

Maintaining the high diversity of pine and oak species in Mexican temperate forests: a new management approach combining functional zoning and ecosystem adaptability

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Abstract: Mexican temperate forests, at the southernmost end of the distribution range of this ecosystem, are the world's centre of diversity of pine and oak, with 55 and 161 species, respectively. Such forests are threatened by land-use change, unsustainable forest management practices, and climate change; these threats reduce their diversity, alter the distribution ranges of species, modify disturbance regimes, and reduce ecosystem adaptability. This paper briefly reviews (*i*) the ecology of the Mexican temperate forests, (*ii*) the ecological basis for the unique diversity of pine and oak species, (*iii*) the main disturbances as well as the main drivers of global changes affecting these forests, in particular climate change, and (*iv*) the social, economic, and cultural factors to be considered in proposing a new forest management approach. It proposes a new conceptual framework to manage Mexican temperate forests that are in line with (*i*) their natural dynamics, (*ii*) the rapidly changing and uncertain global environmental, social, and economic conditions, and (*iii*) the complex adaptive system approach. This new forest management combines functional zoning, multispecies plantations, and sylvicultural interventions to increase the adaptive capacity of forests as a way to balance the increasing need for timber products with the need for other ecosystem services facing rapidly changing and uncertain future environmental, social, and economic conditions.

Key words: adaptability, biodiversity, climate change, disturbances, fire regime, forest income.

Résumé: Les forêts tempérées mexicaines, situées à l'extrême sud de l'aire de répartition de cet écosystème, sont le centre mondial de la diversité de pins et de chênes comptant 55 et 161 espèces, respectivement. Ces forêts sont menacées par la façon dont elles sont utilisées, par des pratiques de gestion de forêts non durable et dû au changement climatique; ces menaces réduisent leur diversité, modifient les aires de répartition des espèces, modifient les régimes de perturbations et réduisent l'adaptabilité de l'écosystème. Cet article examine brièvement (*i*) l'écologie des forêts tempérées mexicaines, (*ii*) la base écologique de la diversité unique d'espèces de pins et de chênes, (*iii*) les principales perturbations ainsi que les principaux moteurs des changements globaux qui affectent ces forêts, en particulier le changement climatique, et (*iv*) les facteurs sociaux, économiques et culturels, à prendre en considération, en proposant une nouvelle approche de la gestion forestière. Cet article propose un nouveau cadre conceptuel pour gérer les forêts tempérées mexicaines conforme avec (*i*) leur dynamique naturelle, (*ii*) l'approche adaptative du système complexe. Cette nouvelle gestion forestière combine un zonage fonctionnel, des plantations multi-espèces et des interventions sylvicoles pour augmenter la capacité d'adaptation des forêts afin d'équilibrer la nécessité croissante des produits forestiers avec la nécessité de d'autres services écosystémiques exposés à des conditions environnementales, sociales et économique et incertaines.

Mots-clés : adaptabilité, biodiversité, changement climatique, perturbations, régimé de feu, revenu de la forêt.

Mexican temperate forests

Mexican temperate forest ecosystems include single-species or mixed forests of pine (*Pinus* spp.), oak (*Quercus* spp.), and many other genera such as *Abies*, *Pseudotsuga*, *Picea*, *Cupressus*, and *Juniperus* and species of more specific origin (*Arbutus xalapensis*, *Alnus firmifolia*, *Prunus capuli*) or restricted distribution (*Pinus hartwegii*), and endemics (*Crataegus mexicana*) (Fig. 1) (Perry 1991; Farjon and Styles 1997). Three subgenera of the genus *Quercus* occur in Mexico: *Erythrobalanus* (white oaks); *Lobatae* (red oaks); and *Protobalanus* (intermediate oaks). Mexican temperate forests also harbour about 656 species of amphibians, 1300 species of birds, 1586 species of reptiles, and 146 species of mammals, many of which are restricted to temperate forest habitats (Challenger 1998; Ceballos et al. 2002).

While pine and oak forests are widely distributed throughout the northern hemisphere (North America, Europe, and Asia), reaching farther south to Central America (Richardson et al. 2007), Mexico is recognized as the major diversity centre for both genera. Of the 110 pine species and 450 oak species known worldwide, some 46 and 170 species, respectively, are indigenous to Mexico, making this country the major diversity and evolutionary centre for pine and oak species in the American continent (Perry 1991; Rzedowski 1993; Farjon and Styles 1997; Zavala Chávez 2007). It is estimated that some 24 pine species and 109 oak species are

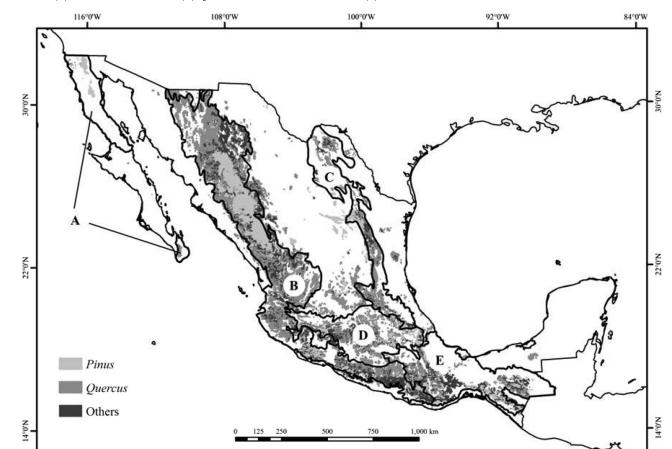
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Received 20 December 2014. Accepted 6 May 2015.

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100°0'W

Fig. 1. Distribution of Mexican temperate forests. Letters indicate locations of geographical regions: (A) Baja California, (B) Sierra Madre Occidental, (C) Sierra Madre Oriental, (D) Eje Neovolcánico Transversal, and (E) Sierra Madre del Sur.

endemic to Mexico; this represents 55% and 68% of the world's pine and oak endemic species, respectively (Rzedowski 1978; Perry 1991; Farjon and Styles 1997; Zavala Chávez 2007). By contrast, the United States (US) and Canada together harbour 87 oak species, 52 of which are also found in Mexico. Canada and the US are home to 9 and 25 pine species, respectively, whereas Mexico harbours 21 and 45 pine species not shared with the US or Canada, respectively (Richardson et al. 2007).

108°0'W

116°0'W

Mexican temperate forests host many commercially valuable timber species (Food and Agriculture Organization of the United Nations (FAO) 2010). Pine and oak species accounted for 78% and 10%, respectively, of the country's timber production during the period 2000-2010 (Comisión Nacional Forestal (CONAFOR) 2012). Pine timber is mainly used for planks and furniture, whereas oak timber is primarily used for construction work, charcoal production, local handcrafts, and furniture (CONAFOR 2012). Pine and oak forests also sustain community forestry, providing timber and nontimber forest products and services (Bray and Merino 2005), including materials (wood, fibre, and food), energy resources (firewood), and a number of ecosystem services such as groundwater recharge, climate regulation, and lessening of land degradation (Galicia and Zarco-Arista 2014). However, only about 12% of these forest communities are subject to environmentally sound management according to CONAFOR. Community forestry in Mexico must adopt a more holistic approach in developing a forestry program as proposed by CONAFOR (2012). CONAFOR, in its proposal to the National Strategy for Sustainable Forest Management for Increasing Production and Productivity 2013-2018 (ENAIPROS) and the 2025 Strategic Forest Program (PEF 2025), considers that

sustainable forest management in Mexico must harness and increase the productivity of forest ecosystems through improved silvicultural practices but must also recognize and generate alternatives for other benefits (biodiversity conservation, maintenance of water and soil contribution to the global carbon cycle, and multiple socioeconomic benefits). This is to be ensured through regulation, incentives, financing, and other policy instruments to achieve the goal of sustainable forest management. Mexican temperate forests have received little attention in theoretical reviews of forest resources, forest ecology, and global climate-change models at a regional level (Bréda et al. 2006; Gómez-Mendoza and Arriaga 2007; Richardson et al. 2007; Gómez-Díaz et al. 2011). Autoecological studies in Mexican temperate forests are also scarce (Eguiluz-Piedra 1985; Farjon and Styles 1997). In fact, forestry research in Mexico has focused primarily on estimating wood volume and timber extraction (Bray and Merino 2005), with little information on forest ecology and the panoply of environmental goods and services provided by forests (Galicia and Zarco-Arista 2014). This paper focuses on describing the interactions between ecosystem processes, species distribution and diversity of mainly oak and pine species, and the dynamics of natural (wind and fire) and anthropogenic (timber harvest and climate change) disturbances. It serves as a basis for proposing a new forest management approach that is compatible with natural processes, the rapidly changing and uncertain social, economic, and environmental conditions, and action plans to prevent further degradation of these ecosystems in Mexico.

92°0'W

84°0'W

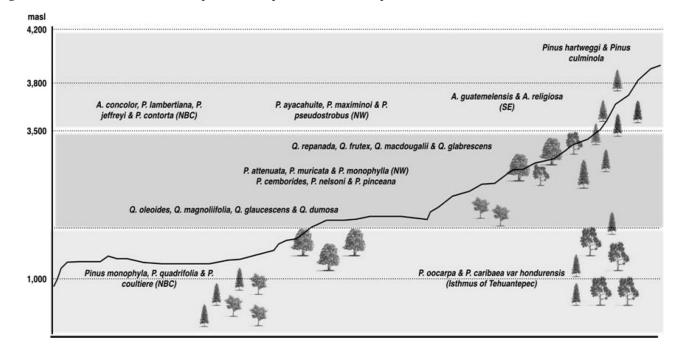


Fig. 2. Altitudinal distribution of several pine and oak species in Mexican temperate forests.

Ecological basis for this high biological diversity of oaks and pines and conservation status

Geological and paleoclimatic evidence suggests that together natural barriers to gene flow and naturally induced climate change in the past explain the high number of pine and oak species that coexist today in Mexico (Farjon and Styles 1997; González-Rodríguez et al. 2004). For pines, occasional shelter during glacial periods allowed the conservation of many species that expanded their distribution during interglacial periods of recolonization (Eguiluz 1982; Perry 1991; Rzedowski 1993; Farjon and Styles 1997). The high species richness of the genus Pinus can be explained by the existence of two diversification centres: (1) the Trans-Mexican Neovolcanic Belt, which bore three polymorphic species (P. devoniana, P. montezumae, and P. pseudostrobus) that have further radiated throughout many mountainous regions in Mexico; and (2) northeastern Mexico, characterized by adaptations to arid conditions, formation of mountain islands, and local endemism (Fig. 1) (Eguiluz-Piedra 1985; Rzedowski 1993; Farjon and Styles 1997). The Sierra Madre Occidental, which stretches from the Sonora-Arizona border to the Transvolcanic Belt, is particularly rich in diversity as it has the country's largest area of temperate forests and a wide variety of habitats. There are 24 species of pine (46% of the national total) and 54 species of oak (34%) (González-Elizondo et al. 2012). For the genus Pinus, the diversification centres, along with migration processes, resulted in five distinct regions that differ in endemism, species richness, composition, diversity, and ecology (Fig. 1). Unlike the wide distribution ranges and low diversity of pine and oak species in boreal regions (Farjon 1990; Farjon and Styles 1997), in Mexico, these species are broadly distributed with distinct ecological ranges. Pine species are found at elevations ranging from 100 m above sea level (a.s.l.) (P. caribaea) to over 4000 m a.s.l. (P. hartwegii), and annual rainfall ranges from 200 mm (P. lambertiana) to 2500 mm (P. pinceana) (Fig. 2). At local and regional scales, the structure and composition of vegetation is determined by local environmental characteristics such as geologic substratum, soil type, elevation, topography and microclimate conditions, soil fertility and quality, humidity, and temperature (Eguiluz-Piedra 1985; Challenger 1998; Sánchez-González 2008).

Genetic diversity has been assessed in commercially valuable, wide-ranging timber species such as P. patula, P. oocarpa, P. greggii, P. pinceana, P. leiophylla, Pseudotsuga menziesii, and Cedrela odorata (Aguirre-Planter et al. 2000; Molina-Freaner et al. 2001; Parraguirre-Lezama et al. 2002; Dvorak et al. 2009; Rodríguez-Banderas et al. 2009). These studies highlight the high genetic diversity of Mexican pine species (Farjon and Styles 1997; Delgado et al. 2007; Moreno-Letelier and Piñero 2009). Delgado et al. (1999) suggest that most conifers have high levels of genetic variation and relatively little genetic differentiation among populations. The principal explanation for the low genetic differentiation found in conifer species is based on the reproductive systems particular to this group (seed and pollen are wind dispersed, which allows a more efficient gene flow among distant populations). However, this pattern can be modified by other factors such as environmental fluctuations and microspatial habitat selection.

For example, P. leiophylla, a widely distributed species, possesses a high genetic diversity due to its outcrossing breeding system and an intense gene flow between populations (Rodríguez-Banderas et al. 2009). It has also been reported that two P. radiata populations growing in contrasting environments displayed the same level of genetic variability but differed significantly from each other (Moran et al. 1998). Molina-Freaner et al. (2001) reported that P. pinceana, P. laguanae, and P. muricata are rare species with high levels of genetic variability, as indicated by their high heterozygosity and high between-population differentiation. This has favoured selection of high-yielding genotypes for commercial plantations and reforestation programs in Mexico and other countries (Molina-Freaner et al. 2001). Sánchez-Velásquez et al. (2009) suggested that P. maximinoi and P. patula might be useful for restoration works in mountainous areas, whereas exotic species such as P. sylvestris and P. radiata var. binata can serve as nurse plants to facilitate the regeneration of other natural pine species. Owing to its rapid growth and good adaptation to different environments, P. greggii has been widely used in reforestation. These differences among species may be associated with adaptation to different degrees of variation between and within provenances or populations, including variations in growth relative to soil pH (Ramírez-Herrera et al. 2005). For example, to determine the degree of genetic isolation between populations, the southern stands (Puebla, Hidalgo, and Querétaro) grow at lower elevations, with higher mean annual temperature and precipitation (±1.720 m, ±17.5 °C, and ±1.370 mm, respectively) than the northern stands (Coahuila and Nuevo Leon) (±2.450 m, ±13 °C, and ±640 mm, respectively) (Ramírez-Herrera et al. 2005).

In America, the genus Quercus is distributed from southern Canada to Colombia. Geological history has created specific discontinuities due to climate changes and gene barriers (Nixon 1993). During the most recent glacial period in North America, some 12 000 years ago, oak species migrated northward. As a result, closely related species are now commonly found in geographically separated regions (Sauer 1988; Zavala Chávez 1998) (Table 1). In temperate regions, colder temperatures during glacial periods may have caused population decline because many oaks that do not undergo winter dormancy have limited cold tolerance (Cavender-Bares et al. 2011). Fragmentation and isolation of populations, along with limited gene flow, would have naturally followed. In contrast, less drastic changes in climate may have limited such impacts in Central America (Cavender-Bares et al. 2011). In Mexico, oak species grow in temperate and tropical zones, but the highest species richness is found in temperate zones, particularly in the central and southern parts of the country where up to 75 oak species occur (Challenger 1998); it is in these regions and the Sierra Madre Oriental that the largest number of pine species also occurs. Oak forests are widely distributed in Mexican mountain ranges, covering approximately 5.5% of the country's surface area (Challenger 1998). The highest diversity of oak species, 95% of the known Mexican species, occurs at elevations ranging between 1200 and 2800 m, although oak species can be found from 200 to 3500 m (Fig. 2). White oaks are widely distributed in the northeastern zone, whereas red oaks mostly occur in western and southern Mexico (Nixon 1993; Zavala Chávez 1998; Valencia 2004). The genus Quercus displays a remarkable floristic, physiognomic, and ecological diversity, including entirely deciduous and fully evergreen species.

For example, *Q. laceyi*, a medium-stature tree, ranging in height from 3 to 8 m, typically colonizes hot, dry sites and is both the lowest ranging tree species growing in Sierra del Carmen, Coahuila, Mexico, and the dominant low-elevation oak in savannahs and riparian areas. *Quercus sideroxyla* is the dominant high-elevation oak in Sierra del Carmen (Nixon 1993; Valencia 2004). Genetic diversity, as assessed by nuclear microsatellites, is higher in the tropical species *Q. oleoides* than in the temperate *Q. virginiana*, but neutral genetic differentiation between populations is higher in the latter (Cavender-Bares et al. 2011). In addition, oak species are morphologically highly variable, display a high phenotypic plasticity, and have great potential for hybridization and genetic introgression (Cavender-Bares 2007). However, no conservation strategies for gene banks exist in Mexico (Cavender-Bares 2007; Cavender-Bares et al. 2011).

Finally, pine and oak forests are the ecosystems least represented in protected areas in Mexico, far below the 12% recommended by some authors (CONABIO 2007) (CONABIO: Comisión Nacional de Áreas Naturales Protegidas y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad & The National Commission for Knowledge and Use of Biodiversity Commission]). Arriaga-Cabrera et al. (2009) estimated that protected areas cover <5% of the temperate forests, with only 5.9%, 5.4%, and 4.6% of the pine, oak, and pine-oak forests, respectively, being protected. However, the pine-oak forests have a higher percentage of protection (7.1%). Temperate forest protection should be increased because together oak forests represents high beta diversity for the country. On the other hand, Aguirre-Gutiérrez and Duivenvoorden (2010) concluded that although high-elevation species (e.g., P. hartwegii) are well represented in protected areas, low-elevation species (P. attenuata, P. cembroides subsp. cembroides, P. radiata var. binata, P. rzedowskii, and P. muricata) are poorly represented in these

Table 1. Distribution of oak species in five regions of Mexico.

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Region	Species	Exclusive	Е	L	Р
Northwest	47	16	19	25	3
Northeast	45	8	17	28	0
West	53	1	25	28	0
Central	66	1	33	33	0
Southeast	49	9	27	22	0

Note: E, species of the subgenus *Erythrobalanus*; L, species of the genus *Lepidobalanus*; and P, species of the genus *Protobalanus*.

areas. It has been suggested that efforts should be made to protect pine species growing in the Sierra Madre Occidental and Sierra Madre del Sur. Delgado et al. (2008) have suggested on the basis of phylogenetic, genetic, and demographic data that they should also be protected in Baja California.

Stand dynamics and disturbance impacts

In Mexico, some 1582 040 ha of temperate and tropical forests were burned in the 1970s, 2 579 760 ha in the 1980s, and 2 516 979 ha in the 1990s. Within that period, the year 1998 — an ENSO year - was particularly dramatic, with 14 445 wildfires recorded and 850 000 ha affected (CONAFOR 2008), and the year 2011 had 12 061 wildfires recorded and 954 946 ha affected. The role that wildfire played in structuring the pine and oak forests of Mexico has been discussed but no consensus as to its importance has been reached (Table 2) (Rzedowski 1993; Fulé and Covington 1996, 1998; González-Rosales and Rodríguez-Trejo 2004; González-Tagle et al. 2008; Rodríguez-Trejo 2008). For example, Rzedowski (1993) does not regard wildfires as an integral part of the forest's natural dynamics because they are mostly the result of grassland management and agricultural practices. Indeed, wildfires are often associated with land-use intensity, as shown by the relationship between their highest frequency of occurrence and the agricultural calendar (CONAFOR 2008; Manzo-Delgado et al. 2009; Ávila-Flores et al. 2010; Yocom and Fulé 2012). On the other hand, Fulé and Covington (1998), Rodríguez-Trejo and Fulé (2003), and Richardson et al. (2007) regard wildfire as an integral part of the structure, functioning, and regeneration pattern of temperate and boreal forests, because it promotes organic matter recycling and species succession and creates a mosaic of environmental conditions that fosters ecosystem diversity and stability. However, pine and oak species differ in their response to forest fire (Table 3), particularly in terms of their regeneration from seed; in some species of pine with serotinous cones, fire favours recruitment, whereas in oak species, it reduces seed viability. Some pine and oak species are characterized by frequent nonlethal fires, but a few pine and oak species persist in areas characterized by lethal crown fires. Mexico has established a fire management - fire exclusion policy to encompass any type of fire management strategy, including fire suppression (Fulé and Covington 1994, 1999; Rodríguez-Trejo and Myers 2010). Information on fire adaptation in oak and pine species is limited and based on inferences about climate, growth form, vegetative regeneration, and regeneration niche (Rodríguez-Trejo and Fulé 2003; Rodríguez-Trejo and Myers 2010). In contrast, drought or delays of rainfall in other places have led to a rise in wildfire intensity and hence have promoted the expansion of the distribution ranges of some species and the local extinction of others (Richardson et al. 2007). The debate now is not if but how anthropogenic vs. climate-driven fires affect forest structure given that forest's natural or historic fire regime.

The lack of consensus concerning the role of fire on the structure, composition, and functioning of pine and oak is probably due to the wide spatial heterogeneity in the distribution, presence, and intensity of fires and in the biology and ecology of the species (Table 2). For example, the frequency and intensity of fires

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Table 2. Biological legacies (mature	forest), contemporary threats, and effects or	Table 2. Biological legacies (mature forest), contemporary threats, and effects on structure and function of Mexican temperate forests.	
Mature forest ^a	Land cover change ^b	Forest management ^c	Climate change ^d
Altitudinal distribution	Habitat and biodiversity loss	Change in the composition from pine to oak with selection methods	Change in the distribution ranges of species
Biodiversity (genetic, species and ecosystems)	Fragmentation	Dominance of pine species with prescribed burns	Dominance of pine species less tolerant to water deficit
Functional redundancy	Change in species composition	Loss of mechanisms of stabilization of carbon and nutrients	Migration of pine trees in altitudinal gradient
Carbon pools	Reduction in above- and below-ground carbon pools	Change in the light environment and soil temperature Biodiversity loss and soil moisture	Biodiversity loss
Connectivity	Loss of mechanisms of stabilization of carbon and nutrients	Modification of successional processes	Increase in mortality of mature trees through drought
Resistance and resilience Complexity	Anthropogenic fire regimes Biodiversity loss Loss of surface horizons and soil structure Increase in the dominance of few species	Biodiversity loss Increase in the dominance of few species	Droughts Pests
Spatial and temporal heterogeneity	Spatial and temporal heterogeneity Structural and landscape homogeneity		Extreme meteorological events Alteration of hydrological regime

et al. 2002; Zavala Chávez 2007; Dvorak et al. 2001; Parraguirre-Lezama Farjon and Styles 1997; Aguirre-Planter et al. 2000; Molina-Freaner Rzedowski 1993; mature forest: Perry 1991; ^aFor

et al. 2009;

2007; Nájera-Luna et al. 2011; Saynes et al. 2012. Pfor land use change: Gómez-Pompa 1985; Masera et al. 1997; Challenger 1998; CONABIO 2007; Arriaga-Cabrera et al. 2009; Manzo-Delgado et al. 2009; Ávila-Flores et al. 2010. For forest management: Negreros and Snook 1984; Pineda and Sánchez-Velásquez 1992; Asbjornsen et al. 2004; Jardel-Peláez et al. 2004; Guerra et al. 2007; Nájera-Luna et al For climate change: Villers-Ruíz and Trejo-Vázquez 1998; Gómez-Mendoza and Arriaga 2007; Zacarías-Eslava and del Castillo 2010; Gómez-Díaz et al. 2011; Galicia et al. 2015. Rodríguez-Banderas et al. 2009; González-Elizondo et al. 2012.

is spatially more heterogeneous in the south than in central and northern Mexico (Galicia et al. 2015), but more precise data are lacking. Fire regimes vary spatially and temporally, with lowintensity surface fires or relatively frequent high-intensity fires or infrequent high-intensity fires (Rodríguez-Trejo 2008). Changes in extension, composition, and distribution of oak and pine species in response to fire are influenced by disturbance, climate variability, and modern land use (González-Espinosa et al. 1991; González-Tagle et al. 2011). Hence, tree dynamics are not driven by large-scale fire dynamics as only 10% of fires occur in temperate forests; however, fire is a local driver of tree dynamics in some regions of the country as it creates space among individuals or stands for seed germination in the Sierra Madre Oriental, northern Mexico (González-Tagle et al. 2008).

Tree mortality and species replacement in forests are markedly influenced by natural disturbances other than fire. Gap dynamics is one of the major drivers of regeneration in temperate forests but occurs mostly at a local level as a result of environmental (physical, biological, and resource) heterogeneity (González-Tagle et al. 2011). In southern Mexico, relatively shade-tolerant species such as Q. rugosa and Q. castanea grow better under nurse plants. In fact, it has been suggested that disturbance-free successional paths should lead to mature forests dominated entirely by shadetolerant oak species (Farjon and Styles 1997). Nevertheless, pines can replace oaks in successional areas where oaks are exploited for firewood, thus inhibiting the dominance of shade-tolerant species (García-Barrios and González-Espinosa 2004). In the Baja California Sur region, disturbance patterns are associated with the occurrence of hurricanes. Arriaga (1988) reported that about 18% of the state's surface area had been affected by tree falls, which had led to high mortality (up to 334 individuals ha-1) in the humid season. Unfortunately, species-replacement mechanisms in mature forests are still poorly understood. In northern Mexico, a higher proportion of fires are initiated by lightning (Rodríguez and Fulé 2003; Fulé et al. 2011); however, Meunier et al. (2014) report that recruitment peaks in this region are more closely tied to the local processes of tree recruitment and seedling survival.

Some emerging challenges in Mexican temperate forests

Mexican temperate forests have been negatively affected by land-use change, poor tenure, illegal logging, unsustainable timber extraction, and climate change (Table 2), all of which have considerably reduced their area and species composition (Rzedowski 1978; Gómez-Pompa 1985; Masera et al. 1997; Challenger 1998). Some 40% of the area originally covered by these ecosystems has been converted into agricultural fields and, more recently, into pasturelands for livestock ranching (Challenger 1998). Illegal logging is significant, accounting for 3-5 million m³·year⁻¹ of the total production of 7 million m³·year⁻¹ (Rzedowski 1978; Gómez-Pompa 1985; Masera et al. 1997; Challenger 1998). It is now estimated that 40% of timber production in Mexico comes from illegal logging (World Forest Institute 2015). Together, land-use change and illegal logging are responsible for endangering about 40% of the species of pines in Mexico (P. attenuata, P. caribaea, P. contorta, P. coulteri, P. culminicola, P. jaliscana, P. jeffreyi, P. johannis, P. martinezii, P. maximartinezii, P. monophylla, P. muricata, P. nelsonii, P. pinceana, P. quadrifolia, P. remota, P. rzedowskii, P. strobiformi, and P. strobus) (Challenger 1998; Sánchez-González 2008).

Forest communities and land tenure

Forest land tenure requires social organization and participation. For example, it has been argued that supervision of logging through community forest management and good social organization could avoid the severe deforestation (Bray and Merino 2005). The sustainable use of forest resources can be achieved if communities (*i*) perceive that forest resources are economically

Climate change			Fire		
Sensitive	Moderately sensitive	Not sensitive	Resistant	Not resistant	
Pinus					
P. oocarpa P. chihuahuana P. rudis P. hartwegii	P. patula P. durangensis P. teocote P. ayacahuite P. culminicola P. leiophylla P. herrerae	P. cembroides P. douglasiana P. strobiformis	P. hartwegii P. montezumae P. teocote P. culiminicola P. maximartinezii P. rzedowsky P. cembroides P. lagrunde P. jaliscana P. nelsonni P. arizonica	P. reflexis P arizonica P. lumholtzi P. strobiformis	
Quercus					
Q. crispipilis Q. peduncularis Q. acutifolia	Q. sideroxyla Q. mexicana Q. eduardii Q. castanea Q. laurina Q. rugosa Q. magnoliifolia Q. crassifólia	Q. obtusata Q. durifolia Q. segoviensis Q. elliptica Q. scytophylla Q. laeta	Q. ryshophylla Q. laceyi Q. macrophylla Q. chapmanni Q. crassipes Q. crassifolia Q. rugosa Q. laeta Q. obtusata		

Table 3. Sensitivity of species of Pinus and Quercus to climate change and fire.

Note: Sources: Villers-Ruíz and Trejo-Vázquez 1998; Gómez-Mendoza and Arriaga 2007; Gómez-Díaz et al. 2011; Himmelsbach et al. 2010; Rodríguez-Trejo and Myers 2010; Poulos et al. 2007; Yocom and Fulé 2012.

viable, (*ii*) exercise control over their use, and (*iii*) consider the long-term advantages of using renewable resources (Bray and Merino 2005; Merino-Pérez and Segura-Warnholtz 2007).

For example, the communities of Nuevo San Juan Parangaricutiro in Michoacán and Ixtlán de Juárez in Oaxaca are good examples of forest sustainability. In each case, historical processes have generated political and social changes that have given rise to the emergence of a community-based company; this has the capacity to plan guidelines for managing the exploitation of their forests in balance with economic and social development. In Nuevo San Juan, for more than 20 years, the community has maintained a wide range of successful eco-businesses based on sustainable forestry, involving eco-friendly production of furniture and resins, ecotourism, wood extraction through agroforestry, and wildlife management (González-Carmona et al. 2014).

In Ixtlán de Juárez, a well-organized forestry company maintains tight controls over the forest; a system of registration of timber produced and sold keeps track of the transactions from forest to buyer (Matthews 2002). The distribution of economic benefits as profit sharing is fair, and there is an explicit policy of increasing the added value of the forestry production. Thus, community commitment to forest protection is broadly based on the economic advantages to be derived from forest use. Interest in conservation is also related to the domestic — often traditional uses of the forest and to the perception and valuation of the "environmental services" that forests provide; effective factors include the concern to maintain water production, the perception of the forest as an inheritance for coming generations, and the pure enjoyment of forest areas.

Two decades of community forest management have led, in some cases, to a more balanced approach; in recent years, forest management plans have been more varied, promoting a mixture of intensive forestry, selective logging, and conservation, depending on a set of ecological variables (soils, slope, existing species, and closeness to water bodies). These practices are consistent with the emergence of communities' territorial planning practices and capacities (Bray and Merino 2005; Merino-Pérez and Segura-Warnholtz 2007). On the basis of technical information about the different areas and resources that they own, but also on the basis of traditional knowledge and values and the evaluation or their own needs, communities decide the best uses to be given to the lands and resources that they possess.

This experience could be replicable in other regions of Latin America that share similar fundamental conditions with Mexican forest regions, where forests constitute a key element for community survival (Klooster 1999; Klooster and Masera 2000). Finally, the same conceptual framework of sustainability is essential in the implementation of policies that lead to the development and conservation of temperate forests, together with the procurement of goods and services. It is necessary to promote change and direction for the implementation of sustainable forest management to meet the needs of social groups living on the timber and nontimber forest products, as well as the needs of the forest industry and the regional and national economy.

Current forest management

In general, Mexican forestry focuses on the overextraction of a few timber species (P. arizonica, P. engelmannii, P. montezumae, P. pseudostrobus, P. cooperi, and P. durangensis) (FAO 2010), and this results in the loss of other forest resources (fibres, seeds, roots, and medicinal plants), the local extinction of commercially valuable species, and a loss of diversity (Table 2). Furthermore, the use of species of pines, particularly the uncontrolled extraction of seeds of P. maximartinezii for sale in national and international markets, threatens their natural regeneration and distribution (López-Mata 2001). The use of traditional timber harvesting techniques negatively affects soil fertility and vegetation structure (Table 2). For example, Nájera-Luna et al. (2011) have shown that for every 1 m³ of timber harvested, 0.481 m³ of soil is removed, and this has implications for soil fertility and limits the potential future regeneration of timber species (Nájera-Luna et al. 2011). This is accompanied by changes in the total soil carbon concentration, from 4.7 kg·m⁻² in the old-growth forest to 3.6 kg·m⁻² in thinned stands in Sierra Norte of Oaxaca (Saynes et al. 2012).

Disruption of key natural ecosystem processes reduces forest adaptability and resilience (Table 2). For example, intense and recurrent human-induced disturbances reduce the diversity of disturbance-sensitive species; however, the occurrence of relatively frequent low-intensity fires is believed to be part of the processes of these forests (González-Rosales and Rodríguez-Trejo 2004). In southeastern Mexico, the coexistence of Pinus and Quercus species is often associated with low-intensity disturbances (selective timber extraction, firewood extraction, and cattle grazing). Early-successional species are used for fuel, whereas late-successional species are used for timber (González-Espinosa et al. 1991; Galindo-Jaimes et al. 2002). Asbjornsen et al. (2004) reported that coexistence patterns of Pinus and Quercus seedlings are regulated by a synergic interaction between extreme events (droughts) and fragmentation. Each genus depends on the presence of shrubs to facilitate colonization in the presence of drought, but pines are the more efficient colonizers in highly fragmented landscapes thanks to their ability to rapidly use available resources (Asbjornsen et al. 2004).

Mexico has used two major approaches for managing its temperate forests. First, the Mexican Method of Irregular Forestry Development (MMOBI) is based on selective logging, with cut intensity varying according to the current increase in volume of each stand and with a fixed cutting cycle, respecting the maximum cut of 30%-40% in stocks and a minimum cutting diameter (30 cm for pine) (Zerecero and Pérez 1981; Pineda and Sánchez-Velásquez 1992; Gadow et al. 2004). The aim of the method is to modify the characteristics of forests to obtain a balanced composition of age classes in stands while conserving forest density. Application of MMOBI has resulted in a reduction in stocks of shade-intolerant pines and replacement by the more shade-tolerant oaks and other hardwoods (Hernández-Díaz et al. 2008). Second, the Forestry Development Method (MDS) aims to convert irregular forests with little pine regeneration into pine-dominated forests through the creation of large gaps, shelterwood, or clear-cutting followed by planting of a few commercial pine species. This approach has greatly simplified both the composition and structure of many Mexican temperate forests (Zerecero and Pérez 1981; Negreros and Snook 1984; Hernández et al. 1996). Recently, many ejidos receive some sort of financial support from CONAFOR or the Commission of Natural Protected Areas (CONANP) for conservation projects, specifically from Mexico's payments for ecosystem services programs (PES). However, many pine forests in Mexico remain devoid of any management.

Oaks are rather shade-tolerant, so they can establish successfully in small gaps created by selective logging. Moreover, oaks can re-sprout from stumps left after cutting or burning (Jardel 1985; Negreros and Snook 1984; Jardel-Peláez et al. 2004; Lara-González et al. 2009). In undisturbed mixed oak-pine forests, successional processes proceed from early pine-dominated stages to late stages in which oak is dominant. This process is being accelerated by the effect of selective logging (Table 2) (Negreros and Snook 1984; Jardel-Peláez et al. 2004). Therefore, the use of selective logging as a forest management method is ineffective for maintaining the mixed character of these forests (Negreros and Snook 1984; Pineda and Sánchez-Velásquez 1992). In Mexico, the current sylvicultural treatments have been applied without a good knowledge of the biology and growth patterns of the specific species exploited (Zerecero and Pérez 1981; Islas et al. 1988). Only a few sylvicultural approaches have been used in the temperate forest of Mexico, mainly selective and selection cuts, and this has greatly limited the range of ecological conditions (soil type, topography, and altitude) found in the forest (Table 2) (Negreros and Snook 1984; Pineda and Sánchez-Velásquez 1992; Jardel-Peláez et al. 2004; Guerra et al. 2007).

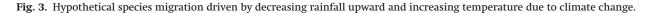
Climate change and forest management

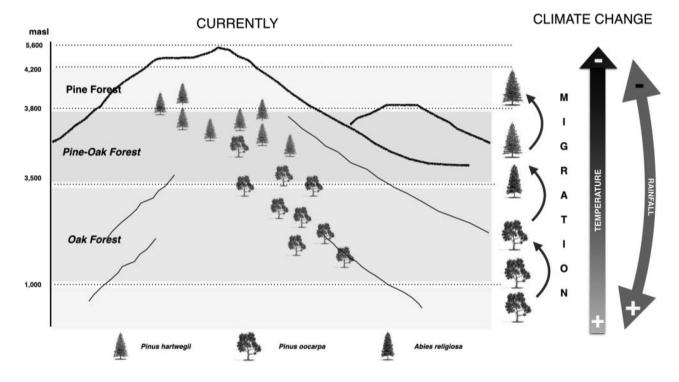
Climate change, too, can affect forest composition, by altering growth, colonization, and successional patterns (Table 3). Mexican temperate forests are among the ecosystems most vulnerable to climate change, at both the ecosystem (Villers-Ruíz and Trejo-Vázquez 1998) and species (Gómez-Mendoza and Arriaga 2007; Galicia et al. 2015) levels. Evidence comes from experimental studies and species modelling under various climate-change scenarios. Global models suggest that temperate forests will be displaced under conditions of climate change (Villers-Ruíz and Trejo-Vázquez 1998), creating new assemblages of species. Gómez-Mendoza and Arriaga (2007), using a statistical downscaling process of the Special Report on Emission Scenarios (SRES) A1 (severe) and B2 (conservative) scenarios, concluded that species of both Pinus and Quercus differ in their sensitivity to climate change (Table 3; Fig. 3). They also suggested that species with a wider geographical range are not less vulnerable to climate change, because the change in a species' geographical range seems to be associated with its own climatic tolerance. For example, P. rudis, P. chihuahuana, P. culminicola, Q. peduncularis, and Q. sideroxyla, which currently occur in semicold, semi-humid climates, are highly vulnerable to climate change, as suggested by reductions of 30%-45% in their geographical ranges by the year 2050 under the scenarios analysed. More recent studies (Himmelsbach et al. 2010, 2012) concluded that P. pseudostrobus is among the Mexican tree species most vulnerable to climate change, particularly in the central-northern region (Table 3)

Climate change signals would also occur over elevation gradients, with high temperature and low rainfall becoming more frequent at high-elevation sites, negatively affecting both tree species composition and recruitment. New climatic conditions in high-elevation zones might reduce frost events, which would favour the upward migration of low-elevation species (Table 3; Fig. 3). By contrast, high-elevation species such as P. hartwegii would be more prone to local extinction as they would not be able to migrate further up in response to climate change. Such distributional shift of species might favour the migration of oak forests towards higher elevations. Zacarías-Eslava and Del Castillo (2010) suggested that, at the foothills of mountains, oak forests might adapt better than pines to climate change. In addition, in several parts of the world, human activities and climate factors associated with climate change have modified fire regimes. The risk of fires in Mexico has been augmented in recent years by climate change. Fire is closely associated with the negative rainfall anomalies now occurring in most parts of northern Mexico and southern USA (Fulé et al. 2012; Galicia et al. 2015). A similar correlation between exceptionally dry periods, as was caused by ENSO in 1998, and exceptionally severe fire seasons has been clearly established for Indonesia, Africa, and Central and South America. So there is an increasing consensus worldwide on the need to develop novel forest management strategies based on scientific knowledge to improve the resilience and adaptability of ecosystems and human well-being under the new conditions of rapid global change (Galicia et al. 2015).

Forest management recommendations: toward a new conceptual framework

Although in Mexico it has been suggested that new forms of forestry and plantations are necessary, with restoration of natural forests, community-based forestry uses, agroforestry, urban forestry, and management of international forest amenities, these proposals have not been implemented. Mendoza et al. (2005) propose an approach to landscape management. Since 2005, forest planning has implemented a new sylvicultural regime — one designed to transform current stand structures back to those that existed before timber-oriented forest management in the region. As discussed, current Mexican forest management approaches are





still rooted in the traditional narrow timber-based approach that has proven inadequate for addressing current and emerging challenges to forest ecosystems. This traditional approach to production forestry was developed to ensure a sustained yield of timber products, disregarding the natural processes that have created and maintained the diversity of structure, function, and species as found in the temperate forests of Mexico (FAO 2005). In fact, few studies have documented the effects of such harvesting on the structure and functioning of these pine and oak forest ecosystems (Saynes et al. 2012). However, Mexican temperate forests are also being managed for other goods and services in addition to timber management (CONAFOR 2010), but we know little about the structural, biological, and climatic complexity, as well as the complex successional processes that are typical of high-mountain temperate forests. We thus propose a new conceptual framework to manage Mexican temperate forests that is more in line with (i) the natural dynamics of these forests, (ii) the rapidly changing global environmental, social, and economic conditions, and (iii) the emerging complex adaptive system approach.

For Mexican temperate forests, the following features and functions should be maintained as a priority: biodiversity, water capture, carbon storage, timber forest resources, and nontimber forest resources (Galicia and Zarco-Arista 2014). To protect biodiversity and forest resources for the future, many forest regions in the world are now advocating forest practices that are emulating the natural disturbances that have created this diversity of forest structure and function in the first place (Harvey et al. 2002). This requires an understanding of the extent, intensity, and frequency of past natural disturbances. However, this approach may be insufficient because future social, economic, and environmental conditions are likely to differ from those in the past. A modification of this forest management based on natural disturbance (Puettmann et al. 2009; Puettmann 2011; Messier et al. 2013) entails complexity science. This approach still recognizes the necessity to maintain the diversity of structure, function, and species naturally found in our forests through a variety of forest harvesting approaches, but instead of looking toward past or current forest conditions and focusing on specific stand structure and species composition, it focuses on adapting the forest to future uncertain environmental conditions. The role of the forest manager, then, is not to impose a strict predetermined structure or composition, but rather to help the forest to change and adapt while maintaining the important structure and function on which we depend. This seems particularly appropriate for temperate Mexican forests because of the high number of oak and pine species adapted to varied environmental conditions. A general description of this approach can be found in Messier et al. (2013).

The need for increasing timber production and for protected areas might be met by functional TRIAD zoning (Seymour and Hunter 1999), as has recently been applied on a large scale in central Quebec, Canada (Messier et al. 2009). TRIAD zoning divides the landscape under management into three zones: one dedicated to intensive forest production, one strictly protected, and the third implementing more natural forestry practices with lower impacts. Despite this division, these three zones must be planned and managed in a coordinated effort to maintain a diverse, productive, and adaptable forest. Both the intensive and extensive forest management areas should be planned to maintain a continuous corridor among protected areas to facilitate species movement and migration. Also, the intensive management areas could grow tree species that are better adapted to future climatic conditions, favoring the overall adaptability of the forest landscape. High timber production could be achieved with fast-growing species, but such plantations should not cover too large an area and should be of as many different species as possible and (or) of mixed species (Paquette and Messier 2010).

A complex adaptive system and zoning for Mexican temperate forest?

Close to Mexico City (in the states of México, Tlaxcala, and Hidalgo), a large area of temperate forest is found with varied climates, soils, and socioenvironmental systems. This region has an intricate network of communal, private, and public properties that are being managed in isolation, without any clear perspectives on larger spatial and temporal scales. Although some mana more integrated and resilience-based approach to face the emerging challenges. We believe that a zoning approach embedded within a complex adaptive system framework may better achieve and maintain the varied objectives required of Mexican forests.

A first step would be to analyze the forest landscape in terms of its spatial configuration, diversity of forest structure and composition, and diversity and spatial extent of ownerships. This would determine where each of the three main forest management zones could be allocated. In areas close to a well establish road system and a possible market, a significant portion of the landscape could be allocated to intensive forest production via plantations; these need not constitute a single species, as multispecies plantations may offer greater productivity and resilience to known and unknown disturbances (Paquette and Messier 2013). The mixtures of pine and oak species should be chosen to produce high quality and quantity in both timber and various ecosystem services. Some conservative migration could also be promoted along the altitudinal gradient to take into consideration the changing climatic conditions. The advantages of mixed forest plantations are the increase in productivity, improvement of soil fertility, increase of forest resilience against pests, diseases, and climatic anomalies, and the potential to generate a much greater variety of ecosystem services (Paquette and Messier 2010). These plantations could connect otherwise unconnected forest fragments and increase the diversity of key but rare functional traits that may allow the extensively managed and protected forests to adapt to global changes.

Protected areas preserve fragile or under-represented species and ecosystems and may help to understand the capability of natural systems to adapt to global changes. For example, in the mountainous regions of central Mexico, trial altitudinal and latitudinal corridors could be created, and environments that could function as buffers against climate change could be identified. Such areas could indicate how species are adapting to global changes. These protected areas should be large enough to allow the greater natural disturbances to occur without affecting the entire area, and they should be evenly distributed across the landscape (Margules and Pressey 2000). This pursues the objective of maintaining the area of primary forests and of protected areas with multiple conservation purposes. It is necessary to establish protected areas in Mexico that aim to preserve biodiversity, functional attributes, and ecosystem services while at the same time ensuring the future forest composition in the face of climate change. A natural consequence of conserving species richness is the maintenance of the ecologic and genetic diversity of pine and oak species (with their different ecological tolerances and morphological and phenotypical variations); this can facilitate species persistence and the formulation of strategies for the maintenance of populations to implement better forest management strategies and restoration projects in the future. Genetic diversity is key for strategies to adapt to climate change (Allen and Holling 2010; Vayreda et al. 2012; Tompkins and Adger 2005). However, a better understanding of the autecology of the various pine and oak species is also necessary, and the possibility of facilitating the migration of some key tree species (Aubin et al. 2011) that could become threatened by a rapidly changing environment should also be evaluated.

The third and normally the largest zone should be managed extensively using a variety of harvesting approaches so as to create a diversity of environmental conditions to allow the forest to "experiment" with different structural and compositional conditions to facilitate adaptation to the novel internal and external biotic and abiotic conditions created by global changes. This is possible owing to the highly heterogeneous forest communities that manage and live in the forests in this region and the different forms of social organization that can allow the establishment of spatially diverse forestry practices and forest (control of small fires, logging, and conservation). Within- and between-stand heterogeneity in ecosystem structure, composition, and function can be favored to recreate natural variability in forest conditions and processes (Puettmann et al. 2009). Forest harvesting should aim not only to replicate the diversity of past natural disturbances, but also to experiment with new disturbances that might help to increase adaptability to future environmental conditions. Once harvested, the forest should be allowed to recover naturally and thereby eventually to develop novel structures and compositions that are better attuned to the emerging environmental conditions. To implement such a management framework in Mexican temperate forests, research should focus on the role that natural disturbances have played in the development of the current diversity of tree species and composition across the various regions where temperate deciduous forest occurs in Mexico. This approach follows a multipurpose forestry objective aiming to meet the needs of as many stakeholders as possible while considering the rapidly changing physical and biological conditions of forests and the future uncertainty; a high diversity of conditions must be maintained to facilitate the adaptation of forests to those new conditions. The current situation of the temperate Mexican forests (few protected areas, low forest management intensity, a need to increase wood production, high tree species diversity, and rapid climate change) provides a near-perfect opportunity to implement a functional zoning approach in conjunction with a complex adaptive system to ensure the future maintenance of the variety of goods and services that this forest provides.

Acknowledgements

This work is part of the sabbatical residency of the first author at McGill University. Leopoldo Galicia acknowledges CONACYT (Grant 150095) for academic support during his sabbatical leave. Funds for this research were provided by PAPIIT-UNAM grant IN 105712.

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