth form	Site			
				MP	PS	RT	AB
Laennecia coulteri	(A. Gray) G.L. Nesom	Asteraceae	Forb	0	0	1	1
Pseudognaphalium macounii	(Greene) Kartesz	Asteraceae	Forb	1	1	1	1
Roldana pennellii	H.Rob. & Brettell	Asteraceae	Shrub/ forb	1	1	1	1
Solidago wrightii var. *adenophora*		Asteraceae	Forb	1	1	1	1
Stevia plummerae	A. Gray	Asteraceae	Forb	1	1	1	1
Verbesina longifolia	A. Gray	Asteraceae	Forb	1	1	1	1
Verbesina parviflora var. *parviflora*		Asteraceae	Forb	0	1	1	0
Verbesina sp. 1		Asteraceae	Forb	0	0	1	0
Verbesina sp. 2		Asteraceae	Forb	1	1	1	1
Viguiera cordifolia var. *cordifolia*		Asteraceae	Forb	1	1	0	1
Viguiera linearis	(Cav.) Sch.Bip. ex Hemsl.	Asteraceae	Forb	1	1	1	1
Lappula sp.		Boraginaceae	Forb	0	0	0	1
Lithospermum calycosum	I.M.Johnst.	Boraginaceae	Forb	0	0	1	1
Draba helleriana	Greene	Brassicaceae	Forb	1	1	0	0
Erysimum capitatum	(Douglas ex Hook.) Greene	Brassicaceae	Forb	1	1	0	0
Pennellia longifolia	(Benth.) Rollins	Brassicaceae	Forb	1	1	1	1
Lonicera aff. *arizonica*	Rehder	Caprifoliaceae	Shrub	0	0	1	0
Cerastium nutans	Raf.	Caryophyllaceae	Forb	1	1	1	1
Silene scouleri	Hook.	Caryophyllaceae	Forb	1	1	1	1
Paxistima myrsinites	(Pursh) Raf.	Celastraceae	Shrub	0	1	0	0
Chenopodium graveolens (*Dysphania graveolens* (Willd.) Mosyakin & Clemants))	Lag. & Rodr.	Chenopodiaceae (Amaranthaceae)	Forb	1	1	0	1
Sedum stelliforme	S. Watson	Crassulaceae	Forb	1	0	1	1
Cyclanthera minima	(S. Watson) Kearns & C.E. Jones	Cucurbitaceae	Vine	0	0	0	1
aff. *Astragalus*		Fabaceae	Forb	1	1	0	0
Cologania angustifolia	Kunth	Fabaceae	Forb	1	1	1	1
*Dalea ananassa**	Barneby	Fabaceae	Forb	0	1	0	0
Fabaceae sp. 1		Fabaceae	Forb	1	1	1	1
Fabaceae sp. 2		Fabaceae	Forb	0	1	1	1
Lotus wrightii (*Hosackia wrightii* A. Gray)	Greene	Fabaceae	Forb	0	1	0	0
Lupinus aschenbornii	S.Schauer	Fabaceae	Forb	1	1	1	1
Phaseolus pauciflorus	Sessé & Moc.	Fabaceae	Forb	1	1	1	1
Phaseolus sp. 2		Fabaceae	Forb	0	0	1	1
Trifolium amabile	Kunth	Fabaceae	Forb	1	1	0	0
Vicia pulchella	Kunth	Fabaceae	Vine/Forb	1	1	1	1
Vicia sp.		Fabaceae	Vine/Forb	1	1	1	1
Gentiana microcalyx (*Gentianella microcalyx* (Lemmon) J.M. Gillett)	Lemmon ex A.Gray	Gentianaceae	Forb	1	1	1	1
Halenia palmeri	A. Gray	Gentianaceae	Forb	0	1	1	1
Geranium atropurpureum	A.Heller	Geraniaceae	Forb	1	1	1	1
Phacelia platycarpa	(Cav.) Spreng.	Hydrophyllaceae (Boraginaceae)	Forb	1	1	0	1

Scientific name (Synonym)	Author	Family (Alternative family)	Growth form	Site			
				MP	PS	RT	AB
Agastache pallida	(Lindl.) Cory	Lamiaceae	Forb	1	1	1	1
Agastache sp.		Lamiaceae	Forb	1	1	0	1
Hedeoma costata	Hemsl.	Lamiaceae	Forb	1	1	1	1
Monarda citriodora	Cerv. ex Lag.	Lamiaceae	Forb	1	1	0	1
Stachys coccinea	Ortega	Lamiaceae	Forb	0	0	1	1
Unknown		Linaceae	Forb	1	1	0	0
Gaura hexandra (*Oenothera hexandra* (Ortega) W.L. Wagner)	Ortega	Onagraceae	Forb	0	0	0	1
Lopezia gracilis	S. Watson	Onagraceae	Forb	1	1	1	1
Unknown		Onagraceae	Forb	1	0	1	0
Oxalis alpina	Rose ex R.Knuth	Oxalidaceae	Forb	1	1	1	1
Oxalis decaphylla	Kunth	Oxalidaceae	Forb	1	1	0	1
Ipomopsis aggregata	(Pursh) V.E. Grant	Polemoniaceae	Forb	0	1	0	0
Eriogonum alatum	G.L. Nesom	Polygonaceae	Forb	1	1	1	1
Chimaphila maculata	(L.) Pursh	Pyrolaceae (Ericaceae)	Forb	0	0	1	0
Aquilegia desertorum	(M.E. Jones) Cockerell ex A. Heller	Ranunculaceae	Forb	0	1	0	0
Delphinium madrense	S. Watson	Ranunculaceae	Forb	1	0	0	0
Thalictrum pinnatum	S. Watson	Ranunculaceae	Forb	1	1	1	1
Ceanothus buxifolius	Willd. ex Schult.	Rhamnaceae	Shrub	0	1	0	1
Ceanothus fendleri	A. Gray	Rhamnaceae	Shrub	0	0	0	1
Frangula betulifolia	(Greene) Grubov	Rhamnaceae	Shrub	1	0	0	1
Fragaria mexicana	Schltdl.	Rosaceae	Forb	0	0	0	1
Potentilla sp.	J.M.Coult. & Rose	Rosaceae	Forb	1	1	1	1
Diodia teres	Walter	Rubiaceae	Forb	1	1	0	0
Galium mexicanum	Kunth	Rubiaceae	Forb	1	1	1	1
Galium microphyllum	A. Gray	Rubiaceae	Forb	0	0	1	0
Heuchera versicolor	Greene	Saxifragaceae	Forb	0	0	1	0
Castilleja patriotica	Fernald	Scrophulariaceae (Orobanchaceae)	Forb	0	0	1	0
Penstemon barbatus var. *torreyi*	(Benth.) D.D.Keck in Kearney & Peebles	Scrophulariaceae (Plantaginaceae)	Forb	1	0	1	1
Physalis philadelphica	Lam.	Solanaceae	Forb	1	1	1	1
Valeriana apiifolia	A.Gray ex S.Watson	Valerianaceae	Forb	1	0	0	1
Glandularia bipinnatifida	Nutt.	Verbenaceae	Forb	0	0	0	1
Viola sp.		Violaceae	Forb	0	0	0	1
Monocotyledons							
Agave sp.		Agavaceae	Rosette succulent	0	0	0	1
Yucca schottii (*Yucca madrensis* Gentry)	Engelm.	Agavaceae	Shrub	0	0	0	1
Commelina dianthifolia	Delile	Commelinaceae	Forb	1	1	1	1
Cyperus fendlerianus	Boeckeler	Cyperaceae	Graminoid	1	1	1	1
Malaxis sp.		Orchidaceae	Forb	0	0	1	0
Bromus anomalus	Rupr. ex E. Fourn.	Poaceae	Graminoid	1	1	1	1
Elymus canadensis	L.	Poaceae	Graminoid	1	1	1	1
Koeleria macrantha	(Ledeb.) J. Schultes	Poaceae	Graminoid	1	1	1	0
Muhlenbergia fragilis	Swallen	Poaceae	Graminoid	0	1	0	0

Scientific name (Synonym)	**Author**	**Family (Alternative family)**	**Growth form**	**Site**			
				MP	**PS**	**RT**	**AB**
Muhlenbergia minutissima	(Steud.) Swallen	Poaceae	Graminoid	1	1	1	1
Muhlenbergia sp. 4		Poaceae	Graminoid	0	1	1	1
Panicum bulbosum	Kunth	Poaceae	Graminoid	1	1	1	1
Piptochaetium pringlei (*Stipa pringlei* Scribn. ex Vasey)	(Beal) Parodi	Poaceae	Graminoid	0	1	0	0

Chapter 5

Forests of the past, present and future: Assessing overstory and understory plant communities in pine-oak forests in a national park and its surroundings in northwestern México

Abstract

México has some of the most diverse pine-oak forests in the world, but despite their relevance as a conservation hotspot they are severely underrepresented in the country's protected area system. We collected data about overstory age and structure, and understory cover and composition in temperate pine-oak forests inside a national park in Northwestern México, Parque Nacional Cascada de Basaseachi, and outside the park, in a logged forest. We used these datasets to evaluate the effectiveness of the park at conserving forest plant community richness and diversity. The forests inside the park had more species rich and diverse overstory communities than the site outside the park. The oldest trees were *Pinus* spp. found inside the park, and established in the early 1700s. We only found evidence of logging outside the park. We conclude that the forest plant communities inside the park are more species rich and diverse than outside the park, contrary to what has been shown in other parts of the world. We propose a model in which regional biodiversity conservation goals could be achieved by combining alternative approaches, such as community-based management, with existing conservation models, such as protected areas.

Introduction

Protected areas (PAs) have been established worldwide to protect biodiversity. However, developing nations often lack the resources to finance their operation, so they can turn into what are called “paper parks.” This concept has been at the heart of a decades-long controversy of “people vs. parks” (e.g. Bruner et al. 2001, Hayes and Ostrom 2005). México is considered a megadiverse country, which increases the difficulty to provide adequate representation of biodiversity in the national PA system (Cantú et al. 2004). Federal PAs in México are managed by the National Commission of Protected Areas (CONANP). Among the short-term challenges faced by PA managers in México are insufficient funding and resources, lack of information for decision-making and institutional instability. Long-term threats are posed by large-scale processes such as land-use change (Challenger et al. 2009), or climate change (Hannah et al. 2007).

Pine-oak forests are underrepresented in the Mexican PA system (Felger and Wilson 1994, Cantú et al. 2004, Arriaga Cabrera et al. 2009, Vazquez and Valenzuela-Galvan 2009). A recent estimate shows that only ~7.1% of the total area of pine-oak forests in México is included in PAs, which is likely to be a poor representation of their high β-diversity (Arriaga Cabrera et al. 2009). The understory of pine-oak forests in México is remarkably varied, with an estimated 50 species in the genera *Castilleja* and *Eryngium*, 52 in *Muhlenbergia*, 60 in *Sedum*, 90 in *Stevia* and 312 in *Salvia* (Challenger 1998). These forests are dominated by trees in the highly diversified genera *Pinus* (44 spp., 44% of the world’s total) and *Quercus* (135-150 spp., 30% of the world’s total) (Koleff et al. 2004).

It is estimated that plant endemism in the pine-oak forests of the Sierra Madre Occidental (SMOc) reaches 70%, which could be the highest among all terrestrial ecosystems in México (Felger et al. 1997). These forests are considered one of the most diverse temperate ecosystems in North America (Van Devender and Reina G. 2005). The SMOc is a mountain range that spans over 1200 km in a northwest-southeast direction, is between 200 and 400 km wide, and sits at ~2000 m of elevation (Ferrari et al. 2007). It is formed mostly of rocks of volcanic origins, and in western Chihuahua it is dissected by deep canyons that rapidly drop to sea level (McDowell and Clabaugh 1979).

Parque Nacional Cascada de Basaseachi (PNCB) is located in the headwaters of the Río Mayo. It was created through a decree published in 1981, and encompasses 5803 ha of forests and canyon habitats (CONANP website). It protects the Cascada de Basaseachi and its surrounding landscape; the *cascada* (waterfall) is the highest perennial waterfall in México at 246 m (Spellenberg et al. 1996). The main vegetation types protected by the park are temperate forests, riparian corridors and subtropical deciduous forest in warm sites that sit at lower altitude, below the waterfall (Spellenberg et al. 1996). The park also hosts diverse forests of mesic genera, such as *Abies*, *Cupressus*, *Acer*, *Ilex*, *Ostrya*, *Prunus* and *Tilia*, intermixed with *Pinus* and *Quercus*, in moister and darker side canyons (Spellenberg et al. 1996).

Documentation about the establishment of PNCB is limited to the published decree and a few records on government websites. The park has been plagued with problems since its establishment due to the land expropriation processes that should follow an NP decree. The Registro de Núcleos Agrarios (RAN 2010) shows that the expropriation decree for the creation of PNCB has not been executed. As a result, there are still permanent human settlements inside the park, comprised mostly of people dedicated to provide services to tourists. Adjacent forests are managed for timber production by ejidos—a collective form of land management—and large mining operations are established in the park's vicinity. Historically, forests in this region provided timber and charcoal for the mining industry since the late 18th century (Sariego Rodríguez 1998). Current mining practices do not depend directly on the availability of wood anymore, but the region is experiencing an increase in its population due to the expansion of mining, which indirectly causes a demand for firewood, building materials and other forest products.

The effectiveness of PAs in México as conservation models has been questioned by several authors (for example,Bray et al. 2003, Porter-Bolland in press). Published studies rely on landscape-level indicators, such as land-use change rates or representation of large ecosystem types (for example, Cantú et al. 2004, Figueroa and Sanchez-Cordero 2008). However, they usually lack site-level indicators such as species richness or diversity represented within PAs.

Species diversity is measured as the frequency of species' occurrence across the set of plots that comprise the sampled community (Magurran 2004). Three commonly accepted scales of species diversity in a given landscape are α, β and γ diversity. α-diversity is a measure of similarity within a basic spatial unit, which can be a plot or sampling point. The heterogeneity of those basic spatial units is β-diversity, and at the landscape-level it is γ-diversity (Whittaker 1972, Jost et al. 2010).

Considering the underrepresentation of temperate forests in the PA system in México, it is important to assess the level of protection that existing PAs provide to the regional biodiversity, despite their management limitations. We present the results of a study that had the goal to compare the overstory and understory in two sites inside PNCB to one site located in logged forest in the park's periphery. We analyzed three suites of plant community data: a chronology of tree establishment across a ~250 year timeline, a dataset of overstory and understory cover and composition, and information about the regeneration stratum, to answer the following questions.

1. Do forests inside the park have a broader range of age, structure and composition characteristics than forests outside the park?
2. Are forests inside the park more diverse than those outside the park?

Methods

Study site

The park is located in central Chihuahua, México, in the headwaters of the Río Mayo, at about ~2000 m of elevation (Figure 5.1). Table 5.1 lists the coordinates, slope and elevation of the sampling sites. Parent material in the area is dominated by rhyolitic ignimbrites (Ferrari et al. 2007), and its soils are shallow, rocky and light colored (Spellenberg et al. 1995). Weather data for the region are very limited. The Concheño weather station, located ~20 km north of the park at ~2130 m of elevation, shows that the annual averages between 1961-1973 were 24.8°C for maximum temperature, 2.4°C for minimum, and 919 mm for precipitation (CSM N.A.).

Ejidos are collectively-managed land units, and with comunidades indígenas, they comprise the social sector, estimated to hold ~80% of México's forests (Bray et al. 2003). The presidential decree that created Ejido Basaseachi was executed in 1936 and originally covered 11,604 ha. The park expropriation decree of 1981, as well as other boundary adjustment processes, left the ejido with 9,340 ha. The ejido actively manages its forests and belongs to a regional union of forest producers. The union provides technical assistance for the implementation of the ejido's forest management plan, and production of seedlings for reforestation and fire management, among other services.

Field methods

We searched the study area on foot, looking for unharvested forest stands that were representative of the landscape conditions found in PNCB and its vicinities. Cañón del Pájaro (CP) and Arroyo La Zorra (AZ) were found in two side canyons within the park boundaries, close to the main rim, and covered a substantial forest area that did not show evidence of mechanical extraction. Arroyo El Estacado (AE) was located inside Ejido Basaseachi and was on the main drainage, and was harvested after the formation of the ejido. At each study site we established twenty plots on a 100 x 100 m sampling grid (N=60 plots), on north facing slopes (Table 5.1). The sites inside PNCB were CP and AZ; AE was on Ejido Basaseachi, close to the park boundary. Access to CP was on foot only, while AZ and AE were adjacent to logging roads.

We established and permanently marked fixed-area circular plots at each grid point and recorded elevation, slope and aspect at the plot center (n=20 at each site, N=60). Plot area was 200 m^2 (7.98 m radius) for overstory measurements and 40 m^2 for nested regeneration plots (3.57 m radius). In each plot we collected data about overstory structure, composition and age; regeneration; and presence-absence and % aerial cover of the understory. We collected overstory data in June of 2008 and understory data in late September-early October 2009. We collected botanical specimens for all plants in the overstory and understory and deposited a full set of our collections (M. Joe and C.

Cortés 2009) at ASC, the Deaver Herbarium of Northern Arizona University. A complete list of overstory and understory plants and botanical authorities is included in Appendix 3.

We recorded species (for some decaying snags we could only record the genus) and diameter at breast height (DBH, 1.3 m) of live and dead trees and snags >1.3 m tall in each 200 m^2 plot, and we measured the DBH of stumps. We tallied all saplings or shrubs <1.30 m tall, in each 40 m^2 subplot using three height classes (1-40 cm; >40-80 cm, >80-130 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 10 cm above ground level. If trees were too small to core (usually <10 cm), we cut a stem section at 10 cm above ground level.

We could not relocate one plot for the understory measurements, so for these datasets N=59. We recorded presence/absence of understory species (shrubs and herbs >1.3 m) in the 200 m^2 overstory plots. We used four 1-m^2 subplots within each overstory plot, located on the perimeter of overstory plots along radial lines that followed cardinal directions, to assess the cover of individual species.

Laboratory methods and data analyses

Experts at ASC determined botanical specimens, or sent them to taxonomic authorities at other herbaria for identification or verification. When identification to species level was impossible, we grouped specimens by morphotype. We used two regional plant checklists (Spellenberg et al. 1996, Martin et al. 1998) and the USDA Plants website (http://plants.usda.gov/java/) to identify exotic or invasive species.

For all living and dead trees we calculated basal area (BA, m^2 ha^{-1}) and tree density (number of trees ha^{-1}) by species, and regeneration density by species group and height class. We reconstructed age distributions from the collected tree cores and sections, which were mounted and sanded with increasingly finer sandpaper grits until individual cells were visible with a microscope. We created a master tree-ring chronology for the area to crossdate each core or section. To establish the number of rings to center for cores that missed the pith, we used a pith locator (a transparent overlay of concentric circles with curvatures that vary as a function of the distance to the pith) (Applequist 1958). We grouped the age data into four categories (*Pinus* spp., Other Conifers, *Quercus* spp. and Other Broadleaved). Other Conifers included all conifers except for *Pinus* spp. and Other Broadleaved all broadleaved species except for *Quercus* spp.

Boxplots and scatterplots clearly showed that the overstory and understory community datasets were not normally distributed so we used methods robust to non-normally distributed multivariate datasets. For diversity analyses we used presence-absence data. To compare the spatial spread of plots on species space we used NMDS (Non Metric Multidimensional Scaling). This method works well with non-normally distributed data and is the primary method recommended for analysis of ecological community datasets (McCune and Grace 2002). The resulting ordination provides a distance-based graphic of an optimal solution to the relationship of species distribution in plots.

We used the NMDS function in PC-ORD (McCune and Mefford 2006) with Sørensen similarity indexes to create the ordinations. For the overstory dataset we relativized BA by plot to equalize the weights for inter-plot analyses (McCune and Grace 2002). For the understory datasets we deleted species present in <5% of the plots, which resulted in N=98 for the presence-absence dataset and N=56 for the % aerial cover dataset. Each ordination was produced through 250 runs with the real data and 250 Monte Carlo randomized runs to ensure that the resulting axes were not a result of chance. To evaluate the association of the NMDS ordinations to environmental variables, we used a second matrix with physical variables (elevation and slope) and overstory information (BA, tree density, fine fuel and coarse woody debris loads). A vector overlay in the ordination graphic depicts strong correlations ($>|0.45|$) between the ordinations and the data in the second matrix.

To test for statistical significance in differences in overstory and understory composition among the three sites, we used the permutational ANOVA function (PERMANOVA) (Anderson 2001) in the vegan package (Oksanen et al. 2011) for R (R Development Core Team 2010). Permutational ANOVA is a multivariate ANOVA analog that makes no assumptions about data distribution, and thus can be used with non-normally distributed data. It uses a pseudo-F as test statistic. The pseudo-F is 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 estimated *p*-values using 9999 permutations, which is well over the minimum 5000 recommended for $\alpha < 0.01$ (Anderson 2001). The PERMANOVA results for the three datasets showed statistical significance, so we conducted paired PERMANOVA tests among all site pairs.

Each site was spatially separated, so we treated each as a different community for β-diversity comparisons. Since incompleteness of sampling can be a problem in areas with high biodiversity (Kessler et al. 2009), we used the program SPADE (Chao and Shen 2010) to assess sample coverage at each site. To assess species richness and diversity at each site we used the data for both overstory and understory plant communities in the three sites. We calculated total species number and Shannon's Diversity Index (H'), and assessed the statistical significance of differences in H' for all site pairs with Hutcheson's *t*-test for H' (Hutcheson 1970). Shannon's Index is the recommended index to compare diversity among communities at the regional level (Jost et al. 2010). We estimated the Morisita Similarity Index for both the overstory and understory communities with the program SPADE (Chao and Shen 2010).

Results

Age structure

The oldest trees at the three sites were *Pinus* spp., and the oldest trees across our sample established in CP in the early 1700s. The most recently established forest was AE, which was mostly comprised of *Pinus* spp. (Figure 5.2). The site had few older trees that established in the second half of the 19th century. However, most of the dated trees established at this site in the early 20th century, with a recruitment peak in the 1920s.

The age distribution graphic for CP (Figure 5.2) shows a recruitment gap from >1710-1830. This was followed by a period of continuous recruitment throughout the 20th century and a spur in the 1970s and 1980s. The oldest live trees in AZ established in the mid-1700s. A 50 year gap in establishment lasted until the early 1800s, followed by another gap in 1820-1840, and two peaks between 1900-1930 and 1990 to 2009 (Figure 5.2).

Overstory composition and structure

Pinus spp. and *Quercus* spp. were dominant in both BA and trees per hectare (TPH) in the three sites. The BA mean values were similar across the four sites: 24.21

for AE, 25.4 for CP and 32.7 for AZ. *Pinus* spp. comprised 56.7% of all trees in AE while 36.3% were *Quercus* spp. Of all the trees present in CP, 44.9% were *Pinus* spp.) and 29.4% were *Quercus* spp. Lastly, in AZ 44.8% of the total trees were *Pinus* spp. and 36.8% were *Quercus* spp. Species richness of the overstory was 22 at both AZ and CP, while AE had 10 (Table 5.2). β-diversity in the overstory was highest at CP, closely followed by AZ and lowest at AE. The Morisita Similarity Index for the overstory was 0.776 for the three communities and 0.82 for AE-CP, 0.71 for AE-AZ and 0.81 for CP-AZ. Hutcheson's t-test results ($p<0.05$) showed that β-diversity of the overstory was statistically significantly different for all pairs of sites.

Pinus spp. and *Quercus* spp. contributed largely to the BAs in the three sites: 80.6% and 17.6% (AE), 56.9% and 26.1% (CP), and 56.0% and 35.5% (AZ). The diameter distributions of live trees were dominated by small trees, declining with successively larger diameter classes in a "reverse-J" shape. Average BA of all dead trees and snags was 4.0 m^2 ha^{-1} in AE, 4.5 in CP and 12.7 in AZ, and average BA of dead trees and snags >30 cm DBH was 5.2 m^2 ha^{-1} at AE, 11.5 at CP and 10.8 at AZ. We only recorded presence of stumps outside the park, in AE, of *Pinus* and unidentified species (2.5 stumps ha^{-1}), corresponding to an average of 5 m^2 ha^{-1} of basal area harvested, ranging from 15-41 cm in diameter.

The final NMDS ordination solution for the overstory dataset (Figure 5.3) had three axes that explained 83.1% of the total variation in the dataset (Axis 1=0.296, Axis 2=0.308 and Axis 3=0.227). It was achieved with stress=16.318, and instability=0.024. Axis interpretation was difficult since environmental data for the study sites were limited to three physical variables (elevation, slope and aspect) that did not have strong correlations to the distance matrix. We attribute the grouping of species in the NMDS graphic along the axes to the inherent variability in each site's composition. Pairwise PERMANOVA comparisons of differences in species composition based on relativized BAs between sites were all statistically significant ($p<0.001$, Bonferroni-adjusted $\alpha=0.017$).

Regeneration

Quercus and *Pinus* dominated the three regeneration height classes (Figure 5.2). Other broadleaved species (*Arbutus* spp., *Fraxinus velutina*, Ilex spp., *Osmanthus americanus, Prunus serotina*) were abundant in the first height class but decreased significantly in the following two.

Understory richness, composition and cover

There were 142 understory plant species across the three sites, representing five life forms (forbs, graminoids, sedges and shrubs), distributed in 38 families. AE had 53 species, CP had 102 and AZ had 89. Shared species between sites were 39 (AE-CP), 36 (AE-AZ) and 57 (CP-AZ). β-diversity was highest at CP, followed by AZ, and lowest at AE. The Morisita Similarity Index for the understory was 0.559 for the three communities and 0.66 for AE-CP, 0.50 for AE-AZ and 0.67 for CP-AZ. Hutcheson's *t*-test results ($p<0.05$) showed that β-diversity of the understory was statistically significantly different between all pairs of sites.

The final NMDS solution for the understory plant community based on species presence-absence (Figure 5.3) had three axes and was the only ordination where a variable from the second matrix (elevation) had a strong correlation to the distance matrix and appeared in the vector overlay. In order to align the vector to Axis 2, we rotated the ordination 14° to the right and assessed the variance explained by the axes with this new configuration. The graphic shows Axis 1 and 2 since these explained 57.7 % of the total variation (Axis 1 = 34.8, Axis 2 = 21.7), the configuration was achieved with stress=18.265 and instability=0.002. The final NMDS solution for the % aerial cover dataset (Figure 5.3) also had three axes that explained 50.8% of the total variation and was achieved with stress=20.486 and instability<0.

Pairwise PERMANOVA comparisons of differences in species composition based on presence-absence and cover between sites were all statistically significant ($p \leq 0.005$, Bonferroni-adjusted $\alpha = 0.017$). Species richness per plot in AE ranged from 2 to 23, 9 to 22 in CP and 18 to 32 in AZ.

Forest community diversity

Muhlenbergia (Poaceae) and *Quercus* (Fagaceae) were the most diversified genera in the three sites, (eight species each, followed by *Pinus* (Pinaceae, six species) and *Ageratina* (Asteraceae, four species). Species richness was highest in Asteraceae (35 species), Poaceae (16 species), Fabaceae (13 species), Fagaceae (eight species), Pinaceae (seven species), Agavaceae (five species) and Ericaceae (five species).

Discussion

Forests of the past

In this section we present the history of forest development across a ~250 year timeline. The dominant genus in the overstory in the three sites was *Pinus*, followed by *Quercus*. The oldest trees in the age reconstruction (250-300 years old) were *Pinus durangensis* found in CP and AZ. Both sites showed relatively stable establishment of *Pinus* since the 19th century, averaging 32 (CP) and 33 (AZ) trees ha^{-1} per decade in the past 160 years. Establishment of *Pinus* spp. trees in AE peaked in the early 20th century in AE, and due to this the site has the highest average tree establishment rate per decade since 1850 (40).

The absence of old trees (>150 years) from AE, along with the age distribution of live trees and the presence of stumps was strong evidence of logging in the late 19th and early 20th centuries. While the sites inside the park had live trees in the >60 diameter classes, the site outside the park did not have any trees in this category. The three sites had most trees concentrated in the smaller diameter categories (<20 cm DBH). Actual species richness and estimated diversity indicators for the overstory were significantly lower for the site outside the park, while the sites inside had higher species diversity and richness. Snags and large trees are important wildlife habitat and their presence in managed forests can be used as an indicator of habitat quality (Miller and Chambers 2007), but their removal is a common practice that has been observed in other logged sites in Chihuahua (Fulé et al. 2011). Snags >30 cm DBH were twice as abundant inside the park than outside the park.

Forests of the present

In this section we discuss the composition and structural characteristics of the sampling sites at the time of data-recording. The two sites inside the park hosted 134 out of the 142 recorded understory species, and 22 out of the 24 recorded overstory species. We only found one exotic species (*Lactuca* sp.: Asteraceae), both inside and outside the park. This is remarkable considering the history of management (including grazing and logging), especially outside the park, and the relative proximity of a paved highway to the three sites. Forest plant communities were significantly richer and diverse in the two sites inside the park, and the lower species richness outside the park could be a consequence of logging and cattle grazing. *Quercus* richness was mostly concentrated inside the park, while all *Pinus* spp. were represented inside and outside the park. While BAs in the three sites are comparable to those of unharvested sites in Chihuahua, tree densities are much higher and are similar to those of harvested sites in the region (Fulé et al. 2011, Cortés Montaño et al. in review). The sites inside the park had diverse shrub and mid-canopy layers, which are also associated to higher habitat quality for wildlife in other sites in the SMOc (Miller and Chambers 2007).

The Morisita Similarity Index showed that AE and AZ hosted the least similar plant communities, which can be observed in the NMDS ordination graphics. Each community was statistically significantly different, which attests to the high landscape-diversity that characterizes this region (Van Devender and Reina G. 2005).

Forests of the future

In this section we discuss the composition and structure of regeneration in terms of its potential contribution to tree recruitment to the overstory. Our results showed that the park encompasses higher forest community diversity than a logged forest outside the park. At the time of sampling, management activities inside the park seemed to focus on the heavily visited waterfall rim area (for example, signage, trail maintenance, waste management). We observed evidence of recent logging outside the park near the access road to one of our sampling sites, but no evidence of recent logging activities inside the park. Officially established protected areas that lack resources (human, material or financial) for implementation are often called “paper parks,” pointing at their ineffectiveness at protecting resources on the ground. Critics also argue that they block access of local communities to natural resources (Hayes and Ostrom 2005). The lack of enforcement of management frameworks often increases the incidence of illegal activities (such as poaching or illegal logging) inside protected areas (Hayes and Ostrom 2005), which could turn them into biodiversity “sinks” instead of “sources.”

Our results showed that despite institutional and management problems faced by PNCB, the park hosted more diverse forests than a managed forest outside the park. While this could be a result of the park’s topography and other physical and environmental factors, the diversity of the park’s plant communities is remarkable. Instead of a “parks vs. community management” dichotomy, we suggest that PNCB and its surrounding forests be viewed as a source-sink model, where the PA provides protection to richer and more diverse forests than those outside the park. If management objectives of the surrounding forests incorporate conservation goals through models such as community management, conservation goals could be maximized at the landscape level.

References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**:32-46.

Applequist, M. B. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry **56**:141.

Arriaga Cabrera, L., V. Aguilar, and J. M. Espinoza. 2009. Regiones prioritarias y planeación para la conservación de la biodiversidad. Pages 433-457 Capital natural de México vol. II: Estado de conservación y tendencias de cambio. CONABIO, México, D.F.

Bray, D. B., L. Merino-Pérez, P. Negreros-Castillo, G. Segura-Warnholtz, J. M. Torres-Rojo, and H. F. M. Vester. 2003. Mexico's Community-Managed Forests as a Global Model for Sustainable Landscapes. Conservation Biology **17**:672-677.

Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. Science **291**:125-128.

Cantú, C., R. Gerald Wright, J. Michael Scott, and E. Strand. 2004. Assessment of current and proposed nature reserves of Mexico based on their capacity to protect geophysical features and biodiversity. Biological Conservation **115**:411-417.

Cortés Montaño, C., P. Z. Fulé, D. A. Falk, J. Villanueva-Díaz, and L. L. Yocom. in review. Linking old-growth forest composition and structure to fire history and climate in northwestern México.

CSM. N.A. Estaciones climatológicas del sistema CLICOM. Comisión Nacional del Agua, Subdirección General Técnica, Coordinación del Servicio Meteorológico.

Challenger, A. 1998. Utilización y Conservación de los Ecosistemas Terrestres de México. Pasado, Presente y Futuro. CONABIO, Instituto de Biología-UNAM, Agrupación Sierra Madre, S.C., México, D.F.

Challenger, A., R. Dirzo, J. C. López Acosta, E. Mendoza, R. Dirzo, A. Lira-Noriega, and I. Cruz. 2009. Factores de Cambio y Estado de la Biodiversidad. Pages 37-73 Capital Natural de México Vol. II: Estado de Conservación y Tendencias de Cambio. CONABIO, México, D.F.

Chao, A., and T. J. Shen. 2010. Program SPADE (Species Prediction And Diversity Estimation).

Felger, R. S., G. P. Nabhan, and R. Bye. 1997. Apachian/Madrean Region of Southwestern North America, Mexico and USA. Mexico and USA: CPD site MA11. Pages 172-180 *in* S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, editors. Centres of Plant Diversity, Volume 3: The Americas. WWF, IUCN, National Museum of Natural History-Smithsonian Institution, European Community, ODA, Cambridge, U.K.

Felger, R. S., and M. F. Wilson. 1994. Northern Sierra Madre Occidental and Its Apachian Outliers: A Neglected Center of Biodiversity. Pages 36-59 *in* Biodiversity and the management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. U.S.F.S. General Technical Report RM-GTR-264, Tucson, AZ.

Ferrari, L., M. Valencia-Moreno, and S. Bryan. 2007. Magmatism and tectonics of the Sierra Madre Occidental and its relation with the evolution of the western margin of North America. Geology of México: Celebrating the Centenary of the

Geological Society of México: Geological Society of America Special Paper 422:1-39.

Figueroa, F., and V. Sanchez-Cordero. 2008. Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. Biodiversity and Conservation **17**:3223-3240.

Fulé, P. Z., M. A. Ramos Gómez, C. Cortés Montaño, and A. M. Miller. 2011. Fire regime in a Mexican forest under indigenous resource management. Ecological Applications **21**:764–775.

Hannah, L., G. F. Midgley, S. J. Andelman, M. Araújo, G. Hughes, E. Martínez Meyer, R. Pearson, and E. H. Williams. 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment **5**:131-138.

Hayes, K., and E. Ostrom. 2005. Conserving the world's forests: are protected areas the only way? Indiana Law Review **38**:595-617.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology **29**:151-154.

Jost, L., P. DeVries, T. Walla, H. Greeney, A. Chao, and C. Ricotta. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions **16**:65-76.

Kessler, M., S. Abrahamczyk, M. Bos, D. Buchori, D. D. Putra, S. R. Gradstein, P. Höhn, J. Kluge, F. Orend, R. Pitopang, S. Saleh, C. H. Schulze, S. G. Sporn, I. Steffan-Dewenter, S. S. Tjitrosoedirdjo, and T. Tscharntke. 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. Ecological Applications **19**:2142-2156.

Koleff, P., J. Soberón, and A. Smith. 2004. Madrean pine-oak woodlands.*in* R. A. Mittermeier, P. Robles Gil, M. Hoffmann, J. D. Pilgrim, T. M. Brooks, C.

Goettsch Mittermeier, J. Lamoreux, and G. A. B. da Fonseca, editors. Hotspots revisited. CEMEX.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford, U.K.

Martin, P. S., D. Yetman, M. Fishbein, P. Jenkins, T. R. Van Devender, and R. K. Wilson. 1998. Gentry's Río Mayo Plants: the tropical deciduous forest and environs of northwest Mexico. The University of Arizona Press, Tucson, AZ. The University of Arizona Press, Tucson, AZ.

McCune, B., and J. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and M. J. Mefford. 2006. PC-ORD. Multivariate analysis of ecological data. MjM Software, Gleneden Beach, Oregon.

McDowell, F. W., and S. E. Clabaugh. 1979. Igninmbrites of the Sierra Madre Occidental and their relation to the tectonic history of western Mexico. Geological Society of America Special Paper **180**:113-124.

Miller, A. M., and C. L. Chambers. 2007. Birds of harvested and unharvested pine-oak forests, Chihuahua, Mexico. Southwestern Naturalist **52**:271-283.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package.

Porter-Bolland, L. in press. Community managed forests and forest protected areas: An assessment of their conservation effectiveness across the tropics.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAN. 2010. Padrón Histórico de Núcleos Agrarios (http://app.ran.gob.mx/phina/).

Sariego Rodríguez, J. L. 1998. Minería y Trabajo Minero en Chihuahua. Pages 221-342 *in* J. L. Sariego, editor. Historia General de Chihuahua V, Periodo Contemporáneo. Trabajo, Territorio y Sociedad en Chihuahua Durante el Siglo XX. Gobierno del Estado de Chihuahua-Centro de Información del Estado de Chihuahua-UACJ-ENAH Chihuahua, Ciudad Juárez, Chihuahua, México.

Spellenberg, R., T. Lebgue, and R. Corral-Díaz. 1996. XIII. A specimen-based, annotated checklist of the vascular plants of Parque Nacional "Cascada de Basaseachi" and adjacent areas, Chihuahua, México. Instituto de Biología-Universidad Nacional Autónoma de México, México, D.F.

Spellenberg, R., T. Lebgue, R. Corral-Díaz, and J. R. Bacon. 1995. Nuevos registros de plantas de las montañas del norte de México. Acta Botanica Mexicana **30**:13-20.

Van Devender, T. R., and A. L. Reina G. 2005. Floristic Comparison of an Arizona Sky Island and the Sierra Madre Occidental in Eastern Sonora: the Huachuca Mountains and the Yécora Area. Pages 154-157 *in* G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster, editors. Connecting Mountain Islands and Desert Seas: Biodiversity and Management of the Madrean Archipelago II. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-36, Tucson, AZ.

Vazquez, L. B., and D. Valenzuela-Galvan. 2009. How well represented are Mexican mammals in the natural protected area network? Revista Mexicana De Biodiversidad **80**:249-258.

Whittaker, R. H. 1972. Evolution and Measurement of Species Diversity. Taxon **21**: 213-251.

Table 5.1. Physical characteristics at the three sampling sites: AE (Arroyo El Estacado), CP (Cañón del Pájaro) and AZ (Arroyo La Zorra). Mean values are bolded, minimum and maximum are in parentheses.

Site	**Latitude (N)**	**Longitude (W)**	**Slope (%)**	**Elevation (masl)**
AE	28° 16’ 36’’	108° 11’ 54’’	**39** (14-61)	**2258** (2122-2420)
CP	28° 10’ 25’’	108° 14’ 6’’	**49** (15-78)	**2020** (1961-2076)
AZ	28° 9’ 2’’	108° 38’ 42’’	**43** (5-83)	**2140** (2087-2214)

Table 5.2. Species richness and diversity of the overstory (O) and understory (U) of the sampling sites. Shannon's Diversity Index is H'. Site labels as in Table 5.1.

Site	**Sample coverage**		**Species richness**		**β-diversity**	
	U	**O**	**U**	**O**	**U**	**O**
AE	95.5	100	53	10	3.77	1.72
CP	91.0	100	102	22	4.56	2.53
AZ	94.7	100	89	22	4.33	2.50

Table 5.3. Overstory species present at each site. Site labels as in Table 5.1. Scientific names and authorities follow the International Plant Names Index (http://www.ipni.org).

Scientific name (Synonym)	Author	Family	Site AE	 CP	 AZ
Coniferopsida					
Cupressus lusitanica (*Callitropsis lusitanica*)	Mill.	Cupressaceae	1	1	1
Juniperus deppeana	Steud.	Cupressaceae	0	1	1
Pinus durangensis	Martínez	Pinaceae	1	1	1
Pinus engelmannii	Carrière		1	1	1
Pinus herrerae			1	1	1
Pinus leiophylla			1	1	0
Pinus lumholtzii			1	1	1
Pinus strobiformis (*P. ayacahuite* var. *brachyptera*)	Engelm.	Pinaceae	1	1	1
Pseudotsuga menziesii	(Mirb.) Franco	Pinaceae	0	1	0
Magnoliopsida					
Ilex rubra	S. Watson	Aquifoliaceae	0	1	1
Ilex tolucana	Hemsl.	Aquifoliaceae	0	1	1
Arbutus arizonica	Sarg.	Ericaceae	0	1	1
Arbutus xalapensis	Kunth	Ericaceae	1	1	1
Quercus arizonica	Sarg.	Fagaceae	0	1	1
Quercus coccolobifolia	Trel.	Fagaceae	0	1	1
Quercus durifolia		Fagaceae	0	0	1
Quercus hypoleucoides	A. Camus	Fagaceae	0	0	1
Quercus mcvaughii	Spellenb.	Fagaceae	1	1	1
Quercus rugosa	Née	Fagaceae	0	1	1
Quercus sideroxyla	Humb. & Bonpl.	Fagaceae	1	1	1
Quercus toumeyi	Sarg.	Fagaceae	0	1	1
Fraxinus velutina	Torr.	Oleaceae	0	1	1
Prunus serotina	Ehrh.	Rosaceae	0	1	1

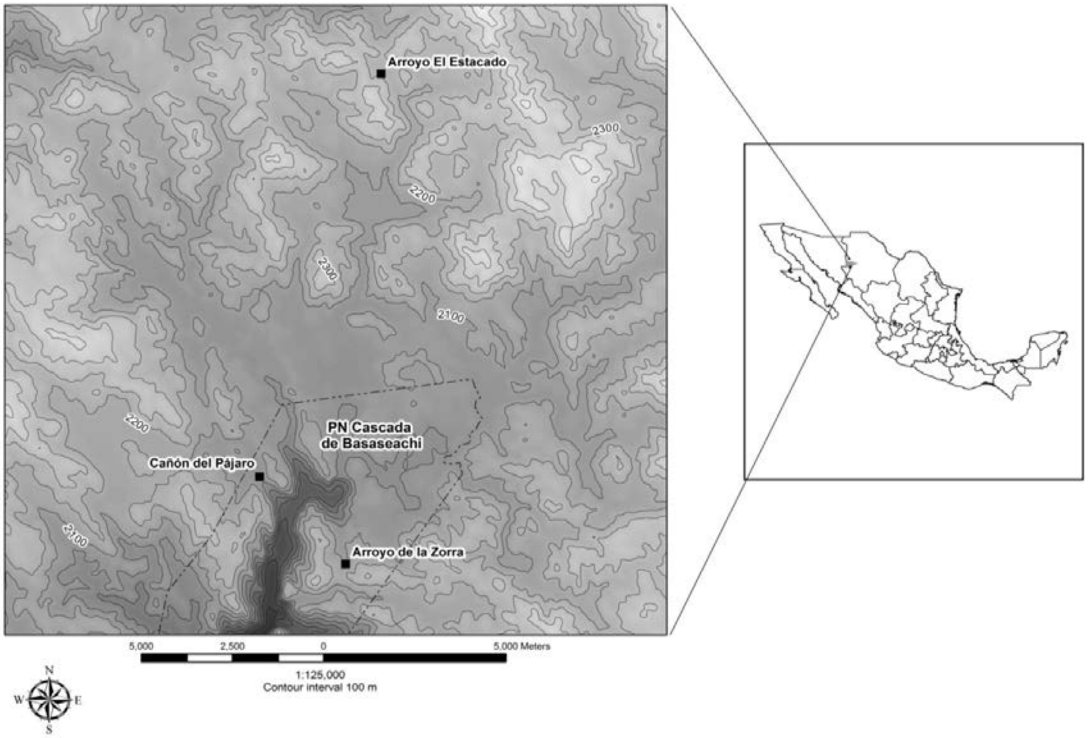

Figure 5.1. Location of the sampling sites in the state of Chihuahua, México.

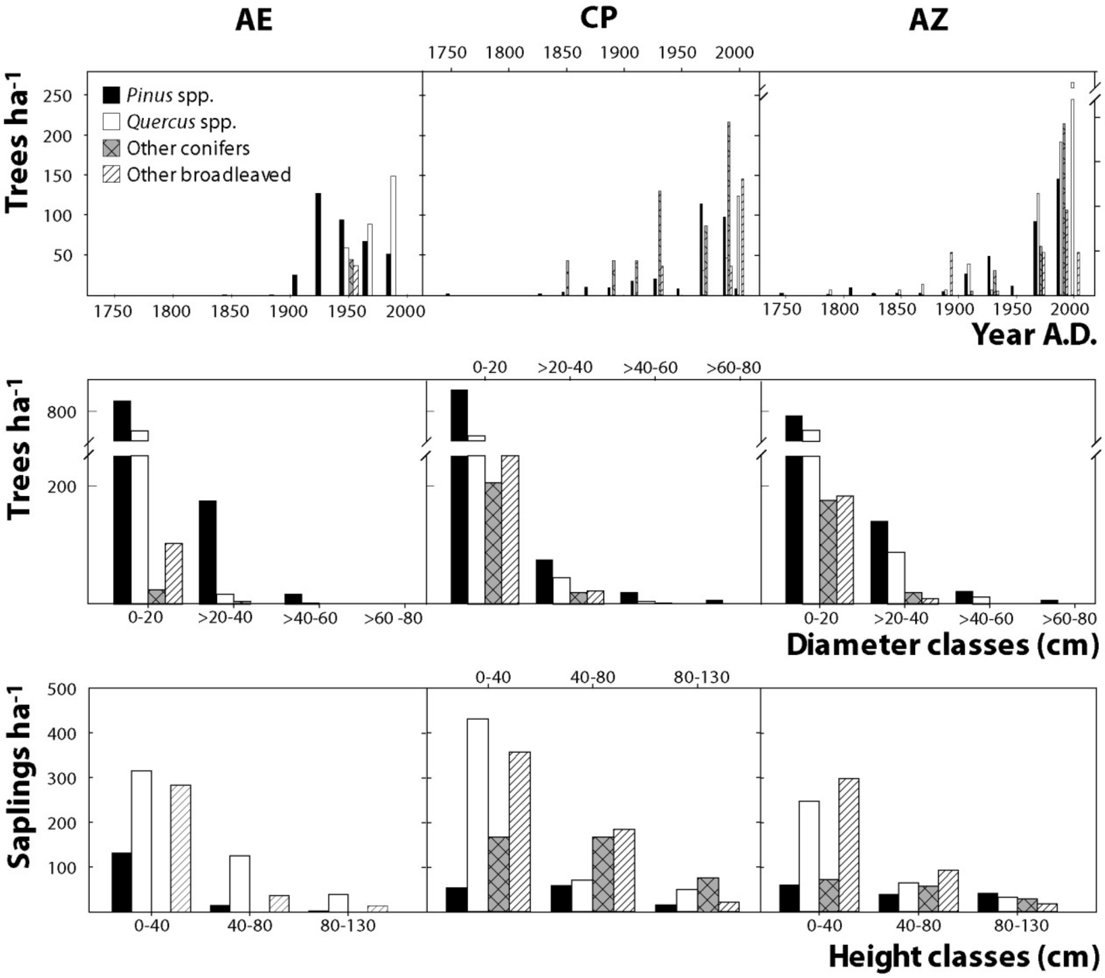

Figure 5.2. Age and diameter distributions of trees and number of saplings in three height classes in the three sites: Arroyo El Estacado (AE), Cañón del Pájaro (CP) and Arroyo La Zorra (AZ). Species groups are *Pinus* spp., *Quercus* spp., Other Conifers (*Juniperus deppeana*. *Cupressus lusitanica* and *Pseudotsuga menziesii*), and Other Broadleaved (*Arbutus* spp., *Fraxinus* velutina, *Ilex* spp., *Osmanthus americanus*).

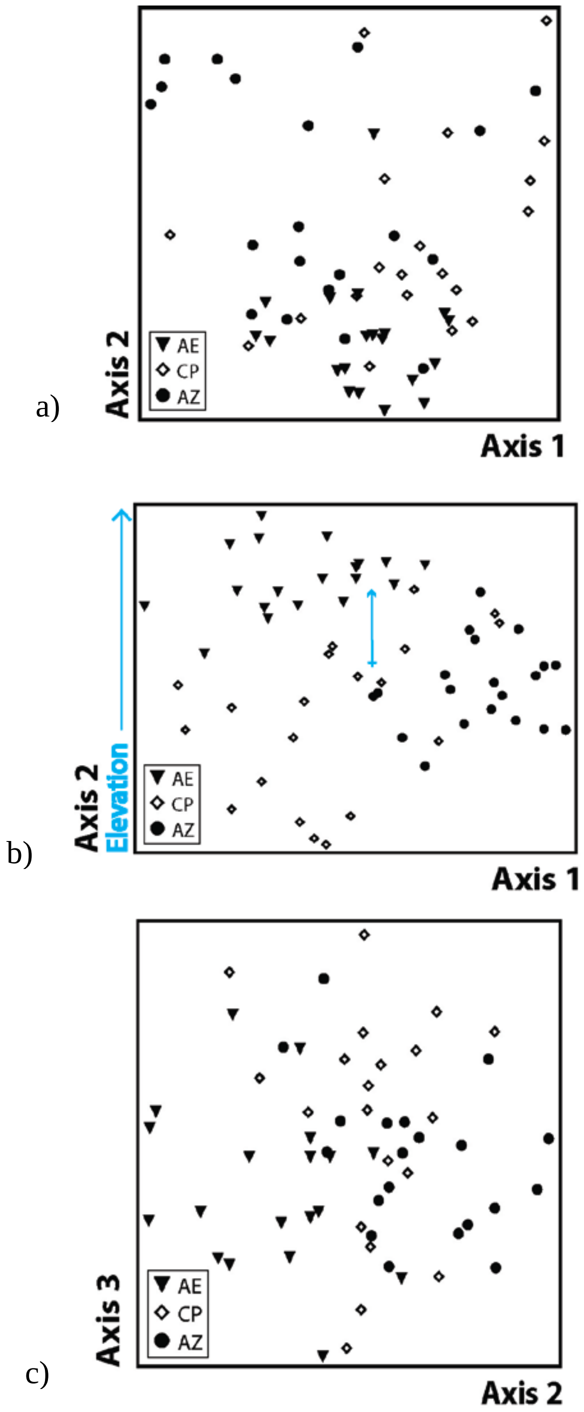

Figure 5.3. Ordinations (NMDS) of overstory based on relativized basal area (a), understory based on species presence-absence (b), and % aerial cover (c) in the three sites. Site labels are as in Table 5.1. All ordinations had three axes, total variance explained by these was 83.1% in a), 72.9% in (b) and 50.8% in (c). Axis 1 explained 29.6% of the variation in (a), 34.8% in (b) and 16.6% in (c). Axis 2 explained 30.8% of the variation in (a), 23.0 in (b) and 17.4 in (c). The ordination based on presence-absence (b) showed that elevation was one of the drivers of Axis 1 (Pearson's *r*>0.35).

Chapter 6
Management Recommendations

This dissertation demonstrates the importance of using a historical, long-term perspective, in the assessment of forest ecological dynamics. Our two study sites in the Sierra Madre Occidental (SMOc) showed that the temperate forests of northwestern México are species rich and diverse. The results discussed here also emphasize the relevance of incorporating multiple components to the study of forests, including understory, overstory, disturbance regimes, climate and their interactions.

It is also important to highlight the active role that humans play in these systems, both historically and presently, and to recognize that human activities such as mining, logging, or cattle grazing, are currently the largest driver of change (Challenger 1998). Evidence from trincheras (retaining walls built with rocks) suggests that humans have occupied the sierras of western Chihuahua since pre-Hispanic times (Herold 1965, Howard and Griffiths 1966). Prior to the arrival of Europeans in the 16th and 17thcenturies, these forests were part of the territories of different indigenous groups (Lartigue 1983, Challenger 1998). Indigenous peoples continue to actively use fire to manage their resources (LaRochelle and Berkes 2003, Fulé et al. 2011).

While the role of humans cannot be excluded from the interpretation of historical evidence, these interpretations must be made carefully. Palynological evidence from a site in western México shows that the appearance of pine forests is related to drier climates, and that naturally occurring fires were part of the ecological dynamics of those systems (Figueroa-Rangel et al. 2008). The historical and current role of human use and management as drivers of change in the forests of the mountains of the SMOc in Chihuahua need to be further studied.

Frequent fire has been an important disturbance agent at Mesa de las Guacamayas in a period that spans at least 250 years. In the SMOc, previous studies have shown that there is high synchronicity between large-scale climatic patterns and fire occurrence, where fire years coincide with dry years and are preceded by wet years that foster accumulation of fine fuels (Heyerdahl and Alvarado 2003, Fulé et al. 2005). "Bottom-up" factors, such as understory vegetation, fuel-loads, and human activities are important drivers of the structural and ecological conditions of a given vegetation type. While the relative importance of these factors can be a matter of scientific debate, it has been suggested that their role shifts once the disturbance regime is altered beyond its historical range of variability (Heyerdahl et al. 2001). It is key that management practices integrate existing information about disturbance regimes to prevent this shift. In the case of temperate forests throughout the SMOc, fire must be incorporated into management practices of conservation areas and managed forests. This could be accomplished by shifting the suppression paradigm to one that includes policies and practices that incorporate wildfire management practices in fire-adapted systems (i.e. integrated fire management).

The old-growth forests of Mesa de las Guacamayas and similar sites in the SMOc have great potential to be used as reference sites. Information about their composition, structure and disturbance regimes can be used to set standards and guidelines to manage similar systems in other parts of the range or in the U.S. Southwest. Logging is still a threat to the old-growth relicts of the SMOc and the biodiversity that they harbor, such as Thick-billed Parrots. A national standard or NOM (Norma Oficial Mexicana) would be a useful tool to grant protection to these systems. This standard should incorporate the characteristics described in Table 6.1, derived from the data generated by this study.

Forests that provide habitat conditions to endangered species that favor old-growth habitats, such as Thick-billed Parrots, should be excluded from logging. A regional-level analysis of high-resolution remotely sensed imagery could be used to identify potential sites with old-growth habitat in order to set them as conservation priorities and to engage land-owners in their protection. An integrated fire management strategy for the SMOc should incorporate the evidence from multiple sites in Chihuahua and Durango that suggests high fire frequencies. Wildfires could be managed and let burn through the landscape in order to maintain or restore the fire frequencies shown by historical ecology records, such as fire scars.

We intentionally looked for sites that were protected areas, such as Basaseachi, or that were included in active conservation processes, such as Mesa de las Guacamayas. In 2009, the federal government published a decree for a new biosphere reserve in Chihuahua, and Mesa de las Guacamayas was included in it. Despite the many problems associated with management of protected areas in México (Bray et al. 2003, Hayes and Ostrom 2005, Porter-Bolland in press), our results showed that the two sites maintain highly species rich and diverse plant communities. While this may be partially due to the inherent diversity of the Sierra Madre Occidental, our data for Basaseachi showed that forests inside the protected area were more diverse than a managed forest near the park boundary.

The fire histories of Mesa de las Guacamayas showed that maintaining fire regimes could be as critical as maintaining the habitat structure for Thick-billed Parrots and other old-growth dependent species, in order to increase the long-term effectiveness of habitat management. Our studies at Mesa de las Guacamayas emphasize the importance of approaching the study of forest plant communities from a holistic perspective that integrates wildlife components.

Much work is needed to improve the management and knowledge of the biodiversity included in the protected areas of México, as shown by our two study sites. Our findings document systems of exceptional value for conservation. It is urgent that managers design and implement research priority plans in order to start filling information gaps, such as species inventories and monitoring of ecological processes. This could be achieved through partnerships with education institutions, NGOs and other groups. In the case of Mesa de las Guacamayas, a bi-national partnership model could be sought with groups interested in the reintroduction of Thick-billed Parrots to the U.S. Southwest. The forests of Parque Nacional Cascada de Basaseachi can be used to set management standards and indicators to improve and monitor management of the surrounding forests.

References

Bray, D. B., L. Merino-Pérez, P. Negreros-Castillo, G. Segura-Warnholtz, J. M. Torres-Rojo, and H. F. M. Vester. 2003. Mexico's Community-Managed Forests as a Global Model for Sustainable Landscapes. Conservation Biology **17**:672-677.

Challenger, A. 1998. Utilización y Conservación de los Ecosistemas Terrestres de México. Pasado, Presente y Futuro. CONABIO, Instituto de Biología-UNAM, Agrupación Sierra Madre, S.C., México, D.F.

Figueroa-Rangel, B. L., K. J. Willis, and M. Olvera-Vargas. 2008. 4200 years of pine-dominated upland forest dynamics in west-central Mexico: human or natural legacy. Ecology **89**:1893-1907.

Fulé, P. Z., M. A. Ramos Gómez, C. Cortés Montaño, and A. M. Miller. 2011. Fire regime in a Mexican forest under indigenous resource management. Ecological Applications **21**:764–775.

Fulé, P. Z., J. Villanueva-Díaz, and M. Ramos-Gómez. 2005. Fire regime in a conservation reserve in Chihuahua, Mexico. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:320-330.

Hayes, K., and E. Ostrom. 2005. Conserving the world's forests: are protected areas the only way? Indiana Law Review **38**:595-617.

Herold, L. C. 1965. Trincheras and physical environment along the Río Gavilán, Chihuahua, México. Department of Geography, University of Denver, Denver, CO.

Heyerdahl, E. K., and E. Alvarado. 2003. Influence of Climate and Land Use on Historical Surface Fires in Pine-Oak Forests, Sierra Madre Occidental, Mexico. Pages 196-217 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W.

Swetnam, editors. Fire and Climatic Change in Temperate Ecosystems of the Western Americas.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial Controls of Historical Fire Regimes: A Multiscale Example from the Interior West, USA. Ecology **82**:660-678.

Howard, W. A., and T. M. Griffiths. 1966. Trinchera distribution in the Sierra Madre Occidental, México. Department of Geography, University of Denver, Denver, CO.

LaRochelle, S., and F. Berkes. 2003. Traditional Ecological Knowledge and Practice for Edible Wild Plants: Biodiversity Use by the Rarámuri in the Sierra Tarahumara, Mexico. International Journal of Sustainable Development & World Ecology **10**:361-375.

Lartigue, F. 1983. Indios y bosques. Políticas forestales y comunales en la Sierra Tarahumara. Ediciones de la Casa Chata, México, D.F.

Porter-Bolland, L. in press. Community managed forests and forest protected areas: An assessment of their conservation effectiveness across the tropics.

Table 6.1. Proposed national standard components (NOM, Norma Oficial Mexicana) for old-growth temperate forests in the SMOc.

Component	**Description**
Overstory composition	Canopy dominated by *Pinus* spp. and *Pseudotsuga menziesii*. A species rich subcanopy of *Quercus* spp. and other broadleaved species is an important component of overstory diversity.
Overstory age	Some trees in the canopy living full natural lifespans (~200-250 years for *Pinus* spp. and *Pseudotsuga menziesii*).
Overstory structure	Basal area concentrated in DBH classes >40 cm. Trees in diameter classes >60 cm must be present. Minimum basal area was 25 m^2. Snags and large logs present.
Understory	Dominated by native species in the Asteraceae, Fabaceae, Poaceae and Lamiaceae.
Indicator species	Presence of indicator species that favor old-growth habitat, such as the Thick-billed Parrot.
Limitations	This standard is based on information generated in two locations in Chihuahua, it needs to be updated as more sites are explored.

Appendix 1. Coordinates (UTM) of sampling sites at Mesa de las Guacamayas and Basaseachi. Both sites are in UTM Zone 12. Coordinates were collected using the NAD27 Datum. Site names at Mesa de las Guacamayas are: Mesa Prieta (MP), Mesa Prieta Sur (PS), Rincón de las Tinajas (RT), and El Abeto (AB). Site names at Basaseachi are: Arroyo El Estacado (AE), Cañón del Pájaro (CP), and Arroyo La Zorra (AZ).

Site	Plot	Easting	Northing
	Mesa de las Guacamayas		
MP	1	735340	3376600
	2	735240	3376600
	3	735440	3376600
	4	735140	3376700
	5	735340	3376500
	6	735240	3376500
	7	735040	3376700
	8	735140	3376500
	9	735040	3376500
	10	735040	3376400
PS	1	736200	3375400
	2	736200	3375500
	3	736100	3375500
	4	736100	3375400
	5	736100	3375300
	6	736000	3375300
	7	736000	3375400
	8	736000	3375500
	9	735900	3375400
	10	736200	3375300
RT	1	725900	3382700
	2	725900	3382800
	3	726000	3382815
	4	725900	3382900
	5	725800	3382900
	6	726000	3382900
	7	725800	3382800
	8	725808	3382717
	9	726000	3383000
	10	725700	3382800

Site	Plot	Easting	Northing
AB	1	728230	3380214
	2	728230	3380314
	3	728230	3380414
	4	728130	3380314
	5	728130	3380414
	6	728230	3380514
	7	728330	3380314
	8	728430	3380314
	9	728330	3380514
	10	728230	3380614
Basaseachi			
AE	1	775064	3130940
	2	774964	3130940
	3	774964	3131040
	4	774964	3131140
	5	774964	3131240
	6	774864	3130840
	7	774864	3130940
	8	774864	3131040
	9	774864	3131140
	10	774864	3131240
	11	774664	3131240
	12	774764	3130840
	13	774764	3130940
	14	774764	3131040
	15	774764	3131140
	16	774764	3131240
	17	774664	3130840
	18	774664	3130940
	19	774664	3131040
	20	774664	3131140
CP	1	771700	3119300
	2	771600	3119300
	3	771600	3119200
	4	771665	3119400
	5	771600	3119400
	6	771600	3119500
	7	771400	3119600
	8	771400	3119400
	9	771500	3119600

Site	Plot	Easting	Northing
CP	10	771500	3119400
	11	771600	3119600
	12	771400	3119500
	13	771600	3119700
	14	771500	3119700
	15	771450	3119700
	16	771300	3119500
	17	771300	3119600
	18	771400	3119800
	19	771300	3119700
	20	771320	3119800
AZ	1	773900	3116800
	2	773900	3117000
	3	773900	3117400
	4	773800	3116800
	5	773900	3117100
	6	773800	3117100
	7	773800	3117400
	8	773700	3116800
	9	773800	3117200
	10	773700	3116900
	11	773800	3117300
	12	773900	3117200
	13	773800	3116900
	14	773900	3117300
	15	773800	3117000
	16	773900	3116900
	17	774000	3117000
	18	774000	3116900
	19	774000	3117165
	20	773700	3116700

Appendix 2. List of flowering plant collections for Parque Nacional Cascada de Basaseachi and Ejido Basaseachi. Site names are AE: Arroyo El Estacado, CP: Cañón del Pájaro, and AZ: Arroyo La Zorra. Scientific names and authorities follow the International Plant Names Index (http://www.ipni.org). Synonyms and alternative families obtained from Van Devender et al. (2010). Numbers in the Site column indicate presence (1) or absence (0) from a site.

Scientific name	**Authority**	**Family (Alternative family)**	**Sites**		
			AE	**CP**	**AZ**
	Overstory				
Coniferopsida					
Juniperus deppeana	Steud.	Cupressaceae	1	1	1
Cupressus lusitanica	Greene	Cupressaceae	0	1	1
Pinus durangensis	Martínez	Pinaceae	1	1	1
Pinus engelmannii	Carrière	Pinaceae	1	1	1
Pinus herrerae	Martínez	Pinaceae	1	1	1
Pinus leiophylla	Schltdl. & Cham.	Pinaceae	1	1	0
Pinus lumholtzii	B.L.Rob. & Fernald	Pinaceae	1	1	1
Pinus strobiformis (*P. ayacahuite* var. *brachyptera* Shaw)	Engelm.	Pinaceae	1	1	1
Pseudotsuga menziesii	(Mirb.) Franco	Pinaceae	0	1	0
Magnoliopsida					
Ilex rubra	S. Watson	Aquifoliaceae	0	1	1
Ilex tolucana	Hemsl.	Aquifoliaceae	0	1	1
Arbutus arizonica	Sarg.	Ericaceae	0	1	1
Arbutus xalapensis	Kunth	Ericaceae	1	1	1
Quercus arizonica	Sarg.	Fagaceae	0	1	1
Quercus coccolobifolia	Trel.	Fagaceae	0	1	1
Quercus durifolia	Seemen	Fagaceae	0	0	1
Quercus hypoleucoides	A. Camus	Fagaceae	0	0	1
Quercus mcvaughii	Spellenb.	Fagaceae	1	1	1
Quercus rugosa	Née	Fagaceae	0	1	1
Quercus sideroxyla	Humb. & Bonpl.	Fagaceae	1	1	1
Quercus toumeyi	Sarg.	Fagaceae	0	1	1
Fraxinus velutina	Torr.	Oleaceae	0	1	1
Prunus serotina	Ehrh.	Rosaceae	0	1	1
	Understory				
Magnoliopsida					
Donnellsmithia juncea	(Humb. & Bonpl. ex Spreng.) Mathias & Constance	Apiaceae	0	1	1
Eryngium yuccifolium	Michx.	Apiaceae	0	1	0
Pseudocymopterus montanus	J.M.Coult. & Rose	Apiaceae	0	0	1
Ageratina calaminthifolia	(Kunth) R.M.King & H.Rob.	Asteraceae	0	1	0
Ageratina lemmonii	(B.L.Rob.) R.M.King & H.Rob.	Asteraceae	1	0	0
Ageratina stricta	(A.Gray) R.M.King & H.Rob.	Asteraceae	1	0	1
Ageratina venulosa	(A.Gray) R.M.King & H.Rob.	Asteraceae	0	1	1
Ageratum corymbosum	Zucc. ex Pers.	Asteraceae	0	1	0

Scientific name	Authority	Family (Alternative family)	Sites		
			AE	CP	AZ
Artemisia ludoviciana	Nutt.	Asteraceae	0	1	1
aff. *Bidens tenuisecta*	A. Gray	Asteraceae	0	1	1
Brickellia betonicifolia	A. Gray	Asteraceae	0	0	1
aff. *Brickellia parvula*	A. Gray	Asteraceae	0	1	0
Carphochaete pringlei var. *pringlei*	(S.Watson) Grashoff ex B.L.Turner	Asteraceae	1	1	0
Carphochaete wislizeni	A.Gray	Asteraceae	1	1	1
Coreopsis sp.		Asteraceae	0	1	0
Erigeron basaseachensis	G.L.Nesom	Asteraceae	0	1	1
Erigeron fraternus	Greene	Asteraceae	1	1	1
Erigeron neomexicanus	A. Gray	Asteraceae	1	0	1
Gutierrezia alamanii var. *megalocephala*	A.Gray	Asteraceae	1	1	1
Gutierrezia megalocephala	(Fernald) G.L.Nesom	Asteraceae	1	1	0
Hieracium fendleri	Sch.Bip.	Asteraceae	1	1	1
Lactuca sp.		Asteraceae	1	1	1
Laennecia spellenbergii	G.L.Nesom	Asteraceae	1	1	1
Leibnitzia lyrata	(Sch.Bip.) G.L.Nesom	Asteraceae	0	0	1
Perityle microglossa	Benth.	Asteraceae	0	1	0
Pseudognaphalium arizonicum	(A.Gray) Anderb.	Asteraceae	0	1	0
Pseudognaphalium pringlei	(A.Gray) Anderb.	Asteraceae	0	1	1
Pseudognaphalium sp.		Asteraceae	0	1	0
Roldana pennellii	H.Rob. & Brettell	Asteraceae	1	1	1
Solidago wrightii var. *wrightii*	A. Gray	Asteraceae	0	1	1
aff. *Solidago*		Asteraceae	0	1	0
Stevia plummerae var. *plummerae*	A. Gray	Asteraceae	1	1	1
Stevia salicifolia	Cav.	Asteraceae	1	1	0
Stevia sp.		Asteraceae	0	1	1
Verbesina sp.		Asteraceae	0	0	1
Viguiera cordifolia	A. Gray	Asteraceae	1	1	0
Viguiera linearis	(Cav.) Sch.Bip. ex Hemsl.	Asteraceae	0	1	0
Wedelia chihuahuana	B.L. Turner	Asteraceae	0	1	0
Lithospermum sp.		Boraginaceae	1	1	1
Unknown cactus sp.		Cactaceae	0	1	0
aff. *Symphoricarpos palmeri*	G.N. Jones	Caprifoliaceae (Adoxaceae)	0	1	0
Cerastium nutans	Raf.	Caryophyllaceae	0	0	1
Drymaria glandulosa	Bartl.	Caryophyllaceae	0	0	1
Drymaria multiflora	Brandegee	Caryophyllaceae	0	1	0
Silene scouleri	Hook.	Caryophyllaceae	0	0	1
Paxistima myrsinites	(Pursh) Raf.	Celastraceae	1	1	1
Helianthemum cf. *glomeratum*	Lag. ex DC.	Cistaceae	0	1	0
Sedum stelliforme	S.Watson	Crassulaceae	0	1	1
Arctostaphylos pungens	Kunth	Ericaceae	1	1	1
Comarostaphylis polifolia	(Kunth) Zucc. ex Klotzsch	Ericaceae	0	1	1
Vaccinium chihuahuense	Wilbur & Luteyn	Ericaceae	1	1	1
Euphorbia sp.		Euphorbiaceae	1	1	1
aff. *Astragalus*		Fabaceae	0	0	1
Cologania angustifolia	Kunth	Fabaceae	1	1	1
Desmodium grahamii	A.Gray	Fabaceae	0	1	1

Scientific name	Authority	Family (Alternative family)	Sites		
			AE	CP	AZ
Desmodium supinum	D.C.	Fabaceae	0	0	1
Desmodium triflorum	(L.) DC.	Fabaceae	1	1	1
Eriosema sp.		Fabaceae	0	1	0
Fabaceae sp. 1		Fabaceae	1	0	0
Fabaceae sp. 2		Fabaceae	1	1	1
Lupinus aschenbornii	S.Schauer	Fabaceae	1	0	0
Lupinus montanus	Kunth	Fabaceae	1	1	1
Phaseolus acutifolius	A.Gray	Fabaceae	0	0	1
Phaseolus sp.		Fabaceae	1	0	1
Vicia pulchella	Kunth	Fabaceae	0	0	1
Garrya ovata	Benth.	Garryaceae	1	1	1
Gentianella wislizeni	(Engelm.) J.M.Gillett	Gentianaceae	1	1	1
Halenia palmeri	A.Gray	Gentianaceae	1	0	1
Geranium atropurpureum (*G. caespitosum*)	A.Heller	Geraniaceae	0	1	1
Agastache pallida	(Lindl.) Cory	Lamiaceae	1	0	1
Hedeoma oblongifolia	(A.Gray) A.Heller	Lamiaceae	0	1	0
Hyptis sp.		Lamiaceae	0	1	1
Prunella vulgaris	L.	Lamiaceae	0	0	1
Linum neomexicanum	Greene	Linaceae	0	0	1
Linum rupestre	(A.Gray) Engelm.	Linaceae	0	0	1
Linum sp.		Linaceae	0	1	0
Monotropa uniflora	L.	Monotropaceae (Ericaceae)	0	0	1
Osmanthus americanus	(L.) Benth. & Hook.f. ex A.Gray	Oleaceae	0	1	0
Lopezia gracilis	S.Watson	Onagraceae	0	0	1
Oenothera flava	Garrett	Onagraceae	0	0	1
Seymeria sinaloana	(Pennell) Standl.	Orobanchaceae	1	0	0
Seymeria sp.		Orobanchaceae	0	1	1
Oxalis decaphylla	Kunth	Oxalidaceae	0	0	1
Oxalis sp.		Oxalidaceae	1	0	0
Polygala sp.		Polygalaceae	0	1	0
Chimaphila maculata	(L.) Pursh	Pyrolaceae (Ericaceae)	1	1	1
Aquilegia chrysantha	A. Gray	Ranunculaceae	0	1	0
Aquilegia desertorum	(M.E.Jones) Cockerell ex A.Heller	Ranunculaceae	0	0	1
Delphinium madrense	S.Watson	Ranunculaceae	0	0	1
Thalictrum pinnatum	S.Watson	Ranunculaceae	0	0	1
Ceanothus coeruleus		Rhamnaceae	1	1	0
Ceanothus depressus	Benth.	Rhamnaceae	1	0	1
Frangula betulifolia	(Greene) Grubov	Rhamnaceae	0	1	1
Potentilla oblanceolata	Rydb.	Rosaceae	0	1	1
Potentilla sp.		Rosaceae	1	1	0
Prunus microphylla	Hemsl.	Rosaceae	1	0	0
Rubus leucodermis	Douglas ex Hook.	Rosaceae	0	0	1
Bouvardia tenuifolia	Standl.	Rubiaceae	0	1	0
Galium microphyllum	A.Gray	Rubiaceae	1	1	1
Heuchera sp.		Saxifragaceae	1	1	1

Scientific name	Authority	Family (Alternative family)	Sites		
			AE	CP	AZ
Agalinis sp.		Scrophulariaceae (Orobanchaceae)	0	1	0
Castilleja ortegae	Standl.	Scrophulariaceae (Orobanchaceae	0	1	0
Penstemon sp.		Scrophulariaceae (Plantaginaceae)	1	1	0
Penstemon wislizeni	(A.Gray) Straw	Scrophulariaceae (Plantaginaceae)	1	1	1
Viola sp.		Violaceae	1	1	1
Vitis arizonica	Engelm.	Vitaceae	1	1	1
Monocotyledons					
Agave filifera ssp. *schidigera*	Salm-Dyck subsp. *schidigera* (Lem.) B.Ullrich	Agavaceae (Asparagaceae)	0	1	0
Agave sp.		Agavaceae (Asparagaceae)	0	1	0
Dasylirion sp.		Agavaceae (Asparagaceae)	0	1	1
Manfreda singuliflora	(S.Watson) Rose	Agavaceae (Asparagaceae)	0	1	1
Yucca sp.		Agavaceae (Asparagaceae)	0	1	0
Bulbostylis juncoides	(Vahl) Kük. ex Osten	Cyperaceae	0	1	0
Cyperus seslerioides	Kunth	Cyperaceae	0	1	0
Cyperus sp.		Cyperaceae	0	1	1
Maianthemum racemosum	Link	Liliaceae (Ruscaceae)	0	0	1
Zigadenus virescens (Anticlea virescens)	J.F.Macbr.	Liliaceae (Melanthiaceae)	1	1	1
Nolina microcarpa	S.Watson	Nolinaceae (Asparagaceae)	1	1	0
Goodyera striata	Rchb.	Orchidaceae	0	0	1
aff. *Habenaria crassicornis*	Lindl.	Orchidaceae	1	0	1
Malaxis sp.		Orchidaceae	0	1	1
Achnatherum sp.		Poaceae	0	1	0
Aegopogon cenchroides	Humb. & Bonpl. ex Willd.	Poaceae	0	0	1
Dichanthelium lanuginosum	(Elliott) Gould	Poaceae	0	1	1
Heteropogon sp.		Poaceae	0	1	0
Muhlenbergia minutissima	(Steud.) Swallen	Poaceae	0	0	1
Muhlenbergia sp. 1		Poaceae	0	1	1
Muhlenbergia sp. 2		Poaceae	0	1	0
Muhlenbergia sp. 3		Poaceae	1	1	1
Muhlenbergia sp. 5		Poaceae	0	0	1
Muhlenbergia sp. 6		Poaceae	0	1	0
Muhlenbergia sp. 7		Poaceae	1	0	0
Muhlenbergia sp. 8		Poaceae	1	1	1
Panicum bulbosum	Kunth.	Poaceae	1	1	1
Schizachyrium cirratum	(Hack.) Nash	Poaceae	0	1	1
Schizachyrium feense	(E.Fourn.) A.Camus	Poaceae	0	1	0
Tripsacum lanceolatum	Rupr. ex Benth.	Poaceae	0	1	1
Smilax moranensis	M.Martens & Galeotti	Smilacaceae	0	1	0