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Recent dynamics of Fagaceae and Pinaceae in temperate forests in Mexico and worldwide

Tesis doctoral

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"Nada es para siempre excepto el cambio"

Heráclito

Abstract

The temperate forests are distributed in the northern hemisphere and are dominated mainly by Pinaceae and Fagaceae. In recent decades, several studies have documented the decline of these forests and the rapid changes they are experiencing because of climate change and anthropogenic disturbances. These studies indicate that, in many cases, the species of Fagaceae are invading areas that were previously dominated by Pinaceae. The main objective of this PhD thesis has been to analyze the relative dynamics of Pinaceae and Fagaceae in temperate forests, both globally and specifically in the case of Mexico, to understand the recent dynamics of these forests and how can be modified in a context of climate change. On a global scale, the specific objectives were: (1a) to establish if there is a directional substitution of Pinaceae by Fagaceae and if this substitution is consistent for all the large biogeographic regions with temperate forests; (1b) to determine whether these directional changes are associated with specific climatic conditions or reflect differences in the historical management of forests between regions. In the case of Mexican forests, the objectives were: (2a) to evaluate if there was a directional change in the relative abundance of Pinaceae compared to Fagaceae in Mexican pine-oak forests; (2b) to identify the environmental factors that determine the recent growth dynamics of Pinaceae and Fagaceae in the study area; (3a) to evaluate the spatial distribution of the recent Pinaceae and Fagaceae regeneration in pure and mixed forests of both groups of species to determine if the current patterns of regeneration suggest directional changes in forest composition; and (3b) to identify the environmental factors that determine the regeneration dynamics of Pinaceae and Fagaceae in these forests, including climatic factors, forest structure and the impact of management and the main disturbances. To achieve these objectives, we used bibliographic data, repeated sampling data from the National Inventory of Forests and Soils of Mexico, and statistical models. We combined analysis of factors and processes at different spatiotemporal scales. At the global level we found that there is a trend of directional change from Pinaceae to Fagaceae in most of the temperate forests of the world that have been studied. This trend is especially pronounced in Europe and East Asia, and much less clear in eastern North America. The drivers of vegetation change were climate stress, succession dynamics and, to a lesser

extent, anthropogenic disturbances. Transitions from Fagaceae to Pinaceae were more common in forests under natural disturbance regimes. In the temperate Mexican forests there is no clear directional pattern showing changes in the relative abundance of Pinaceae and Fagaceae in the tree layer. Growth patterns, however, provide evidence that Fagaceae species are being favored by temperature increases, while Pinaceae are being negatively affected in warmer environments. The spatial patterns of regeneration are affected by forest structure, by climate and by the history of disturbances and land tenure. The regeneration of Fagaceae is in general more abundant than that of Pinaceae and is favored mainly by warm temperatures and presence of fires. Overall, our results suggest an increase in the abundance of Fagaceae to the detriment of Pinaceae in the medium term, especially in the context of climate change. These changes could have important impacts on the functioning of forests and their resilience to environmental changes.

Tabla de Contenidos

Capítulo 1 Introducción general	1
Capítulo 2 Is there a substitution of Pinaceae by Fagaceae in temperate forests at global scale?.....	9
Capítulo 3 Recent dynamics of pine and oak forests in Mexico	27
Capítulo 4 Regeneration dynamics in Mexican pine-oak forests	49
Capítulo 5 Conclusiones generales	67
References	71
Acknowledgments	91

Capítulo 1

Introducción general

La importancia global de los bosques

Los bosques cubren aproximadamente un tercio de la superficie terrestre emergida y nos proporcionan una gran cantidad de servicios ecosistémicos que sustentan, en buena medida, nuestros sistemas socioeconómicos (MA 2005; Bonan 2008). Los servicios que proporcionan los bosques son muy diversos y en general incluyen servicios de provisión (como madera, leña, alimentos), de regulación (del ciclo del carbono, del ciclo hidrológico), de soporte (hábitat para la biodiversidad), y culturales (e.g., valores estéticos y recreativos). A escala global, los bosques absorben aproximadamente un 30% del CO₂ que emitimos a la atmósfera y son por tanto un elemento esencial a la hora de entender y modelizar el calentamiento global y, en general, la dinámica futura del clima (Bonan 2008; Pan et al. 2011). Al mismo tiempo, los bosques son vulnerables al cambio climático y están sometidos a crecientes presiones ambientales, muchas de ellas de origen antrópico (Bonan 2008; Trumbore et al. 2015). Es esencial, por tanto, entender cómo van a responder los bosques al conjunto de presiones derivadas del cambio global (Seidl et al. 2014; Allen et al. 2015; Trumbore et al. 2015).

La dinámica de los bosques en un contexto de cambio global

La distribución de los bosques está determinada a grandes escalas por factores climáticos que limitan el rango geográfico de las especies (Holdridge 1967; Woodward and Williams 1987). En general, los bosques han estado también sometidos a una larga historia de perturbaciones que han moldeado de alguna manera su estructura y composición (Woodward and Williams 1987). Estas perturbaciones van de escalas pequeñas (frecuentes) a grandes escalas (poco frecuentes), y ocurren con diferentes intensidades y frecuencias en espacios geográficos distintos, creando gran variedad de patrones de vegetación en diferentes fases de recuperación (Paine et al. 1998). La capacidad de recuperación de los bosques después de una perturbación, depende de las características genéticas implícitas de

las especies, el tamaño y edad de los individuos, la diversidad de factores ambientales y las condiciones anteriores del bosque (Thompson et al. 2009). Cuando los bosques llegan a un umbral a partir del cual no son capaces de recuperarse se pueden producir cambios catastróficos en su estructura, composición y funcionamiento (Paine et al. 1998; Gauthier et al. 2015; Millar and Stephenson 2015).

La sucesión ecológica tiene lugar cuando se produce un cambio progresivo a lo largo del tiempo en el dominio de las especies (Smith and Huston 1990). Este cambio se da en respuesta a variaciones en la disponibilidad de recursos, entre otros agua, nutrientes y, principalmente, luz (Barton 1993). La dinámica de la sucesión contrapone dos grandes grupos de especies: las especies pioneras intolerantes a la sombra y las especies más tolerantes a la sombra, características de estadios más avanzados de la sucesión (Swaine and Whitmore 1988). En función de la luz y las condiciones biofísicas del suelo estos grupos ecológicos se pueden subdividir en: (i) heliófitas efímeras, especies intolerantes a la sombra que requieren de luz para establecerse y crecer, y tienen una vida muy corta; (ii) heliófitas durables, especies intolerantes a la sombra de vida relativamente larga; (iii) esciófitas parciales, especies que toleran la sombra en las etapas tempranas del desarrollo, pero requieren de iluminación para alcanzar el dosel y pasar de las etapas intermedias hacia la madurez; y (iv) esciófitas totales, especies que se establecen a la sombra y no requieren de altos niveles de iluminación para su crecimiento (Finegan 1992; Chazdon et al. 2010). El proceso de sucesión se inicia con la colonización de plántulas de especies pioneras de vida corta que crecen rápidamente, dando paso sucesivamente a nuevas especies que van siendo reemplazadas por otras de larga vida tolerantes a las nuevas condiciones que se van creando (Finegan 1996). El reclutamiento de plántulas a menudo está fuertemente limitado por la dispersión, mientras que el crecimiento y la supervivencia de los individuos jóvenes son afectados por las variaciones micro-climáticas (Gómez-Pompa and Vázquez-Yanes 1981).

El éxito en el establecimiento y la supervivencia en las fases juveniles viene determinada por la respuesta a condiciones que actúan a nivel local, pero la configuración de la cubierta vegetal a escala de paisaje viene determinada por multitud de factores que operan a diferentes niveles o escalas (Bailey 2004). En primer lugar, el clima (radiación solar, temperatura, disponibilidad de agua) determina la distribución de la vegetación a nivel global,

dando lugar a distintas tipos de vegetación (Holdridge 1967). En segundo lugar, factores topográficos y edáficos, como las características del suelo, la pendiente, la exposición, la orientación y la elevación, influyen en la incidencia de la luz solar, la temperatura y la precipitación, y también regulan los agentes de perturbación como el fuego, el viento, las plagas o los deslizamientos del suelo, dando lugar a diferentes asociaciones de especies de plantas dentro de una zona (Oliver and Larson 1996). Finalmente, las perturbaciones naturales (como huracanes, sequías, incendios, o eventos geológicos) y las humanas (aprovechamientos forestales, ganadería, desmontes, quemadas, entre otros) promueven cambios en la cubierta vegetal, formando mosaicos de vegetación en distintas etapas de desarrollo o sucesión; es decir, cambios temporales en la estructura y composición de especies (Oliver and Larson 1996). Es importante considerar que las perturbaciones forestales se verán modificadas sustancialmente en un contexto de cambio climático, y el impacto de estos cambios en la dinámica de los bosques a medio plazo no se conoce con precisión (Seidl et al.).

Los bosques templados

Los bosques templados se distribuyen en gran parte del hemisferio norte (y en menor medida en el hemisferio sur), extendiéndose sobre las latitudes medias de América del Norte, Asia y Europa, y representan aproximadamente el 26% del área forestal mundial (Olson et al. 2001). Estos bosques se desarrollan en climas con veranos relativamente cálidos e inviernos fríos, con precipitaciones anuales entre los 500 y 3,000 mm, temperaturas anuales promedio de alrededor de 10 °C, y con cambios estacionales muy marcados (Woodward and Williams 1987; Olson et al. 2001). Los bosques templados acostumbran a ser complejos estructuralmente y desempeñan un papel importante en la determinación del clima a escala regional y global (Bonan 2008). Como en otras regiones, los bosques templados influyen en los procesos bioquímicos, los regímenes hidrológicos y los regímenes de incendios, y proporcionan alimentos para la población humana y los animales (Richardson 2000). Así mismo, los bosques templados presentan una historia de manejo generalmente más larga y compleja que los de otros biomas, lo cual determina también unos riesgos específicos en relación a los impactos del cambio global (Millar and Stephenson 2015)

Los bosques templados están compuestos principalmente por árboles planifolios de hoja caduca y coníferas de hoja perenne, representados principalmente por las familias Pinaceae (pinos y especies afines) y Fagaceae (robles, hayas y similares), aunque especies de muchas otras familias pueden ser también localmente importantes dependiendo de la región (Woodward et al. 2004). Pinaceae es la familia más importante entre las coníferas y se divide en 11 géneros y aproximadamente 225 especies (Christenhusz et al. 2011). El género *Pinus* es el más diverso y abundante de la familia y comprende aproximadamente 110 especies (Eckenwalder 2009). Los pinos son componentes importantes y con frecuencia dominantes de los bosques templados, y en muchas zonas tienen un gran valor económico como fuentes de productos maderables. La mayor concentración de especies de todos los géneros de Pinaceae se encuentra en América del Norte y Asia oriental (Richardson 2000). Por otra parte, la familia Fagaceae está representada por ocho géneros y alrededor de 927 especies (Christenhusz and Byng 2016). *Quercus* es el género más diverso dentro de la familia, con más de 500 especies. Las zonas con mayor diversidad de Fagaceae se concentran en el sudeste asiático, donde hay siete géneros diferentes, y en Norteamérica, donde se halla el mayor número de especies endémicas (Nixon 2006).

Históricamente, los impactos por actividades antropogénicas en los ecosistemas templados han sido muy importantes, debido entre otros factores al rápido crecimiento de la población humana y el consumo de los recursos asociados (Ellis and Ramankutty 2008). La agricultura, el pastoreo, la extracción de minerales y el desarrollo urbano han originado cambios en los ecosistemas forestales, afectando su funcionamiento a múltiples escalas, desde la local (degradación de los suelos y los sistemas hidrológicos) a la global (cambio climático) (Ellis et al. 2010). Las perturbaciones como los incendios o las sequías intensas están incrementado con el cambio climático (Reyer et al. 2017; Seidl et al. 2017) y su impacto puede ser especialmente elevado en sistemas templados (Paine et al. 1998). Numerosos estudios han informado que estas perturbaciones causadas por el cambio climático están provocando cambios importantes en los bosques templados, incluyendo: expansión del límite de árboles hacia el norte (Boisvert-Marsh et al. 2014), migración ascendente de especies en zonas de montaña (Ortega-Rosas et al. 2008), invasión de especies y alteración de los patrones de regeneración (Anderson-Teixeira et al. 2013), cambios en la composición y la estructura de los bosques (Lines et al. 2010; Anderson-Teixeira et al. 2013; Zhang et al. 2018), cambios en

la distribución geográfica de las especies (Kelly and Goulden 2008); (Brecka et al. 2018), entre otros.

Las Pináceas y las Fagáceas a menudo coexisten en áreas de latitudes medias y ambientes fríos. Ambas familias han desarrollado estrategias ecofisiológicas contrastadas que les permiten crecer en estos ambientes. Por ejemplo, las Pináceas están bien adaptadas para soportar las bajas temperaturas: sus características anatómicas (xilema) les permiten tener amplios márgenes de seguridad que les hacen menos susceptibles al embolismo por congelación (Carnicer et al. 2013). Otros rasgos como la estructura de la hoja y su capacidad fotosintética resultan en tasas de fotosíntesis máximas similares o incluso más altas en las Pináceas que las de las angiospermas (Brodrribb et al. 2012). Por su parte las Fagáceas a menudo están mejor adaptadas a las condiciones cálidas, y generalmente tienen un control estomático menos estricto que les permite mantener niveles sustanciales de transpiración durante las sequías de verano (Carnicer et al. 2013; Augusto et al. 2014).

Diversos estudios recientes sugieren que el cambio climático reciente está afectando positivamente a las Fagáceas, mientras que las Pináceas parecen estar en clara desventaja en un contexto de aumentos de temperatura y largos periodos de sequía (Rigling et al. 2013). Aunque la variabilidad climática, en particular la sequía, es determinante en la dinámica reciente de muchos de estos bosques, el historial de perturbaciones antropogénicas tales como los aprovechamientos forestales y los cambios en el uso del suelo también juegan un papel importante y promueven cambios en los bosques que difícilmente se pueden separar de los climáticos (Bond-Lamberty et al. 2014; Vayreda et al. 2016). Las tendencias recientes en la dinámica Pináceas-Fagáceas y los factores que la determinan son mucho menos conocidos en los bosques templados de América, particularmente en los bosques hiperdiversos de Centroamérica.

Importancia de los bosques de pino-encino mexicanos

Los bosques mexicanos poseen una gran cantidad de especies florísticas que los sitúan en los primeros lugares en cuanto a diversidad de plantas se refiere. Se estima que existen aproximadamente 30,000 especies distintas de plantas en México (Rzedowski 1991). La ubicación geográfica, la geología modelada por grandes sucesos paleo-históricos, el relieve

irregular dominado por sistemas topográficos complejos, la variedad de tipos de suelo y los diferentes tipos de clima han creado las condiciones necesarias para generar esta gran variedad y abundancia de especies vegetales (Ramamoorthy 1994).

En México, los bosques templados mixtos se distribuyen en las zonas montañosas de clima templado y frío, lluvioso subhúmedo, con lluvias en verano y una estación seca bien definida en invierno y primavera, con temperaturas promedio de 10-20 °C y con precipitaciones anuales entre 500 y 3000 mm al año (Miranda and Hernández 1963; Rzedowski 2006). Se estima que los bosques templados mexicanos contienen cerca de 7,000 especies de plantas. Éstos se caracterizan por la dominancia de especies del género *Pinus* en asociación con especies de *Quercus* (bosques de pino-encino). En el país existen alrededor de 61 especies de pinos y 125 especies de encinos (Debreczy and Rácz 1995; Valencia-A 2004; Nixon 2006; Eckenwalder 2009; Gernandt and Pérez-de la Rosa 2014; Romero-Rangel et al. 2015), que representan el 50% de especies de pinos y cerca del 25% de encinos del mundo. La alta diversidad biológica y la gran cantidad de endemismos es una de las principales características de los bosques templados mexicanos. El 70% de las especies son consideradas endémicas y un gran porcentaje se encuentra en alguna categoría de protección especial (Espinosa and Ocegueda 2008).

Los bosques de pino-encino mexicanos representan una fuente de bienes y servicios para los poseedores de la tierra, además de ser una fuente de empleo e ingreso para las comunidades locales, ya que el 70% de la superficie del bosque (aproximadamente 27 millones de hectáreas) están bajo el régimen de propiedad social, es decir ejidal o comunal (Chapela 2012; Jardel 2012). El sistema de manejo de bosques, pastizales y aguajes es colectivo, y la gestión de los asuntos principales se maneja a través de asambleas comunitarias (Segura 2000).

Los cambios en los usos del suelo, la tala ilegal, la extracción no sostenible de madera y el cambio climático, entre otros factores, han reducido considerablemente el área de distribución y han modificado la composición de los bosques de pino y encino en México (Rzedowski 2006; Challenger and Soberón 2008). Aproximadamente el 40% de los bosques de pino-encino han sido convertidos en campos agrícolas y, más recientemente, en pastizales para la cría de ganado (Challenger and Soberón 2008). Los incendios forestales forman parte

de la dinámica natural de estos bosques, aunque también se asocian con las prácticas agrícolas y el manejo de pastizales (Rzedowski 2006). El patrón de regeneración causado por el fuego promueve la sucesión de especies, favoreciendo el reclutamiento de algunas especies de pino con conos serotinos, mientras que reduce la viabilidad de las semillas de encinos (Fulé and Wallace Covington 1998; Rodríguez-Trejo and Myers 2010; Yocom and Fulé 2012). Diversos estudios indican que la regeneración de *Pinus* en general se ve favorecida en zonas con perturbaciones antropogénicas frecuentes pero de baja intensidad (Ramirez-Marcial et al. 2001; López-Barrera and Newton 2005; Meunier et al. 2014b). Sin embargo, la capacidad de rebrote de muchas quercíneas hace que la dinámica de la vegetación a medio plazo sea muy dependiente de las condiciones ambientales y del régimen de perturbaciones, y por tanto difícil de predecir. En buena medida se desconoce cómo los cambios en los regímenes de perturbaciones asociados al cambio climático afectaran la dinámica de los bosques de pino-encino mexicanos a medio y largo plazo.

Objetivos y estructura de la tesis

El objetivo general de esta tesis ha sido analizar la dinámica relativa de las especies de Pináceas y Fagáceas en los bosques templados, tanto a escala global como específicamente en el caso de México, con la finalidad última de comprender mejor la dinámica reciente de estos bosques y como se puede ver modificada en un contexto de cambio climático.

A nivel global (**Capítulo 2**) los objetivos específicos han sido: (2a) establecer si existe una sustitución direccional de Pináceas por parte de Fagáceas y si esta sustitución es consistente para todas las grandes regiones biogeográficas con bosques templados; (2b) determinar si estos cambios direccionales están asociados con condiciones climáticas específicas o reflejan las diferencias en el manejo histórico del bosque y el uso de la tierra entre regiones. Para lograr estos objetivos se realizó una revisión bibliográfica de los trabajos publicados que han estudiado la dinámica relativa de especies de Pináceas y Fagáceas en los bosques templados de todo el mundo entre 1850 y 2016. Los datos resultantes se analizaron mediante modelos estadísticos y se relacionaron con distintos factores climáticos y biogeográficos.

En segundo lugar, se analizó la dinámica reciente de los bosques templados mexicanos, (**Capítulo 3**), con el objetivo de: (3a) evaluar si hay un cambio direccional en la abundancia

relativa de Pináceas frente a en los bosques de pino-encino Mexicanos; (3b) identificar los factores ambientales que determinan la dinámica de crecimiento reciente de Pináceas y Fagáceas en el área de estudio, centrándonos en el efecto de la estructura forestal y los patrones de sucesión, el manejo, las perturbaciones, el clima y las tendencias climáticas recientes. Estos objetivos se abordaron utilizando datos de dos mediciones repetidas del Inventario Nacional de Bosques y Suelos de México (INFyS) e información ambiental complementaria obtenida de distintas fuentes.

Finalmente, se estudió la regeneración de Pináceas y Fagáceas en los bosques de pino-encino Mexicanos (**Capítulo 4**) con el objetivo de: (4a) evaluar la distribución espacial de la regeneración reciente de Pináceas y Fagáceas en bosques puros y mixtos de ambos grupos de especies para determinar si los patrones actuales de regeneración sugieren cambios direccionales en la composición del bosque; y finalmente (4b) identificar los factores ambientales que determinan la dinámica de regeneración de Pináceas y Fagáceas en estos bosques, incluyendo factores climáticos, la estructura forestal y el impacto del manejo y las principales perturbaciones. Para alcanzar estos objetivos se utilizaron nuevamente datos del INFyS (considerando conjuntamente los resultados de los dos últimos apeos) combinados con modelización estadística.

Capítulo 2

Is there a substitution of Pinaceae by Fagaceae in temperate forests at
global scale?

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Abstract

Reports on forest decline, changes in species composition and the distribution of forests in response to changes in climate and land use are increasing worldwide. Temperate forests are largely dominated by two tree families: Pinaceae and Fagaceae. These two families have distinct functional properties and different responses to environmental factors. Several local and regional assessments, particularly in Europe, have found that species of Fagaceae are invading areas previously dominated by Pinaceae. The main aim of this synthesis study is to analyze the relative dynamics of Pinaceae and Fagaceae species in temperate forests around the world, with the following specific objectives: (1) establish if there is a consistent directional substitution of Pinaceae by Fagaceae worldwide; and (2) determine whether these directional changes are associated with specific climatic conditions or certain geographic regions, reflecting differences in historical forest management and land use. A bibliographic review was performed, and 51 papers were found that met the search criteria, including a total of 121 case studies in which the relative dynamics of Pinaceae and Fagaceae were evaluated. Our results show that the relative abundance of Fagaceae increased in 71% of cases (P→F dynamics), whereas Pinaceae relative abundance increased in 17% of cases (F→P) and 12% of cases did not show clear changes. Increases of Fagaceae relative to Pinaceae occurred preferentially in areas where vegetation dynamics were less clear in areas where vegetation dynamics were driven by natural disturbances. Our results indicate a widespread increase in dominance of Fagaceae species at the expense of Pinaceae across northern temperate forests, with the exception of Eastern North America. The potential implications for ecosystem function and forest resilience under ongoing climate change are large and clearly deserve further study.

Keywords: *broadleaves, conifers, global change, Quercus, Pinus, vegetation dynamics.*

Introduction

There is an increasing number of studies reporting episodes of forest decline worldwide associated to climatic extremes (Allen et al. 2010; Reyer et al. 2015; Trumbore et al. 2015). This climatic signal, however, is usually difficult to separate from other drivers of forest change, particularly past changes in forest management and land use (e.g., Vayreda et al. 2016), as most of the world's forests have been extensively modified by human intervention. The interactions between climate change and land use changes may modify disturbance regimes and alter forest structure and functionality. Important disturbances, including drought, fire, and insect and pathogen outbreaks, may interact with each other causing cascading effects (Dale et al. 2001; Thompson et al. 2009). The compounded effects of disturbances can lead to new ecosystem states, resulting in changes in dominant species (Bahamondez and Thompson 2016; Torres et al. 2016; but see Martínez-Vilalta and Lloret 2016). A new state may be entered, for instance, when the system has not recovered from the first disturbance before a second perturbation occurs, leading to a new, long-term condition (Paine et al. 1998).

Temperate forests account for 26% of forest area worldwide (Keenan et al. 2015; Riitters et al. 2016) and cover large areas of the northern hemisphere, dominating mid-latitudes in North America, Asia, and Europe (Olson et al. 2001). This biome is dominated by deciduous broadleaf trees and evergreen conifers, mostly belonging to two families: Fagaceae (angiosperm) and Pinaceae (gymnosperm) (Woodward et al. 2004). Despite substantial ecological differences, these two families can coexist in large areas characterized by distinct seasonality, including a marked dry season in some regions (Manos and Stanford 2001; Eckenwalder 2009). Pinaceae is a diverse conifer family with 11 genera and 225 species (Tsai et al. 2013). The genus *Pinus* is the most diverse and abundant of the family, and comprises approximately 110 species (Eckenwalder 2009). Fagaceae is represented by eight genera and about 927 species (Christenhusz and Byng 2016). *Quercus* is the most diverse genus within the family, consisting of over 500 species and having a great ecological and economic importance (Nixon 2006).

It has been hypothesized that conifers in general, and Pinaceae in particular, are largely restricted to areas where growth of angiosperm competitors is reduced, such as high

latitudes and elevations (cold environments) or nutrient-poor soils (Bond 1989). However, this paradigm does not seem to explain contemporary forest dynamics in some regions, where Pinaceae have been aggressive competitors capable of dominating entire regions, often to the exclusion of angiosperm trees (Brodribb et al. 2012). Pinaceae species are well adapted to freezing, thanks mostly to their wood anatomy (small xylem conduits highly resistant to freeze-thaw embolism) and their leaf morphology and photosynthetic physiology. Conifers, however, can also sustain maximum photosynthetic rates that are similar or even higher than those of associated angiosperm trees (Brodribb et al. 2012). Many Fagaceae are well adapted to warm conditions, and generally have a less strict stomatal control and are able to maintain substantial transpiration levels during summer drought (Carnicer et al. 2013; Augusto et al. 2014).

Both Fagaceae and Pinaceae are showing signs of decline in some areas, including reduced growth, leaf area reductions, and increasing tree mortality (Carnicer et al. 2011; Rigling et al. 2013; McIntyre et al. 2015). Given the large functional differences between Pinaceae and Fagaceae, and the ecological importance of both families, the question of whether they will respond differently to ongoing climate change becomes highly relevant. Some reports suggest that contrasting trait syndromes between these families may be associated to different responses to recent changes in temperature in SW Europe, with positive growth responses to increases in temperature for Fagaceae but not for Pinaceae (Carnicer et al. 2013). Other studies, however, give more prominence to anthropogenic drivers, including historical changes in forest management and land use, in explaining recent forest dynamics in the same region (Vayreda et al. 2016; Searle and Chen 2017).

Two important research questions emerge from the previous considerations: (1) are the dynamics of replacement of Pinaceae and Fagaceae observed in some European regions (Rigling et al. 2013; Vayreda et al. 2016) generalizable to other temperate regions worldwide? (2) what would be the ecological implications of this directional replacement, both in terms of ecosystem function (and provision of ecosystem services) and in terms of the future vulnerability of temperate forests to warmer and drier conditions? Here, we focus on the first of these two issues. We compiled a database of published studies analyzing the relative dynamics of Pinaceae and Fagaceae in temperate forests worldwide. We then analyzed this

data to: (1) establish whether there is a consistent directional trend in recent decades towards greater abundance of Fagaceae relative to Pinaceae species in temperate forests worldwide, and whether this trend has led to a change in the dominant tree family in these forests; and (2) determine whether these changes are associated to specific conditions or certain geographic regions, reflecting differences in climate, historical forest management or land use.

Methods

Bibliographic review

A systematic review was performed at the global scale using bibliographic data available from the Web of Knowledge (<http://apps.webofknowledge.com>, accessed 28th February 2018). We targeted peer-reviewed journal articles on the comparative dynamics of Pinaceae and Fagaceae species in temperate forests worldwide. The following search terms were used, which include all genera in the two families studied: ((*Castanea* OR *Castanopsis* OR *Chrysolepis* OR *Fagus* OR *Lithocarpus* OR *Notholithocarpus* OR *Quercus* OR *Trigonobalanus*) AND (*Pinus* OR *Cedrus* OR *Cathaya* OR *Picea* OR *Pseudotsuga* OR *Larix* OR *Pseudolarix* OR *Tsuga* OR *Nothotsuga* OR *Keteleeria* OR *Abies*) AND (forest\$) AND (dynamics OR succession OR regeneration OR recruitment) AND (survey\$ OR substitution OR replacement OR change\$)). This literature survey approach is complementary to studies using consolidated datasets such as those obtained from national forest inventories, which have already been used for similar purposes in some regions (e.g. Vayreda et al. 2016). Clearly, forest inventories provide more systematic and comparable experimental designs and data collection protocols. However, they are only available for a small and biased fraction of the world's forests, they tend to cover relatively short periods of time, they are not easily integrated across countries, and they offer limited information on potential drivers of vegetation change. A systematic literature survey as the one conducted here has the potential to overcome some of these limitations.

We included studies written in English or other languages (with English abstract). This search resulted in a total of ~1250 papers. The initial list of papers was then filtered according to the following criteria: (i) studies concerned 'natural' vegetation (forest plantations and modeling

studies were excluded), (ii) Pinaceae or Fagaceae were dominant (in terms of stem density or basal area) at the beginning or the end of the study period, (iii) the study period was well-defined, with clear dates for initial and final vegetation surveys, (iv) changes in vegetation were assessed between 1850 and 2016, (v) the study period was longer than three years, (vi) the study measured or made some inference on vegetation changes by species or groups of species using a quantitative measure of abundance (e.g., basal area, stem density, distribution area), and (vii) both families were clearly represented at the beginning or at the end of the study period (studies were removed when the proportion of Fagaceae relative to (Fagaceae + Pinaceae) remained $< 5\%$ or $> 95\%$ throughout the study period).

We obtained a final list of 51 papers matching these criteria. Since many of these papers included more than one study area, we considered unique combinations of paper by study area as our basic study unit ($N = 121$). The source of variability associated to the paper level in the hierarchical structure of the dataset was accounted for in our statistical analyses (see below). One of the studies (Vayreda et al. 2016) provided a synthesis of forest inventory data for Spanish forests. Since this was not directly comparable to the other datasets included in our analyses, which typically represented much smaller areas, we split the original dataset used in Vayreda et al. (2016) by administrative region, giving 12 different study cases.

The following information was recorded from the original papers for each of the study units (the complete dataset is given in Table S1, Electronic Supplementary Material): complete reference; geographic location (country, state or region, geographic coordinates); characteristics of the study area (vegetation type, dominant species); method used to assess vegetation change (permanent plots, forest inventory, aerial photography, satellite images); area covered by the study (i.e., total area sampled) (ha); baseline year; end date of the study; main drivers of vegetation change during the study period; type of variable used to quantify abundance; and the initial (baseline) and final value of the abundance variable for Pinaceae and Fagaceae, combining all values for the species belonging to each family.

The variables that were used to quantify abundance were: basal area (in $\text{m}^2 \text{ha}^{-1}$ or % of total basal area, $N = 60$ study cases), stem volume (in $\text{m}^3 \text{ha}^{-1}$ or % of total stem volume, $N = 23$), tree density (in stems ha^{-1} , $N = 20$), importance percentage (Choung et al. 2004; Lee et al. 2012; Jang et al. 2013) ($N = 12$), and distribution area (in ha or %, $N = 6$). When more than

one of the previous variables was reported in a paper, the variables were prioritized in the same order given above and only the first one was considered. Drivers of vegetation change, as specified by the authors of each study, were classified in the following four categories: climate stress (e.g., temperature, drought), natural disturbances (e.g., wildfires, pests and pathogens, windstorms), direct anthropogenic disturbances (e.g., fire suppression, forest management, grazing), and successional dynamics in the absence of major disturbances.

Assessing vegetation change

Changes in relative abundance between Pinaceae and Fagaceae were assessed using the following index of change (C):

$$\text{Index of change} = \frac{A_{end}^F}{(A_{end}^P + A_{end}^F)} - \frac{A_{ini}^F}{(A_{ini}^P + A_{ini}^F)}$$

where A refers to the value of the measure of abundance; the super-indices F and P denote Fagaceae and Pinaceae, respectively; and the sub-indices end and ini indicate the values at the end and at the beginning of the study period, respectively. A positive value of index of change indicates that Fagaceae abundance increases more (or decreases less) relative to Pinaceae ($P \rightarrow F$), whereas a negative value indicates the opposite ($F \rightarrow P$) and $C = 0$ indicates identical changes in the two families (no change, NC). Besides using this quantitative index of change, in some analyses we also used the corresponding categorical variable with three levels: Pinaceae to Fagaceae ($P \rightarrow F$), Fagaceae to Pinaceae ($F \rightarrow P$), and no change (NC). As low values of $|C|$ indicate very small relative changes that are unlikely to be biologically meaningful, we compared different threshold values of $|C|$ to determine which cases corresponded to the no change situation (NC), including 0.02, 0.025 and 0.03 (the overall distribution of C ranged between -0.6 and 0.5, with mean = 0.077 and median = 0.074). Results were identical in all cases and thus we only report those using $|C| = 0.025$ as a threshold. We also assessed when changes in the abundances of the two families led to changes in overall dominance. A change in dominance occurred when the family with the highest abundance (Pinaceae or Fagaceae, measured as described above) changed between the beginning and the end of the study period.

Climate data

To complement the data extracted from the articles, we also obtained total annual precipitation ($L\ m^{-2}$) and mean annual temperature ($^{\circ}C$) using the geographic coordinates of each study site, as given in the original papers. These additional data layers were obtained from WorldClim Weather-Global climate data (30 arc-seconds resolution) for current conditions 1950-2000 (<http://www.worldclim.org/current>).

Data analysis

We used chi-square tests to assess whether there was a preferential vegetation change (P→F vs. F→P, excluding NC) globally or for each main region (corresponding to continents except in the case of North America, which was split between Eastern and Western territories). We also tested whether dominance changes were more frequent for sites initially dominated by Fagaceae or Pinaceae.

Classification trees are a statistical modelling technique to determine a set of conditions (from a set of explanatory variables) that allow accurate classification of cases in relation to a discrete response variable (De'ath and Fabricius 2000), and were used here to determine which variables were associated to different directions of vegetation change (the response variable, with three discrete classes: P→F, F→P and NC). Explanatory variables included total annual precipitation, mean annual temperature, driver of change, region and type of variable used to quantify abundance. This latter variable was included to account for potential methodological effects associated to the way abundance was assessed in each study.

Finally, a mixed-effects model was fit with the quantitative index of change as response variable and total annual precipitation, mean annual temperature, driver of change, region, type of variable used to quantify abundance, and length of the study period (in years, ranging from 3 to 159 years) as explanatory variables. Preliminary analyses showed that the effect of the size of the study area was not significant ($r = -0.09$, $P = 0.34$) and, since this variable was unavailable for a few case studies, we decided not to include it in the final model. Study was included as a random factor in the model to account for the fact that many of the studies (papers) included in our dataset contained more than one study case, which likely shared common experimental conditions and thus were not independent. Both the response

variable (index of change) and the model residuals were approximately normally distributed. Significant differences were accepted whenever $P < 0.05$. All analyses were conducted using the R software environment (v.3.4.3, The R Project for Statistical Computing).

Results

The 121 cases obtained were distributed throughout the northern hemisphere, with 64 cases in Europe, 31 in East North America, 10 in West North America and 16 in (East) Asia (Figure 1). Of those, 71% corresponded to changes in the relative abundance from Pinaceae to Fagaceae ($P \rightarrow F$), 17% corresponded to the change from Fagaceae to Pinaceae ($F \rightarrow P$) while 12% of the cases did not show clear changes (NC). Changes from Pinaceae to Fagaceae were significantly more frequent than the opposite trend, both globally ($P < 0.001$) and in all regions except East North America ($P < 0.001$ in Europe, $P = 0.032$ in (East) Asia, $P = 0.034$ in West North America and $P = 0.705$ in East North America) (Figure 2). These changes in relative abundance, however, have not lead to significant changes in dominance in neither Pinaceae nor Fagaceae forests ($P \geq 0.05$ in all cases).

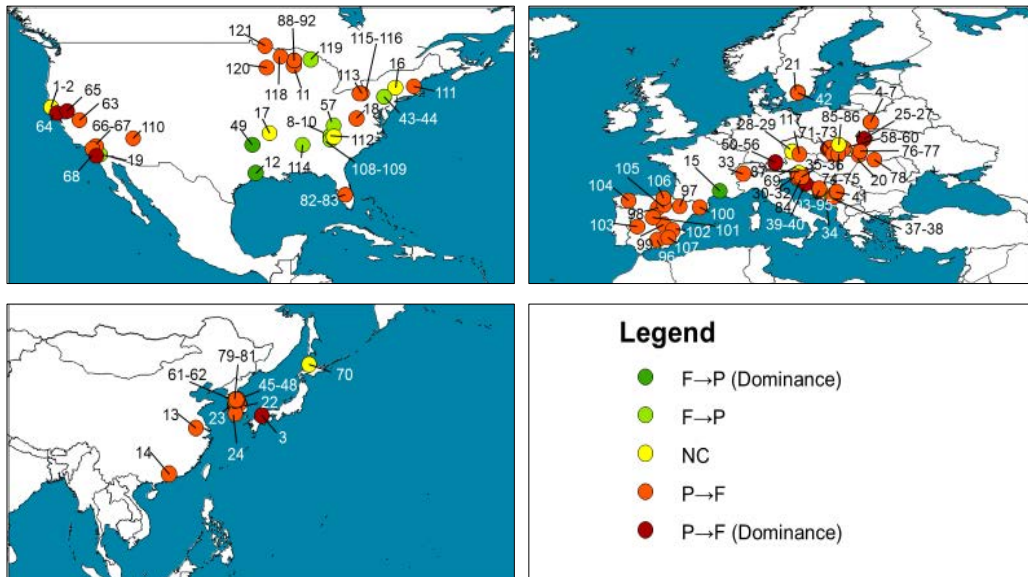


Figure 1. Approximate locations of the 121 case studies of relative Pinaceae vs Fagaceae dynamics included in the study. Different colors indicate the direction of vegetation change ($F \rightarrow P$ indicates increased Pinaceae abundance; $P \rightarrow F$ indicates increased Fagaceae abundance; and NC denotes no change in the relative abundance of the two families, $|C| < 0.025$). Darker green or red colors indicate changes in dominance (see text for details).

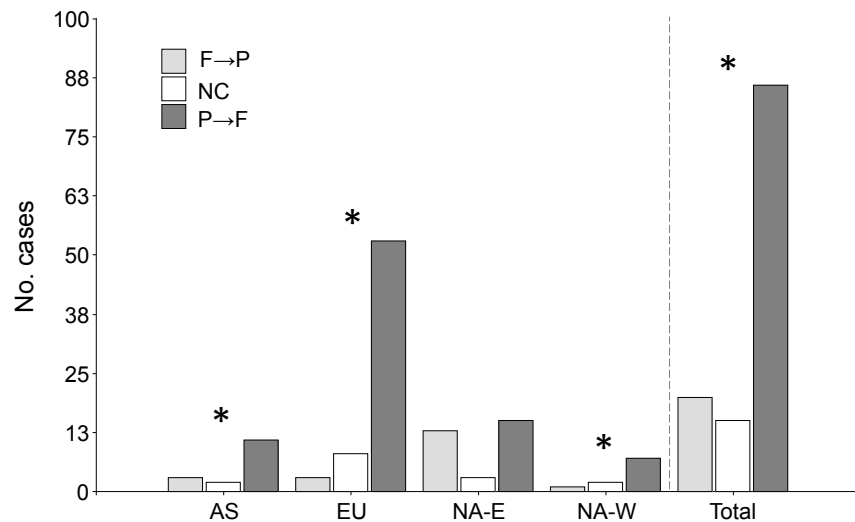


Figure 2. Number of study cases by direction of vegetation change (F→P indicates increased Pinaceae abundance; P→F indicates increased Fagaceae abundance; and NC denotes no change in the relative abundance of the two families, $|C| < 0.025$) worldwide and by region (AS: East Asia, EU: Europe, NA-E: East North America, NA-W: West North America). An asterisk indicates significant differences between directions of change (F→P vs P→F), globally and by regions.

The distribution of drivers of change differed among regions, with anthropogenic disturbances and successional dynamics being particularly common in Europe, successional dynamics being also common in (East) Asia and East North America, and natural disturbances being also common in East North America (Figure 3). No obvious association was observed between the direction of vegetation change and climate, defined by total annual precipitation and mean annual temperature (Figure S1, Electronic Supplementary Material).

The classification tree results indicated that the only explanatory variable that was retained in the model (out of annual precipitation, temperature, driver of change, region and type of variable) was the driver of change. This variable alone allowed a reasonably good classification of the direction of vegetation change, with natural disturbances being associated to relative increases in Pinaceae or no changes (88% of cases within that group corresponded to F→P or NC) and all the other drivers being associated to increased Fagaceae abundance, the most common outcome (80% of cases within that group corresponded to P→F dynamics) (Figure 4).

IS THERE A SUBSTITUTION OF PINACEAE BY FAGACEAE IN TEMPERATE FORESTS AT GLOBAL SCALE?

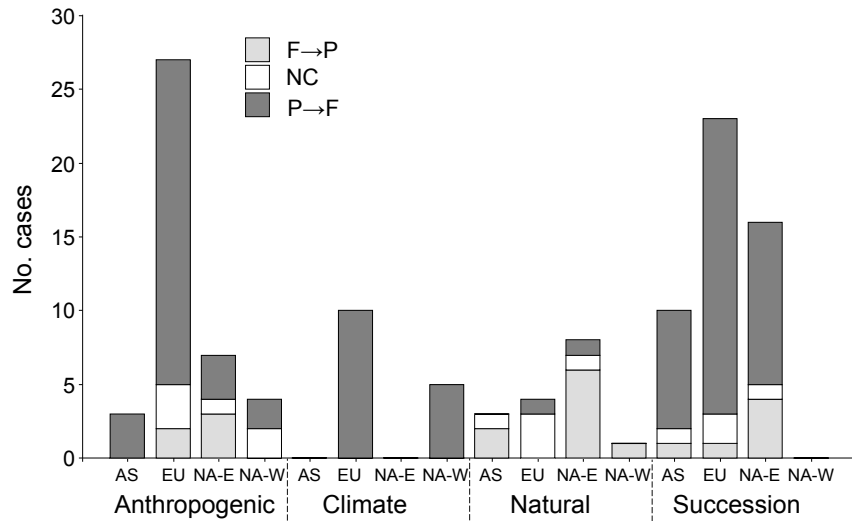


Figure 3. Number of study cases by direction of vegetation change as a function of region (AS: East Asia, EU: Europe, NA-E: East North America, NA-W: West North America) and driver of change (Anthropogenic disturbances, Climate stress, Natural disturbances or Succession; see text for details). F->P indicates increased Pinaceae abundance, P->F indicates increased Fagaceae abundance, and NC denotes no change in the relative abundance of the two families ($|C| < 0.025$).

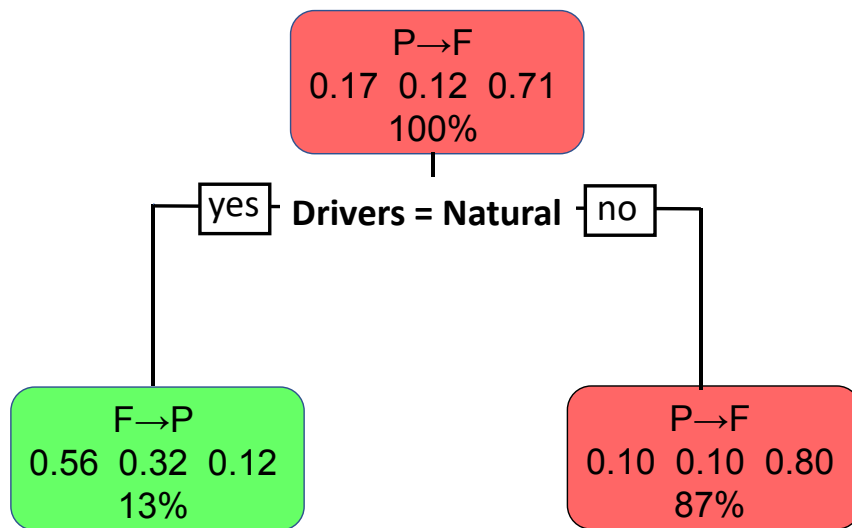


Figure 4. Classification tree with direction of vegetation change as response variable (F->P: increased Pinaceae abundance, P->F: increased Fagaceae abundance) and driver of change as the only significant explanatory variable. The numbers indicate the proportion of cases in each category that correspond to each direction of vegetation change (in the order: F->P, no change, P->F) and the overall percentage of cases in each category.

The analyses using the (quantitative) index of vegetation change largely confirmed the results obtained for the discrete variable categorizing the direction of vegetation change. Positive average values of the index of change, indicating preferential P→F dynamics, were observed in all combinations of region and driver of change except for natural disturbances in East North America and Asia, and anthropogenic disturbances in East North America (Figure 5). The mixed-effects model allowed us to assess the statistical significance of the previous patterns and showed that the only two variables with a significant effect on the index of change (C) were driver and region (marginal $R^2 = 0.28$) (Table 1). Natural disturbances were the only driver of change for which the model predicted negative C values on average (using least-squares means estimation), implying preferential F→P dynamics. Predicted C values were significantly lower for natural disturbances than for climate stress and successional dynamics ($P < 0.05$), whereas anthropogenic disturbances showed intermediate values. Regarding region effects, predicted C values were all positive, but were significantly higher for (East) Asia than for Europe or East North America ($P < 0.05$). The effects of variable type, length of the study period, and precipitation and temperature climatology were not significant (Table 1).

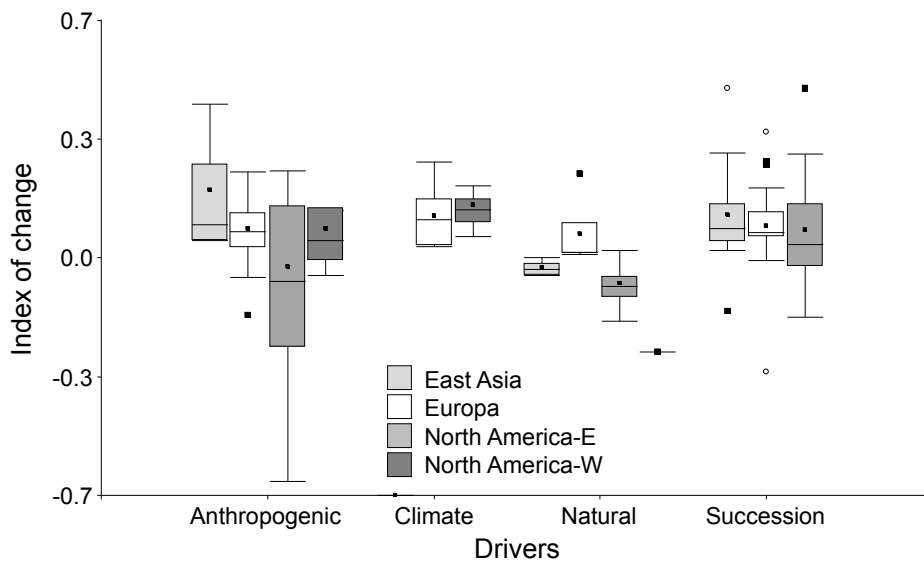


Figure 5. Index of change (C) as a function of driver of change and region. A positive value indicates that Fagaceae abundance increases more (or decreases less) relative to Pinaceae ($P \rightarrow F$), whereas a negative value indicates the opposite dynamics ($F \rightarrow P$) and $C = 0$ indicates identical changes in the two

families. The horizontal line and black dot inside the box give the median and the mean, respectively, the edges of the box are the lower and upper quartiles, the two whiskers extend up to 1.5 times the interquartile range from the top/bottom of the box, and the dots beyond the end of the whiskers represent outliers.

Table 1. ANOVA table for the linear mixed-effects model predicting index of change (C) as a function of type of variable used to assess abundance, region, driver of change, mean annual temperature, annual precipitation, and length of the study period.

Variable	numerator degrees of freedom	denominator degrees of freedom	F-value	p-value
(Intercept)	1	64	38.40	<0.0001
Type of variable	4	43	1.87	0.1325
Region	3	43	3.65	0.0197
Driver of change	3	64	5.50	0.0020
Temperature	1	64	1.04	0.3116
Precipitation	1	64	2.54	0.1157
Study period	1	64	2.31	0.1335

Discussion

We report a generalized increase in Fagaceae species at the expense of Pinaceae in temperate forests, particularly in Europe and (East) Asia. The patterns are less clear in East North America, which is associated to a different dominant driver of vegetation change in this region (see below). These prevailing P→F dynamics were not significantly affected by the length of the study period. This result suggests that compensatory dynamics (which could promote stability in the long term, Lloret et al. 2012) were not a dominant factor explaining the observed vegetation changes, although they were observed in some cases. For instance, forest composition in central Massachusetts experienced a variety of successional stages ranging from late-successional *Tsuga canadensis* assemblages to assemblages dominated by early successional to mid-successional taxa such as *Castanea*, *Quercus*, and *Pinus*; but with similar relative abundances of Pinaceae and Fagaceae at the beginning and end of the study period (McLachlan et al. 2000).

Our results show that there is a directional change from Pinaceae to Fagaceae in most forests worldwide and, in particular, in areas where vegetation dynamics are driven by climatic stress, successional dynamics and, to a lower extent, (direct) anthropogenic disturbances.

This directional pattern disappears in areas where natural disturbances drive vegetation change. The higher frequency of F→P dynamics under natural disturbance regimes is consistent with the fact that many Pinaceae, particularly those belonging to the *Pinus* genera, are considered early-successional species (Vayreda et al. 2016; Searle and Chen 2017). A similar argument explains why the opposite, P→F change dominates areas driven by natural succession. It is less clear why anthropogenic and climate-driven disturbances may promote Fagaceae at the expense of Pinaceae. Possible explanations are that the legacies from past anthropogenic disturbances and climate warming directly contribute towards the observed composition changes. For example, in some areas of Europe, the replacement of firewood (obtained mostly from Fagaceae) by fossil fuels has indirectly promoted broadleaves (Vayreda et al. 2016). Also, in Europe, less intense forest management and abandonment of lands formerly used for cultivation or grazing has resulted in successional dynamics towards forests increasingly dominated by Fagaceae, particularly *Quercus* species (Rigling et al. 2013; San Roman Sanz et al. 2013; Morales-Molino et al. 2017). In SW North America, changes in fire regimes since European settlement have also led to an increase of Fagaceae (*Quercus* species) relative to Pinaceae in *Pinus ponderosa* forests (Fule et al. 1997).

Despite the fact that our simplistic analysis did not detect any effect of average climate on the observed vegetation dynamics, it is likely that climate extremes have a role in the observed patterns, at least in some areas. Increased temperature and drought has been associated with forest mortality episodes, in many cases affecting Pinaceae species, whereas Fagaceae appear less affected (Gimmi et al. 2010; Ruiz-Benito et al. 2013; Carnicer et al. 2014; McIntyre et al. 2015; McDowell et al. 2016). In a recent global synthesis, drought legacy effects on radial growth have been reported to be more prevalent in Pinaceae relative to Fagaceae (Anderegg et al. 2015a), possibly reflecting different strategies to face drought stress (Ruiz-Benito et al. 2014; Anderegg et al. 2016; Cailleret et al. 2017). Although these latter results pertain only to growth responses, radial growth dynamics and tree mortality are tightly associated (Cailleret et al. 2017). Finally, the high recruitment capacity of most Fagaceae likely confers them an additional advantage (relative to Pinaceae) in face of disturbance (Eugenio and Lloret 2004; Ruiz-Benito et al. 2017a; Abrams et al. 2017).

Several factors likely explain why changes towards increased dominance of Fagaceae were less clear in East North America compared to Europe and (East) Asia. Firstly, our own results indicate that natural disturbances appear to be a particularly important driver of vegetation change in this region, and this is the only type of disturbance not associated to P->F dynamics. This would be consistent with the view of Pinaceae as relatively early-successional species compared to Fagaceae. In addition, late-successional Pinaceae species (e.g., many *Abies*, *Picea* and *Tsuga* species, as opposed to relatively early-successional *Pinus*) are particularly common in North America, which could also cause increased Pinaceae as a result of successional dynamics in this region (Chen and Luo 2015; Searle and Chen 2017). Finally, many of the recent changes in forest management and land use that have promoted broadleaves in Europe (e.g., land abandonment) have not been observed (or are much more recent) in North America (Paulson et al. 2016). Although not captured in our literature review, Pinaceae encroachment upon savannas and woodlands formerly dominated by Fagaceae have been also observed in NW North America, mostly associated to changes in fire frequency, introduction of exotic species, and grazing intensification (Gedalof et al. 2006; Devine and Harrington 2013; Copes-Gerbitz et al. 2017).

The fact that Fagaceae and Pinaceae have contrasted functional traits (Brodribb et al. 2012; Carnicer et al. 2013; Ruiz-Benito et al. 2017) implies that the observed changes in the relative abundance of the two groups may have important implications for ecosystem function and the provision of forest ecosystem services (Vayreda et al. 2016). Possibly even more important are the implications of these compositional changes in terms of future forest resilience to ongoing climate change. On one hand, conifers in general and Pinaceae in particular are frequently considered more capable to withstand extreme abiotic stress (e.g. Coomes et al. 2005) and, in relation to drought stress, tend to operate with wider hydraulic safety margins than angiosperms (Choat et al. 2012). On the other hand, some attributes, including higher resprouting capacity, may favor Fagaceae under warmer and drier climates (Carnicer et al. 2013). Palynological evidence shows that oaks (Fagaceae) have indeed increased in abundance during warm interglacial periods, at least in some regions (McIntyre et al. 2015). However, the net result of all these contrasting responses remains highly uncertain.

In conclusion, we report a widespread increase in dominance of Fagaceae species at the expense of Pinaceae across northern temperate forests, with the exception of East North America. Although our results appear consistent and summarize, to the best of our knowledge, all published reports worldwide, we acknowledge that the number of case studies on which we base our synthesis is low and possibly not representative at the global scale, as large areas of the temperate forest biome are not well represented (e.g., most of the Asian continent, NW North America). The driver of vegetation change emerges as an important factor determining the direction of observed vegetation dynamics, with transitions from Pinaceae to Fagaceae dominating in all cases except for natural disturbances. Different disturbance histories, as well as differences in regional floras, likely determine the dominant direction of vegetation transitions in different temperate regions. If the pattern of directional change observed here proves to be general for the temperate biome, the potential implications for ecosystem function and forest resilience are large and clearly deserve further study.

Capítulo 3

Recent dynamics of pine and oak forests in Mexico

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Abstract

Temperate forests worldwide are dominated by two families, Pinaceae and Fagaceae. In the last decades, temperate forests are experiencing rapid changes and, in some regions, a directional increase in Fagaceae abundance at the expense of Pinaceae has been detected. Here, we analyze the recent forest dynamics of Pinaceae and Fagaceae in Mexican forests to assess whether there is a directional change in the relative abundance of these two families and identify the environmental factors that are determining their recent growth dynamics. We take advantage of repeated surveys data from the Mexican National Forest and Soil Inventory (INFyS), obtained in 2004-2007 and 2009-2014. Our results show that, at present, there is no overall directional trend in the changes of the relative abundance of Pinaceae and Fagaceae in the temperate forests of Mexico, which likely reflects a complex mixture of forest dynamics, locally dominated by different types of disturbance or successional dynamics. At the same time, however, we find evidence that the growth of Fagaceae species is responding more favorably than that of Pinaceae to currently rising temperatures in Mexico. Although these results need to be confirmed by longer-term studies, the resulting changes in composition could potentially have strong impacts on forest ecosystem function in the mid-term.

Keywords: *Climate change, Fagaceae, Forest dynamics, Forest inventory, INFyS, Mexico, Pinaceae, Temperate forests.*

Introduction

Temperate forests cover large areas of the northern hemisphere, dominating mid-latitudes in North America, Asia, and Europe (Olson et al. 2001). These forests are dominated by deciduous broadleaf trees and evergreen conifers, mostly belonging to two families: Fagaceae (angiosperm) and Pinaceae (gymnosperm) (Woodward et al. 2004). Pinaceae is represented by 11 genera and 225 species (Tsai et al. 2013) and Fagaceae by eight genera and about 927 species (Christenhusz and Byng 2016). Angiosperm and gymnosperm species in general, and Pinaceae and Fagaceae in particular, tend to differ in their ecology and habitat requirements, as well as in their functional properties (Bond 1989; Brodribb et al. 2012; Carnicer et al. 2013; Augusto et al. 2014).

In the last decades, temperate forests are experiencing rapid changes, largely driven by global change and the corresponding anthropogenic impacts (Bonan 2008). These impacts are modifying the disturbance regime of many temperate forests, including higher occurrence of extreme climatic events, natural fires, pests and diseases, and land use changes (Dale et al. 2001; Seidl et al. 2014). These alterations, including recent changes in forest management, are modifying the composition and functional properties of temperate forests at the stand to regional scales (Carnicer et al. 2014; Vayreda et al. 2016; Ruiz-Benito et al. 2017; Stambaugh et al. 2017). Importantly, resulting functional changes are largely determined by the balance between Fagaceae and Pinaceae in the composition of these forests (Carnicer et al. 2013; Vilà-Cabrera et al. 2015; Ruiz-Benito et al. 2017b).

Several reports have identified a recent trend of increasing Fagaceae (mostly oaks) at the expense of Pinaceae (mostly pines) in several temperate regions. These changes seem to be largely driven by direct anthropogenic factors, including historical changes in forest management and land use (Vayreda et al. 2016). Some studies, however, stress also a climatic component, reflected in positive growth responses to increases in temperature for Fagaceae but not for coexisting Pinaceae (Carnicer et al. 2013). A recent synthesis including data from 51 studies in temperate forests worldwide indicates that the pattern of increased Fagaceae abundance (relative to Pinaceae) is widespread and seems to be dominant in all regions except Eastern North America (Alfaro Reyna et al. 2018). Increases of Pinaceae relative to Fagaceae seem to be largely restricted to areas where vegetation dynamics are driven by

natural disturbances, which are a particularly important driver of vegetation change in Eastern North America (Alfaro Reyna et al. 2018).

Temperate forests of North America, distributed from Canada through the United States and Mexico to southern Nicaragua, encompass a great diversity of environmental gradients, which has resulted in a great diversity of species across forest landscapes. The humid mountain regions of Mexico harbor the greatest diversity of *Pinus* and *Quercus* species worldwide (Rzedowski 2006; González-Abraham et al. 2015). It is estimated that in Mexico there are about 60 pine species and 125 oak species (Valencia-A 2004; Romero-Rangel et al. 2015). Although these temperate forests in Mexico and Central America have high levels of endemism and are considered centers of species diversity, there is little information on their recent community dynamics. In this area, the main anthropogenic disturbances are mostly associated with the collection of firewood, extensive grazing, and conversion of forest lands for cultivation or livestock (FAO 2010; Barsimantov and Antezana 2012; González-Abraham et al. 2015; Correa Ayram et al. 2017). Pines and oaks may respond differently under these different types of disturbance (Fulé and Covington 1998).

Climatic variability influenced by ENSO (El Niño Southern Oscillation) is another important factor in the region, as ENSO causes either dry or extremely wet conditions depending on its phase (Yocom Kent et al. 2017). This climatic oscillation of wet-dry periods favors increased frequency of forest fires (Drury and Veblen 2008; Yocom Kent et al. 2017), which is a key factor for the successful recruitment of pines and oaks in the region (Meunier et al. 2014a). In some areas exposed to frequent fires, oaks tend to be more abundant in the early post-fire stages, while in later stages both pines and oaks are usually codominant (González-Tagle et al. 2008).

The main objective of this study is to analyze the recent forest dynamics of Pinaceae and Fagaceae in Mexican temperate forests, using repeated surveys data from the Mexican National Forest and Soil Inventory (INFyS). Firstly, we assess whether there is a directional change in the relative abundance of pines vs oaks in these forests. Secondly, we identify the environmental factors that are determining recent growth dynamics of pines and oaks in the study area, focusing on the effect of forest successional patterns and land use, long-term climate and recent climate trends. Based on previous research, we hypothesize that oaks will

be increasing their abundance (relative to pines) in most areas, and that this trend will be particularly noticeable under dry conditions, both in terms of historical climate and recent warming.

Materials and methods

Study area

Forests throughout Mexico (between 24° 34'W and 98° 25'W and 14° 20'N and 92° 05'N), extend through a large variety of climates and topographies and cover approximately 32 million ha (40% of the country's surface). We focused specifically on Mexican pine-oak forests, which are mainly distributed through the temperate climate (*Cw*, according to the Köppen's classification; Garcia 1964), characterized by dry winters, mean temperatures between 12 and 23° C and annual precipitation between 800 and 2,000 mm per year. These forests are dominated predominantly by the genera *Pinus* and *Quercus*, which account for 88% of the basal area of temperate Mexican forests. Mexican pine-oak forests A low proportion of pine-oak forests, however, can also be found in the humid subtropical zone (*Cf* type), a wet area where it rains throughout the year. Pine-oak forests are distributed mostly in the Sierra Madre Occidental and in the Volcanic Axis, but also in the eastern slopes of the Sierra Madre Oriental and some parts of the southern mountain systems and the humid subtropical zone (Miranda and Hernández 1963; INEGI 2014).

National Forest and Soil Inventory of Mexico

The study is based on the information obtained from the National Forest and Soil Inventory of Mexico, hereinafter INFyS. This inventory contains around 26,000 sampling units distributed homogeneously throughout the country, following a rectangular grid with a distance between plots that varies from 5 km in temperate regions up to 20 km in arid zones (CONAFOR 2015). The INFyS follows a systematic stratified sampling scheme, using conglomerates of plots as the basic sampling units. Conglomerates have a circular shape (56.42 m radius; 1 ha). Each conglomerate is composed of four subplots distributed geometrically as an inverted "Y", with a sampled area of 400 m² (0.04 ha) each (totaling 1600 m² per conglomerate). This study uses data from the two last INFyS surveys, conducted in

2004-2007 and in 2009-2014. The two surveys were generally conducted on the same conglomerates and thus provided true resampling of the same sampling units (see below).

The following variables were recorded and averaged at the conglomerate level for each survey: tree density, diameter at breast height (1.30 m; DBH) and basal area, considering only trees with DBH > 7.5 cm. These variables were computed considering only Pinaceae species, only Fagaceae species or all trees present in the conglomerate plots, regardless of their family. In addition, we recorded species richness (total number of tree species per conglomerate) and structural richness (total number of 5 cm diameter classes per conglomerate). Recorded site and soil conditions included altitude (masl); slope (estimated as the maximum % slope in the center of the conglomerate); soil depth in the center of each conglomerate (in cm); land tenure (public, state-owned; private property; and social, including the 'ejido' and the communal properties); and disturbance history, including wildfires, pests and diseases, grazing, and wood extractions. The intensity of each disturbance type was assessed in the INFyS as a five-level ordinal scale. For simplicity, we aggregated these levels in two categories for each disturbance type: low impact (no, barely appreciable or low impact) and high impact (medium or high impact as recorded in at least one of the surveys). Preliminary analyses showed that alternative categorizations did not modify the results.

Out of all conglomerates sampled in the INFyS, we selected those that fulfilled the following criteria: (i) the same plots had been measured (resurveyed) in the two inventories; (ii) Pinaceae and Fagaceae were present (in terms of basal area) in at least one of the two inventories; (iii) basal area $\geq 2 \text{ m}^2 \text{ ha}^{-1}$ in the first survey so that very open forests were excluded; (iv) human structures, including roads, were not present; (v) severe disturbances, including power lines, mining activities, human settlements, floods, opening of roads, land-use change and hurricanes affecting more than 66% of the conglomerate surface had not been recorded. A total of 3,953 conglomerates were selected for further analyses (Figure 1). The measurement interval between the two inventories for a given sampling unit was on average 6 years but varied between 3 and 10 years depending on the conglomerate.

Climatic data

Two climatic datasets were used. The first one, characterizing the average (long-term) climate at each conglomerate, was extracted from Worldclim (Hijmans et al. 2005), a free database of global climate layers with a spatial resolution of about 1 km². The geographic coordinates of all conglomerates were superimposed to Worldclim climatic layers from the 1950-2000 period using the ArcGis software to obtain their total annual precipitation (mm) and average annual temperature (°C).

The second set of climatic data characterized recent climate trends (anomalies of temperature and precipitation) and was downloaded from the Climatic Research Center of the University of Delaware <https://climatedataguide.ucar.edu/climate-data> (Legates and Willmott 1990; Lawrimore et al. 2011), with a spatial resolution of 0.5 x 0.5 degrees. Climatic anomalies of precipitation and temperature were calculated for each conglomerate relating the values for the study period (average for the period between surveys for each conglomerate) with the long-term climate average for the period 1960-1990 (reference period). The temperature anomaly was defined as the absolute difference between the temperature during the study period and the reference one. The anomaly of precipitation was calculated as a percentage change.

Data analysis

To evaluate the changes in relative abundance of Fagaceae vs. Pinaceae we calculated the difference between the basal area increments of Pinaceae and Fagaceae in each conglomerate, divided by the period of time (BA_{dif}) as:

$$BA_{dif} = \frac{(BA_{end}^F - BA_{ini}^F) - (BA_{end}^P - BA_{ini}^P)}{(BA_{ini}^F + BA_{ini}^P) \cdot Period} \quad (\text{Eq. 1})$$

where BA is basal area; the super-indices *F* and *P* denote Fagaceae and Pinaceae, respectively; the sub-indices *end* and *ini* indicate the values at the end and at the beginning of the study period (first or second INFyS survey), respectively; and *Period* refers to the length of the time period between surveys in years.

To assess in more detail the drivers of the differential growth dynamics of Fagaceae vs. Pinaceae we modelled basal area in the second INFyS survey as a function of Family (Fagaceae, Pinaceae), the basal area in the first INFyS survey, and a set of environmental explanatory variables. Since some environmental variables were highly cross-correlated, we used principal components analysis (PCA) to reduce the number of explanatory variables in our model. A first PCA comprised stand variables as measured in the first INFyS survey, including total tree density (by family), average DBH (by family), basal area (by family), species richness and structural richness. Basal area and average DBH were approximately orthogonal and characterized the first and second axis of the PCA, respectively (Figure S1), and were thus selected to be included in the models below. A second PCA summarized environmental variables at the conglomerate level, including slope, soil depth, mean annual temperature, annual precipitation, temperature anomaly and precipitation anomaly. The results showed that mean annual temperature and temperature anomaly were roughly orthogonal and characterized the first two axes of the PCA (Figure S2) and were thus selected for further analyses.

The explanatory variables in the final model included Family (Fagaceae, Pinaceae) and its interaction with: the length of the time period between surveys (in years), the basal area in the first INFyS survey (per family), mean DBH in the first survey (per family), mean annual temperature, temperature anomaly, land tenure (Public, Private, Social), wildfires (low vs. high impact), pests and diseases (low vs. high impact), grazing (low vs. high impact), and wood extractions (low vs. high impact). We also included two-way interactions between structural and climatic variables (basal area * mean temperature, DBH * mean temperature, basal area * temperature anomaly, and DBH * temperature anomaly). We used mixed-effect models with Conglomerate nested in State (N = 28) as random factors. The former variable was included to account for the fact that data for the two families (Fagaceae, Pinaceae) was paired at the conglomerate level; whereas the latter variable accounted for the effect of spatial autocorrelation at relatively large spatial scales (the average size of a Mexican state is 63,481 km²).

We applied step-by-step model selection to simplify the previous model, beginning with the saturated model and removing the least significant variables until a minimum adequate

model was found in terms of the Akaike Information Criterion (AIC). Some variables were transformed before analyses to ensure normality and/or linearize their relationship with the response variable (see Table 1). Model residuals showed no obvious pattern. All statistical analyses were carried out with the R software (version 3.2.2, The R Foundation for Statistical Computing).

Results

The most abundant species in the study forests were *Quercus sideroxyla*, *Quercus laeta* and *Quercus crassifolia* for Fagaceae and *Pinus durangensis*, *Pinus engelmannii* and *Pinus cembroides* for Pinaceae (Figure 2). Average plot basal area and, particularly, the contribution of Pinaceae and Fagaceae to total basal area, increased between the two inventories. However, the proportion corresponding to Pinaceae and Fagaceae remained similar between inventories (Figure 3).

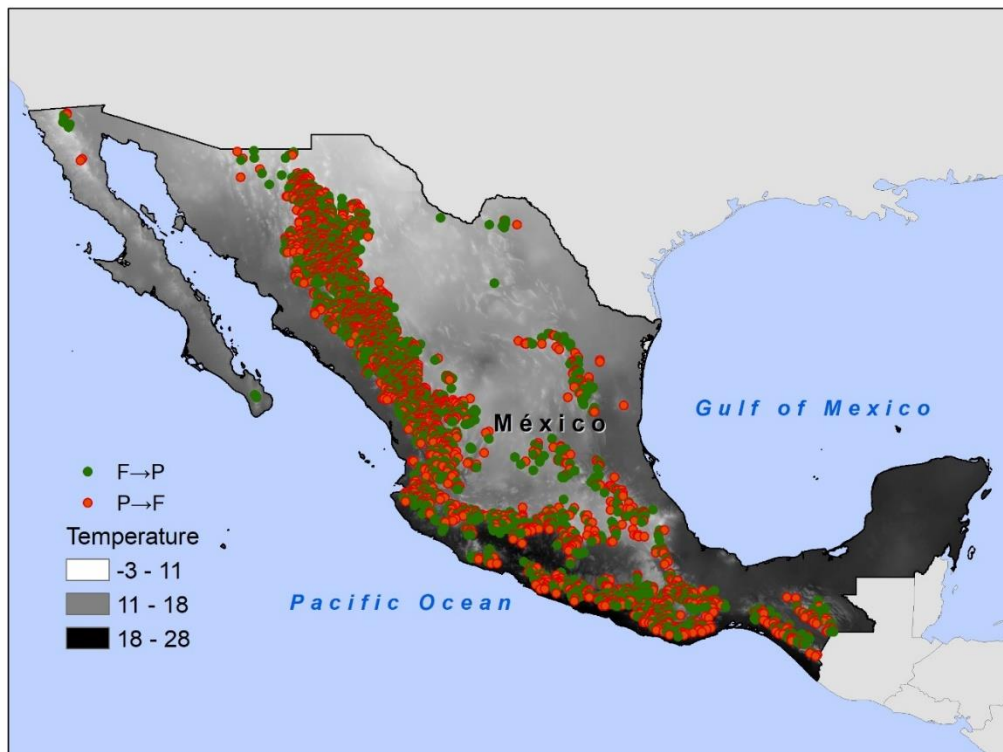


Figure 1. Location of the 3,953 INFyS conglomerates that were used to assess the recent dynamics of Pinaceae vs Fagaceae in Mexico, plotted over an annual mean temperature ($^{\circ}\text{C}$) map. Different colors indicate the direction of vegetation change in terms of basal area (Eq. 1) (F→P indicates increased Pinaceae abundance; P→F indicates increased Fagaceae abundance).

Table 1. ANOVA table for the linear mixed-effects model of final basal area (second INFyS) (square-root transformed) as a function of family (Pinaceae or Fagaceae), initial stand structure (initial basal area, mean DBH), climate variables (mean temperature and recent anomaly of temperature), land tenure and several disturbance types (pests, wood extractions). Conglomerate nested in state were included as random factors (see text). Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. This model corresponds to the minimum adequate model after simplification based on AIC.

	numDF	denDF	F-value	p-value
(Intercept)	1	3946	6201.65	<.0001
Family	1	3946	63.41	<.0001
Sqrt (Initial basal area)	1	3946	28632.74	<.0001
Sqrt(DBH)	1	3916	53.02	<.0001
Log (Mean temperature)	1	3916	11.95	0.0006
Anomaly of temperature	1	3916	4.43	0.0354
Land tenure	2	3916	2.06	0.1275
Pests	1	3916	6.19	0.0129
Wood extractions	1	3916	16.91	<.0001
Family: Sqrt (Initial basal area)	1	3946	12.32	0.0005
Family: Sqrt(DBH)	1	3946	7.10	0.0078
Family: Log (Mean temperature)	1	3946	24.28	<.0001
Family: Anomaly of temperature	1	3946	11.34	0.0008
Sqrt (Basal area): Log (Mean temperature)	1	3946	98.37	<.0001
Sqrt (DBH): Log (Mean temperature)	1	3916	11.95	0.0006
Sqrt (DBH): Anomaly of temperature	1	3916	3.34	0.0676

However, the proportion corresponding to Pinaceae and Fagaceae remained similar between inventories (Figure 3). Accordingly, the difference between the basal area increments of Pinaceae and Fagaceae in each conglomerate (BA_{dif}) was distributed around zero (Figure 4) and did not show obvious geographical patterns (Figure 1), indicating that there is no consistent increase in dominance of either of the two families. Negative values, corresponding to relative increases of Pinaceae, corresponded to 53% of values; whereas 47% of values (relative increase of Fagaceae) were positive. Most values were small, with 5% and 95% quantiles equaling -0.09 and 0.10 year^{-1} , respectively, indicating that large changes (relative to the initial BA) were rare. These results were very similar if only the conglomerates for which the period between surveys was >7 years were considered (average period between surveys = 8 years, $N = 1119$) (not shown).

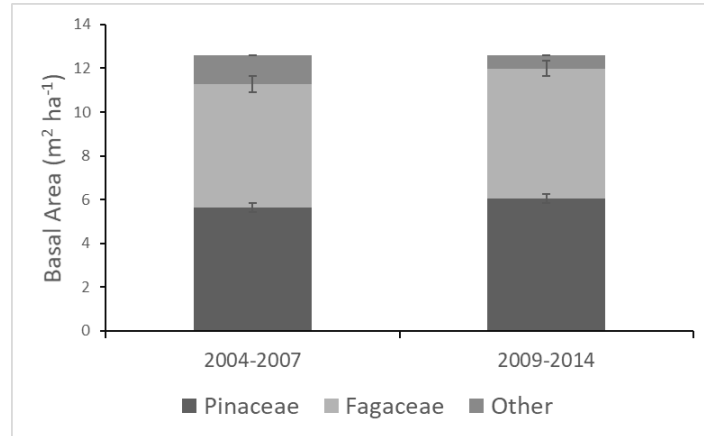


Figure 3. Average plot basal area at the two INFyS surveys, indicating the proportion corresponding to Pinaceae, Fagaceae and other families.

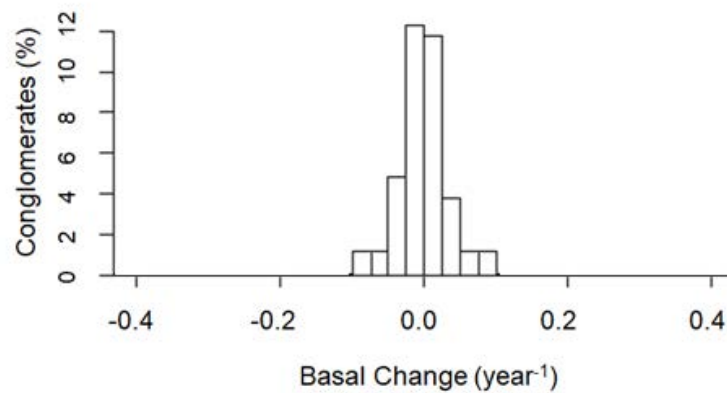


Figure 4. Overall basal area change (year⁻¹) of Pinaceae vs. Fagaceae between the two INFyS surveys studied. Positive values indicate increasing abundance of Fagaceae, negative values indicate increasing abundance of Pinaceae.

As expected, initial basal area was the strongest determinant of final basal area according to the results of the mixed-effects model (Table 1, Figure S1), with a positive effect that tended to saturate at large initial basal areas (Figure S3). In addition, DBH, mean temperature and temperature anomalies had all negative effects overall. However, some of these variables showed significant interactions. The (positive) effect of initial basal area tended to be stronger at low temperatures, and the negative effect of temperature occurred particularly at large initial basal areas (Figure 4). Similarly, the negative effect of DBH was stronger at high

temperatures, and the negative effect of temperature was apparent only at large DBH (Figure 5). Finally, the negative effect of temperature anomaly was particularly strong at large DBH, whereas the effect was almost neutral at lower DBH values (Figure 6). Pests and wood extractions had a significant, negative effect on final basal area (Table 1, Figure S1).

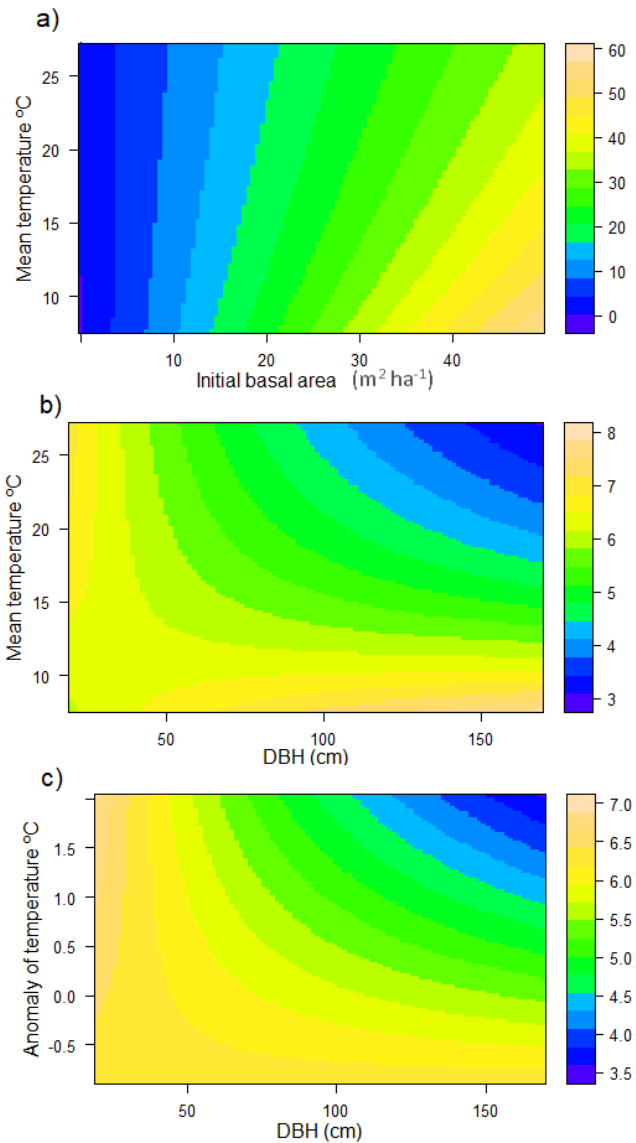


Figure 5. Effect of the interaction between a) mean annual temperature ($^{\circ}\text{C}$) and initial basal area ($\text{m}^2 \text{ha}^{-1}$), b) mean annual temperature ($^{\circ}\text{C}$) and average DBH (cm), and anomaly of temperature ($^{\circ}\text{C}$) and average DBH (cm) on final basal area (square-root transformed), according to the model presented in Tables 1 and S1.

Family also had a very significant effect on final basal area, according to the mixed-effects model. In addition, the effects of initial basal area and DBH interacted with Family, but the

qualitative patterns were similar for the two families in both cases (Figures S3, S4). Climatic effects also interacted with Family, but in this case the patterns were contrasted for the two families, with strong negative effects of both mean temperature and temperature anomaly in Pinaceae and no effect on Fagaceae (Figure 7, 8). These results remained qualitatively unchanged (negative effects of mean temperature and temperature anomaly for Pinaceae, neutral or positive effects for Fagaceae), and overall model fit worsened, when we refit the model using total conglomerate basal area instead of splitting this variable by family (Table S2, Figure S5).

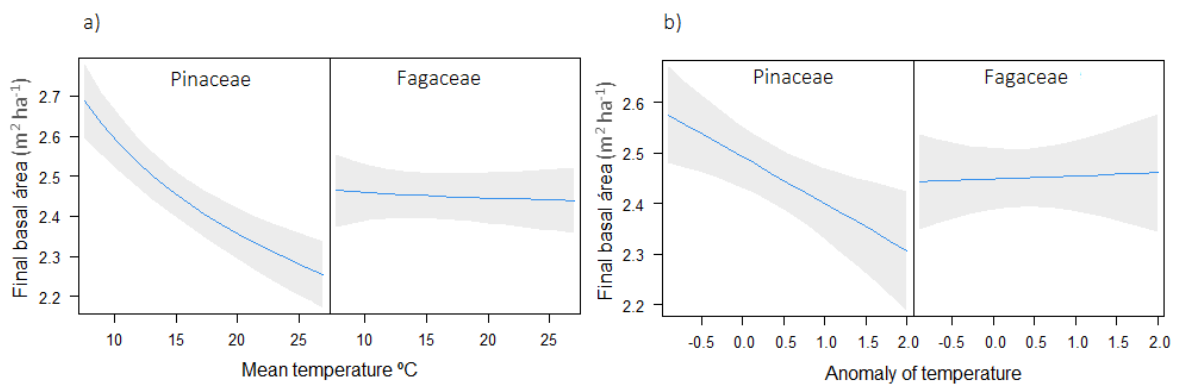


Figure 8. Effect of family (Fagaceae, Pinaceae) on the relationship between final basal area (square-root transformed) and mean annual temperature (°C) (a, left) and anomaly of temperature (°C) (b, right), according to the model presented in Tables 1 and S1.

Discussion

Our results show that, at present, there is not clear directional pattern in the changes of the relative abundance of Pinaceae and Fagaceae in the temperate forests of Mexico. This is not consistent with the global patterns reported by Alfaro et al. (2018), but appears similar to the lack of clear directional changes observed in that study for Eastern North America. Previous studies conducted in Mexico at local to regional scales show mixed results regarding the relative dynamics of these two families (González-Espinosa et al. 1991; Goforth and Minnich 2008; Olvera-Vargas et al. 2010; Ávila-Flores et al. 2014), consistent with the relative stasis suggested by our country-level analysis. Although exceptions exist, the majority of Pinaceae in Mexico (particularly pines) are considered relatively early-successional species that require

comparatively open environments relative to the more shade-tolerant and late successional oaks (Galindo-Jaimes et al. 2002; Almazán-Núñez et al. 2016). In this context, our results can be interpreted to indicate a complex mixture of forest dynamics, locally dominated by different types of disturbance or successional dynamics, but without a clear overall trend (cf. Fulé and Covington 1998; Park 2001).

The relatively short period between forest inventory surveys (average of 6 years, ranging between 3 and 10 depending on the plot) is an important limitation of our analysis and may contribute to explain the lack of clearer directional trends. However, we obtained similar results when only the conglomerates with relatively long (> 7 years) periods between surveys were considered. This time period is similar to the one used in other national forest inventories for which clear directional trends have been identified (e.g. Vayreda et al. 2016). In addition, the time period between surveys did not have a significant effect in the basal area increment model, which altogether suggests that this temporal limitation was not critical in explaining the lack of directional short-term patterns in our case.

Our results show that the recent growth dynamics of pines and oaks in Mexico are largely driven by forest structure, with saturating effects of initial basal area and mean DBH that likely reflect increasing competition. Although these effects differed between families, differences were quantitatively small (Figures S3, S4) and did not reflect the expected lower growth of pines at higher basal areas due to their lower competitive ability (Bond 1989; but see Brodribb et al. 2012). This could be explained by the fact that total basal area was not accounted for in our main models (*i.e.*, basal areas were split by family). However, the distribution of basal area was similar between families (Figure 3) and when we refit the model using total conglomerate basal area instead of splitting this variable by family, we got similar results. In fact, these models showed a clearer trend towards lower final basal area for Fagaceae in conglomerates with very large initial basal area, contrary to expectations (Table S2). Interestingly, stand structure effects interacted with climate, so that the positive effect of basal area tended to be reduced at warmer sites and the negative effect of average DBH was highest under warmer conditions, both in terms of average climate and in terms of higher temperature anomalies. These effects suggest an impact of increased competition for water

under warmer environments, consistent with previous reports in other regions (e.g. Linares et al. 2010; Vilà-Cabrera et al. 2011).

The negative effect of forest extractions is consistent with the fact that 75% of forest wood production in Mexico comes from temperate forests, particularly conifers (Segura 2000). On the other hand, forest pests affect both Conifers and Fagaceae, although greater relevance has been given to pest effects on conifers due to their economic importance (FAO 2009). Some reports indicate that there is an increase in the affectation of Mexican forests by pests and diseases, closely related to rising temperatures and forest fires (Rubin-Aguirre et al. 2015; Marín et al. 2018). In particular, Mexican forests affected by forest fires are more prone to pests and diseases, causing a double affectation due to the increase of tree mortality produced by pest infestations, such as the pine bark beetle (*Dendroctonus ponderosae*) (Rubin-Aguirre et al. 2015). Although we could not assess this interaction with our experimental design, this type of interactive effects are likely to become increasingly important for forest dynamics under climate change (cf. Anderegg et al. 2015b).

Pinaceae and Fagaceae responded very differently to mean annual temperature and to temperature anomaly. Whereas pine basal area was strongly reduced under warmer conditions these variables had little effect on the oaks. Previous studies have reported differential pine-oak dynamics depending on the region in Mexico. In the semi-humid forests of southern Mexico, where conditions of high humidity and temperature dominate, oak species tend to replace pines during succession and pine dominance appears to be restricted to highly disturbed areas (Ramirez-Marcial et al. 2001; Galindo-Jaimes et al. 2002; Almazán-Núñez et al. 2016). In contrast, in areas with lower humidity and temperature, such as the center and northeast of the country, where the extraction of wood, firewood or charcoal are more frequent, pine dominance appears also to be more common (Segura 2000; Heyerdahl and Alvarado 2003; Cortés Montaña et al. 2012). The pine-oak forests that are distributed further north under drier and colder conditions are affected by the wet-dry climate oscillations, which promotes an increase in the frequency of forest fires (Drury and Veblen 2008; Yocom Kent et al. 2017). Although in many northern areas forest fires tend to promote pine dominance, this is not always the case depending on complex interactions between fire frequency, local environmental conditions and species identity, resulting in frequent

situations in which oaks and pines are codominant (Fulé and Covington 1994; Fulé and Covington 1998; Fulé et al. 2000; Park 2001; González et al. 2007; González-Tagle et al. 2008; Meunier et al. 2014).

The fact that Fagaceae seem to be favored not only in warmer places but also where conditions have become warmer over last decades (higher temperature anomalies) suggests that climate change may favor oak dominance in current pine-oak forests. Similar results have been reported in other temperate regions (Carnicer et al. 2013), although interactions with changing disturbance regimes, including management, are likely to play also a key role (Vayreda et al. 2016). In Mexican forests, changes in wildfire regimes will be critical and increased fire frequencies under warmer conditions (due to higher climatic fire risk) could counterbalance, at least in part, the trend towards increased oak dominance reported here (Fulé and Covington 1998; González-Tagle et al. 2008). In addition, it should be noted that our analysis focused on changes in basal area, which does not allow disentangling recruitment, growth and mortality responses and may therefore mask subtler demographic responses to temperature.

In conclusion, our study provides evidence that Fagaceae species may be responding more favorably than Pinaceae to currently rising temperatures in Mexico, which could potentially lead to changed forest structure, composition and function in the mid-term. If confirmed, this trend could have major ecological, economic and social consequences, as pine-oak woodlands in Mexico are considered biodiversity hotspots and provide major ecosystem services, including subsistence goods to several indigenous communities and 75% of all wood extractions in the country (Segura 2000; FAO 2015). The dynamics of pine-oak woodlands in Mexico under ongoing climate change clearly merit further investigation.

Appendix

Table S1. Estimated coefficients of the linear mixed-effects model of final basal area (second INFyS) (square-root transformed) as a function of family (Pinaceae or Fagaceae), initial stand structure (basal area, DBH), climate variables (average temperature and recent temperature anomaly) and several disturbance types (see Table 1 in main text for the corresponding ANOVA table). Conglomerate nested in state were included as random factors (see text). Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. This model corresponds to the minimum adequate model after simplification based on AIC. Coefficient values are given relative to the reference level for each factor (Family='Pinaceae', Land tenure='Private', no disturbance for all disturbance types).

	Value	Std.Error	DF	t-value	p-value
(Intercept)	-4.7287	1.1576	3946	-4.0848	0.0000
Family Quercus	-1.7151	0.3010	3946	-5.6969	0.0000
Sqrt(Initial basal area)	2.1443	0.1312	3946	16.3395	0.0000
Sqrt(DBH)	0.5281	0.1497	3916	3.5262	0.0004
Log(Mean temperature)	1.0567	0.2263	3916	4.669	0.0000
Anomaly of temperature	0.1223	0.1194	3916	1.0241	0.3058
Land tenure "Public"	-0.0911	0.0927	3916	-0.9825	0.3259
Land tenure "Social"	0.0244	0.0145	3916	1.6794	0.0931
Pests	-0.0377	0.0184	3916	-2.0482	0.0406
Wood extractions	-0.0748	0.0159	3916	-4.6940	0.0000
Family Quercus: Sqrt(Initial basal area)	-0.0386	0.0114	3946	-3.3775	0.0007
Family Quercus: Sqrt(DBH)	0.0205	0.0101	3946	2.0112	0.0444
Family Quercus: Log(Mean temperature)	0.3215	0.0596	3946	5.3934	0.0000
Family Quercus: Anomaly of temperature	0.0987	0.0330	3946	2.9889	0.0028
Sqrt(Basal area): Log(Mean temperature)	-0.2448	0.0261	3946	-9.3457	0.0000
Sqrt(DBH): Log(Mean temperature)	-0.1123	0.0292	3916	-3.83882	0.0001
DBH: Anomaly of temperature	-0.0295	0.0161	3916	-1.8283	0.0676

Table S2. Estimated coefficients of the linear mixed-effects model of final basal area (second INFyS) (square-root transformed) as a function of family (Pinaceae or Fagaceae), initial stand structure (initial basal area, DBH), climate variables (average temperature and recent temperature anomaly), the time period between surveys, and several disturbance types. Conglomerate nested in state were included as random factors (see text). The only difference between this model and the one presented in Tables 1 and S1 is that in this case total conglomerate basal area was used instead of splitting this variable by family (Pinaceae vs Fagaceae). Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. This model corresponds to the minimum adequate model after simplification based on AIC. Coefficient values are given relative to the reference level for each factor (Family='Pinaceae', Land tenure='Private', no disturbance for all disturbance types).

	Value	Std.Error	DF	t-value	p-value
(Intercept)	-1.7359	1.1043	3940	-1.5718	0.1161
Family Quercus	-2.9052	0.3347	3940	-8.6787	0.0000
Time period	0.0175	0.0098	3940	1.7836	0.0746
Sqrt(Basal area) (Total)	1.3897	0.1546	3911	8.9837	0.0000
Sqrt(DBH)	0.1647	0.1482	3911	1.1110	0.2666
Log(Mean temperature)	0.6162	0.3915	3911	1.5737	0.1156
Anomaly of temperature	-0.046	0.2055	3911	-0.2262	0.821
Land tenure "Public"	0.1540	0.2198	3911	0.7005	0.4836
Land tenure "Social"	0.1441	0.0346	3911	4.1636	0.0000
Wildfires	0.1831	0.0317	3911	5.7763	0.0000
Grazing	-0.1076	0.0321	3911	-3.3488	0.0008
Pests	-0.0712	0.0446	3911	-1.5946	0.1109
Wood extractions	0.1692	0.0384	3911	4.4012	0.0000
Family Quercus: Time period	-0.0212	0.0138	3940	-1.5315	0.1257
Family Quercus: Sqrt(Basal area) (Total)	-0.2362	0.0220	3940	-10.7179	0.0000
Family Quercus: Sqrt(DBH)	-0.0120	0.0200	3940	-0.6007	0.548
Family Quercus: Log(Mean temperature)	1.5595	0.1104	3940	14.1201	0.0000
Family Quercus: Anomaly of temperature	0.1562	0.0625	3940	2.4986	0.0125
Family Quercus: Land tenure "Public"	-0.5375	0.3083	3940	-1.7431	0.0814
Family Quercus: Land tenure "Social"	-0.2057	0.0480	3940	-4.2868	0.0000
Family Quercus: Wildfires	-0.2782	0.0440	3940	-6.3104	0.0000
Family Quercus: Grazing	0.1691	0.0450	3940	3.7522	0.0002
Family Quercus: Pests	0.0700	0.0626	3940	1.1181	0.2636
Family Quercus: Wood extractions	-0.4509	0.0537	3940	-8.3942	0.0000
Sqrt(Basal area) (Total): Log(Mean temperature)	-0.26348	0.0554	3911	-4.7519	0.0000
Sqrt(Basal area) (Total): Anomaly of temperature	-0.00351	0.0336	3911	-0.1042	0.917
Sqrt(DBH): Log(Mean temperature)	-0.07608	0.0524	3911	-1.4509	0.1469
Sqrt(DBH): Anomaly of temperature	-0.00767	0.0300	3911	-0.2549	0.7988

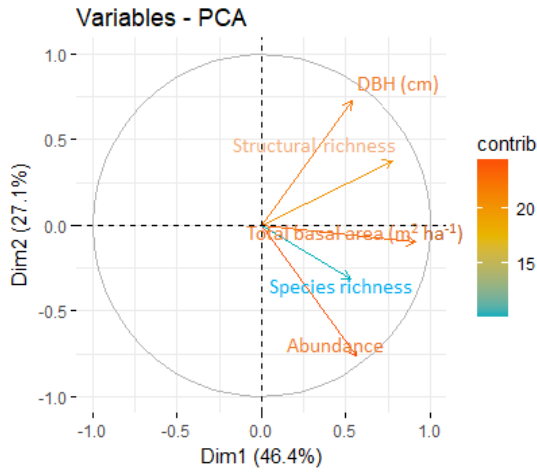


Figure S1. Principal component analysis of plot structural variables, including total tree density (Abundance), species richness, structural richness, average DBH and basal area. The color legend indicates the overall contribution to explained variance.

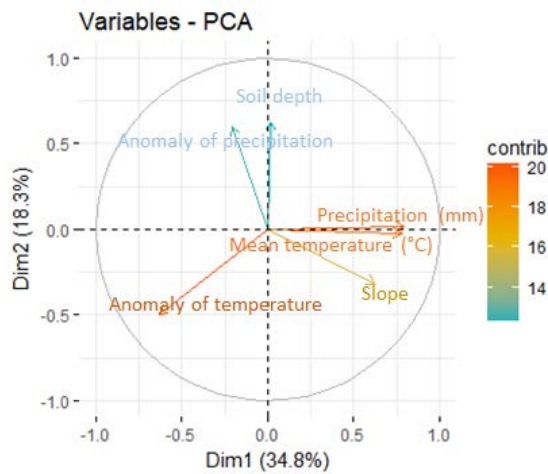


Figure S2. Principal component analysis of environmental variables, including soil depth, slope, precipitation, anomaly of precipitation, mean temperature, anomaly of temperature. The color legend indicates the overall contribution to explained variance.

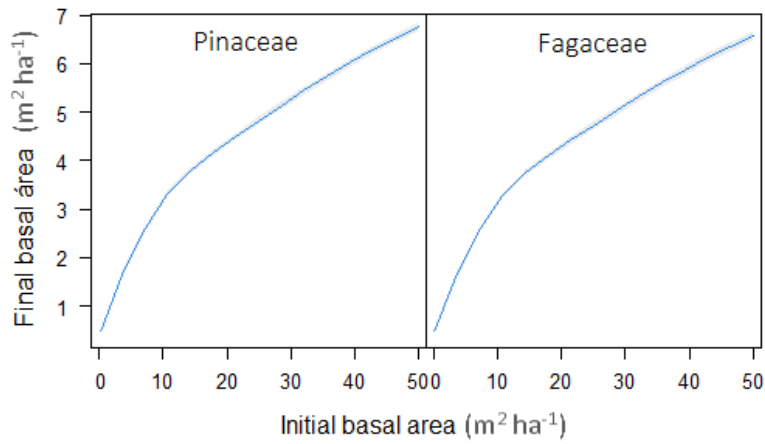


Figure S3. Effect of family (Fagaceae, Pinaceae) on the relationship between final basal area (square-root transformed) and initial basal area, according to the model presented in Tables 1 and S1.

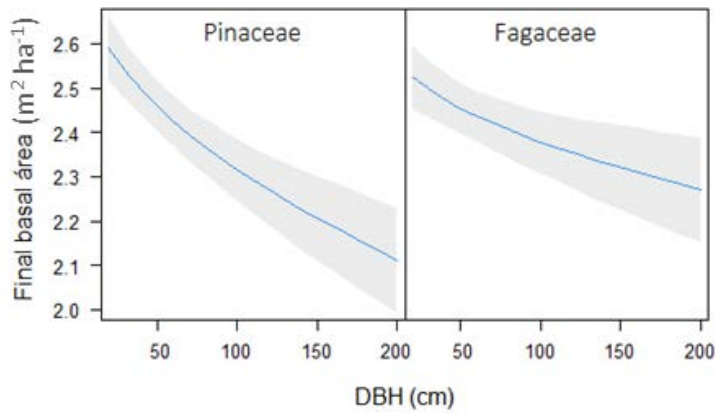


Figure S4. Effect of family (Fagaceae, Pinaceae) on the relationship between final basal area (square-root transformed) and initial DBH, according to the model presented in Tables 1 and S1.

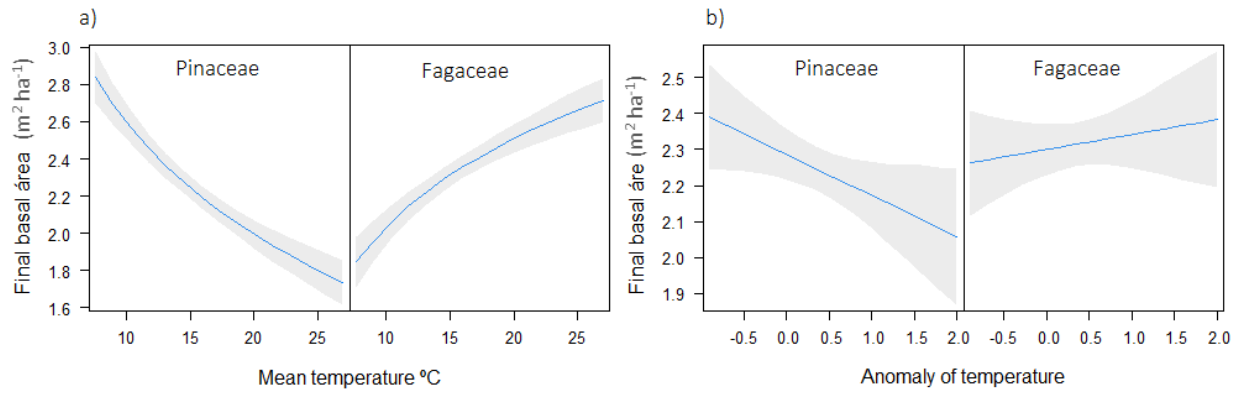


Figure S5. Effect of family (Fagaceae, Pinaceae) on the relationship between final basal area (square-root transformed) and mean temperature (°C) (a, left) and the anomaly of temperature (°C) (b, right), according to the model presented in Table S2.

Capítulo 4

Regeneration dynamics in Mexican pine-oak forests

**Teresa Alfaro Reyna
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Abstract

Global change is causing an increase in the incidence of natural and anthropogenic disturbances on forests, which frequently interact synergistically and promote substantial changes in forest structure, composition and functioning. In this study we evaluate the regeneration of Pinaceae and Fagaceae species in pure and mixed forests in Mexico to determine if current regeneration patterns are indicative of forest composition shifts, as observed in other temperate regions. We also identify the environmental factors that determine the regeneration dynamics of Pinaceae and Fagaceae species in these forests. We use data from two consecutive surveys of the National Inventory of Forests and Soils of Mexico (INFyS), obtained in 2004-2007 and 2009-2014. As expected, our results show that the spatial patterns of regeneration are affected by forest structure, by climate and by the history of disturbances and land tenure. Importantly, the presence and abundance of Fagaceae regeneration is generally higher than that of Pinaceae, and it is favoured (relative to Pinaceae) under warmer climates and by the presence of wildfires, conditions that are likely to increase under ongoing climate change. These changes suggest a progressive increase in the abundance of Fagaceae at the expense of Pinaceae in Mexican temperate forests, which could have important impacts on the functioning of forests and their resilience to future environmental changes.

Keywords: *regeneration dynamics, Oak, Pine, Forest inventory, Mexico*

Introduction

Climate change is causing an increase in the incidence of disturbances such as drought, natural fires, pests and diseases (Brecka et al. 2018; Právělie 2018), which can drive rapid changes in forests (Allen et al. 2015). On the other hand, recent anthropogenic changes due to forest exploitation, extensive grazing and land use changes are also modifying the composition and structure of forest ecosystems (Burgi et al. 2000; Gimmi et al. 2010; Easterday et al. 2018). These drivers frequently interact synergistically, promoting substantial changes in forests in response to the new conditions created (Donato et al. 2016). Examples include the increase of fast-growing and drought-tolerant species in tropical and temperate environments (Feeley et al. 2011; Allen et al. 2012; Zhang et al. 2018), changes in composition from late-successional to early-successional conifers caused by the increase in the frequency of fires associated with climate change (Carcaillet et al. 2001; Searle and Chen 2017) or the transition from conifers to broadleaf species at medium altitudes in temperate forests (Vayreda et al. 2016).

To understand and forecast shifts in forest composition, it is essential to characterize the regeneration patterns of tree species (cf. Martínez-Vilalta & Lloret 2016 for the specific case of drought-induced forest decline), including the conditions that allow the growth and survival of new recruits of different species, as well as their response under different natural and anthropogenic disturbance regimes (Denslow 1980). Regeneration dynamics can be explained in terms of tolerance to limiting resources, such as the availability of water and nutrients or the exposure to light (Agyeman et al. 1999; Woodward et al. 2004). Light availability is one of the most important factors affecting the establishment of tree species (Swaine and Whitmore 1988). Responses to light availability are largely determined by the efficiency of light interception and photosynthetic capacity (Swaine and Whitmore 1988; Woodward et al. 2004). Shade-intolerant species have a higher growth rate under direct light conditions and usually dominate the low canopies initially, and then they are typically replaced by species that tolerate more shaded conditions, at least in their early stages of development, which are usually classified as late-successional species (Swaine and Whitmore 1988).

Temperate forest ecosystems occupy 26% of the world's forest cover and dominate large areas of the northern hemisphere (Keenan et al. 2015; Riitters et al. 2016). These forests are represented mainly by the Fagaceae and Pinaceae families. Many Pinaceae are characterized as being intolerant to shade; that is, they require open areas with little plant cover to establish (Ramirez-Marcial et al. 2001; Quintana-Ascencio et al. 2004; Coomes et al. 2005), although many exceptions exist (e.g., Stephens and Gill 2005; González-Tagle et al. 2008). In xeric environments, Pinaceae may require tree protection or nursery for the successful recruitment of seedlings. Edaphic properties combined with water availability significantly influence the establishment of *Pinus* species (Barton 1993; Carnicer et al. 2014; Marín et al. 2018). On the other hand, most Fagaceae are considered semi-tolerant to shade, as they can live under closed canopies during the juvenile and adult stages, although in the early stages of life the requirements of light are sometimes greater (Galindo-Jaimes et al. 2002; Berg et al. 2018). On the other hand, in general oaks have a greater range of tolerance to drought than pines (Rigling et al. 2013; Montes-Hernández and López-Barrera 2013; Carnicer et al. 2014) and they also have a high capacity of resprouting from stumps or roots after a disturbance, which makes them good competitors against pines under highly disturbed conditions (Cooper et al. 2018). Several studies have reported increased regeneration of oaks relative to pines in temperate forests where these two groups coexist, particularly under warm and dry conditions in Southern Europe (Vayreda et al. 2013; Carnicer et al. 2014).

Temperate forests of Mexico, due to their high diversity, are considered a center of origin and diversification of pines and oaks (Govaerts et al. 1998; Challenger and Soberón 2008). Pinaceae are represented in Mexico by four genera and 60 species, half of which are considered endemic. There are 125 species of Fagaceae in Mexico, and more than 60% are considered endemic and/or are under some protection status (Valencia-A 2004; Valencia-A and Gual-Díaz 2014). Despite their high biodiversity and ecological importance and the ecosystem services they provide, more than 50% of pine-oak forests in Mexico have suffered some type of degradation (FAO 2015) and/or are classified as secondary forests (CONAFOR 2010). The patterns of distribution of these forests reflect the historically common disturbances in the region such as forest thinning, grazing and fires (Marín et al. 2018). Several studies have analyzed the local regeneration patterns of pine-oak forests after clearcuts or wildfires in Mexico (Galindo-Jaimes et al. 2002; Rodríguez-Trejo and Fulé 2003;

González-Tagle et al. 2008; Marín et al. 2018), or the reproduction by seeds and the incorporation of seedlings after forest exploitation (Asbjornsen et al. 2004; López-Barrera and Newton 2005). However, there is little information on the regeneration of both groups at a regional scale for different forest types and how it may be influenced by changing climate.

In this study we analyze the dynamics of Pinaceae and Fagaceae regeneration in Mexican forests, using data from two consecutive surveys of the National Inventory of Forests and Soils of Mexico (CONAFOR 2015). Firstly, we evaluate the regeneration of Pinaceae and Fagaceae in pure and mixed forests to determine if current regeneration patterns are indicative of forest composition shifts, as observed in other temperate regions. Secondly, we identify the environmental factors that determine the regeneration dynamics of pines and oaks in these forests. We hypothesize that Fagaceae will tend to regenerate better than Pinaceae in all forest types where these two species types coexist, and that this pattern will be exacerbated under warmer conditions and in areas subjected to intense disturbance regimes.

Materials and methods

Study area

The study area (Figure 1) covers the Pinaceae and Fagaceae forests of Mexico (between 24 ° 34'O and 98 ° 25'O, and 14 ° 20'N and 92 ° 05'N), which are mainly distributed in the Sierra Madre Occidental, in the eastern slope of the Sierra Madre Oriental and in some parts of the southern mountain systems and the humid subtropical zone (Miranda and Hernández 1963; INEGI 2014). These forests are mainly dominated by species of the *Pinus* and *Quercus* genera. They are distributed mainly in regions of temperate and cold climates, rainy or subhumid with summer rains (climate Cw, according to the Köppen classification, García 1964). This climate is characterized by a well-defined dry season in winter and spring, with a mean annual temperature of 10-20 ° C and annual precipitation between 800 and > 2,000 mm per year. In some parts of the eastern Sierra Madre and southern mountain systems, a small proportion of pine-oak forests can be found in the humid subtropical zone (climate Cf), which is characterized by being a very humid area where it rains all year, without a well-defined dry season (Miranda and Hernández 1963; INEGI 2014; Valencia-A and Gual-Díaz 2014), and with

a mean annual temperature of 10-22 ° C and an annual rainfall between 800 and 4700 mm per year.

National Forest and Soil Inventory of Mexico

The study is based on the information obtained from the National Forestry and Soils Inventory of Mexico, hereinafter INFyS. This inventory contains around 26,000 sampling units homogeneously distributed throughout the country, following a rectangular grid with a distance between conglomerates that varies from 5 km in temperate regions to 20 km in arid zones (CONAFOR 2015). The INFyS follows a systematic scheme of stratified sampling, using conglomerates of plots as basic sampling units. The conglomerates are circular with 56.42 m radius (1 ha⁻¹) geometrically distributed in the form of inverted "Y". Each conglomerate contains 4 sites or subplots of 400 m² each, 1600 m² per conglomerate in total. We used the data from the inventories carried out in 2004-2007 and 2009-2014. The interval between the two inventories for a given sampling unit was on average 5 years but varied between 2 and 9 years depending on the conglomerate.

The criteria for the selection of the conglomerates were the following: (i) the same plots had been measured (resurveyed) in the two inventories; (ii) Pinaceae and/or Fagaceae were present (in terms of basal area) in at least one of the two inventories; (iii) basal area was ≥ 2 m² ha⁻¹ in the first survey so that very open forests were excluded; and (iv) those conglomerates that contained human structures and roads and/or where the trees had been seriously affected by environmental impacts such as mining or fires were discarded. Of all the conglomerates sampled in the INFyS, a total of 5,458 met these criteria and were selected for this study.

In each conglomerate a series of plot variables and the regeneration of tree species were measured:

a) Plot variables.

At the conglomerate level, the following variables were recorded: altitude (msnm), slope (estimated as the maximum % slope in the center of the conglomerate), soil depth (measured at the center of each conglomerate), land tenure (public, state owned, private, and social

property, including the "ejido" and the communal properties), total basal area ($\text{m}^2 \text{ha}^{-1}$), and forest type (Oak, for forests where only Fagaceae were present; Pine, for forests where only Pinaceae were present; and Mixt, for forests where the two tree families were recorded). Total basal area was averaged between the two INFyS surveys. The history of disturbances, including forest fires, grazing, wood extractions, and pests and diseases, was also recorded. The intensity of each disturbance was evaluated in the INFyS as a five-level ordinal scale. For simplicity, we reclassified these levels into two categories for each type of disturbance: low (no, barely noticeable or low impact) and high impact (medium or high impact as recorded in at least one of the surveys).

b) Regeneration of tree species.

At the center of each of the 4 sub-plots of 400 m^2 of each conglomerate, a circle of 12.56 m^2 (a total of 50.24 m^2 per conglomerate) was established, where the regeneration was measured. All individuals greater than 25 cm in height were considered as regeneration, up to the height they reached, provided that their diameter at breast height (DBH) was less than 7.5 cm. All individuals of each genus were counted and classified into three height classes: 25-150 cm, 150-275 cm and > 275 cm. In this study, these height categories were reclassified into two classes: the first class was that of 25-150 cm height, which we called "saplings", and the second class included the categories of 150-275 and > 275 height, which we called "small trees". Total Pinaceae and Fagaceae regeneration (individuals ha^{-1}) were averaged between the two INFyS surveys for each conglomerate.

Climatic data

The bioclimatic variables were extracted from Worldclim (Hijmans et al. 2005), a free database of global climatic layers with a spatial resolution of approximately 1 km^2 . The climatic layers were superimposed with the geographical coordinates of all conglomerates using the ArcGis software to obtain the annual precipitation (mm) and the mean annual temperature ($^{\circ}\text{C}$) of each conglomerate location, which were the climatic variables used in our analyses.

Data analyses

The two response variables, sapling regeneration and small tree regeneration, had large proportion of zeros (that is, plots without regeneration of either saplings or small trees) (7.2% for saplings and 27.7 % for small trees), and no transformation could satisfy the normality assumption. For this reason, each of these variables was analyzed in two steps. First, we transformed each variable to a dichotomous one, indicating the presence/absence of regeneration (of saplings or small trees) in each conglomerate. We used generalized linear models (GLM) with a binomial distribution and a logit link function to analyze the presence of both saplings and small trees considered separately. As explanatory variables, we included the Family of the regeneration (Fagaceae, Pinaceae) and its interaction with: forest type (Pine, Mixed, Oak), total basal area ($\text{m}^2 \text{ha}^{-1}$) of the conglomerate, mean temperature ($^{\circ} \text{C}$), annual precipitation (mm), land tenure (public, private, social), forest fires (low vs. high impact), pests and diseases (low vs. high impact), grazing (low vs. high impact), and wood extractions (low vs. high impact). We used mixed-effect models with Conglomerate nested in State ($N = 28$) as random factors. Conglomerate was included to account for the fact that data for the two families (Fagaceae, Pinaceae) was paired at the conglomerate level; whereas State accounted for the effect of spatial autocorrelation at relatively large spatial scales (the average size of a Mexican state is $63,481 \text{ km}^2$).

In a second step, we used general linear models (GLM) to model regeneration abundance (of saplings or small trees) in conglomerates with at least one regenerating individual. As not always there were regeneration values for the two families in each conglomerate, we carried out four different GLM models: two for saplings and small trees of Pinaceae, and two for saplings and small trees of Fagaceae. The explanatory variables were the same than in the previous models except the family of the regeneration (and its interactions with the other variables), which was not considered in this case. We again used mixed-effect models but in this case the only random effect was State. Regeneration abundance was log-transformed in all cases to satisfy normality assumptions. Some explanatory variables were also log- or square root-transformed, as indicated in the corresponding tables in the Results, to improve the distribution of residuals. Stepwise model selection was applied starting from the saturated model and removing the least significant term until there was no further decrease

in the Akaike Information Criterion (AIC). All statistical analyses were carried out with the R software (version 3.2.2, The R Foundation for Statistical Computing).

Results

Regeneration of Pinaceae and Fagaceae in the different forest types

The presence of Fagaceae saplings was very common in the conglomerates of oak and mixed forests, where the percentage of conglomerates with Fagaceae saplings was $> 80\%$ (Fig. 2). Half of the conglomerates in pine forests had Fagaceae saplings (Fig. 2). On the other hand, Pinaceae saplings appeared in 69% and 56% of pine and mixed forests, respectively, but only in 4% of the oak forest conglomerates. These patterns were similar, albeit with lower overall values, for small trees (Fig. 2).

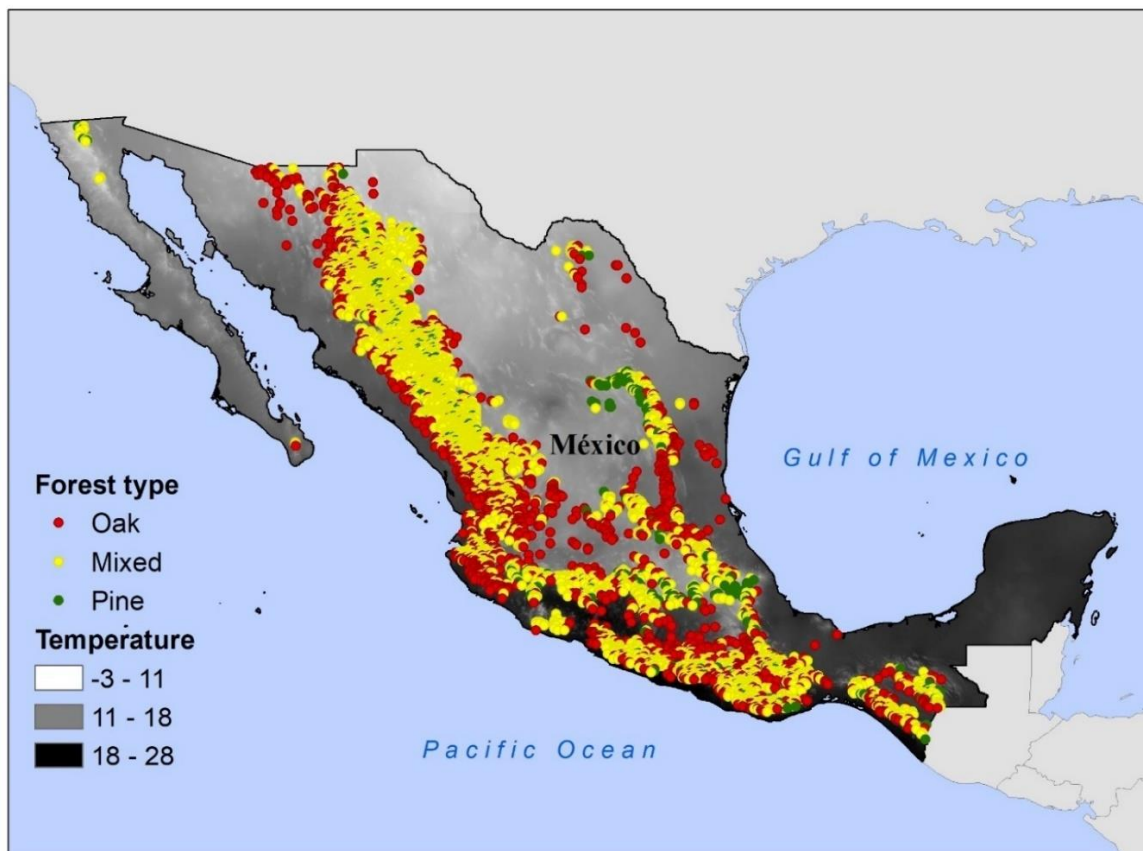


Figure 1. Map of the study area showing the location of the 5458 conglomerates of the INFyS that were used to evaluate the regeneration of Pinaceae vs Fagaceae in Mexico. Sampling plots (dots) are overlaid on a mean annual temperature map. The colour of the dots represents the type of forest: oak (red), pine (green) or mixed (yellow).

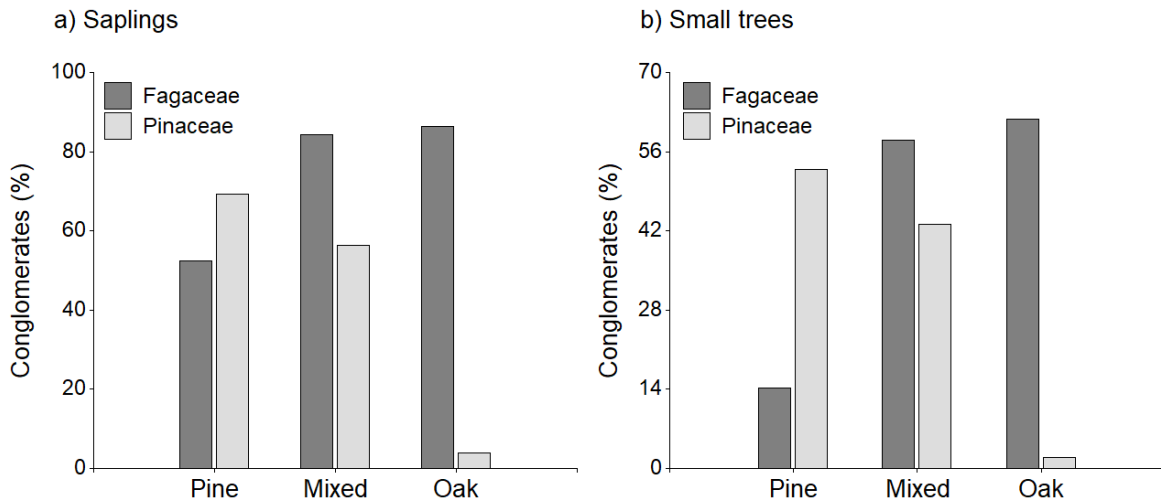


Figure 2. Percentage of conglomerates of the three forest types (pine, mixed, oak) that have regeneration of saplings (a, left) or small trees (b, right) of Fagaceae and Pinaceae.

Densities of Pinaceae and Fagaceae saplings and young trees (for the conglomerates showing regeneration) also varied among the different forest types (Fig. 3). Thus, Fagaceae saplings were more abundant than those of Pinaceae in the three forest types, while those of Pinaceae had a particularly low density in oak forests (Fig. 3). On the other hand, small Fagaceae trees were more abundant than small pines in mixed and particularly in oak forests, where small pines were basically absent (Fig. 3). Only in pine forests the densities of small pine trees were larger (approximately double) than those of small Fagaceae trees (Fig. 3).

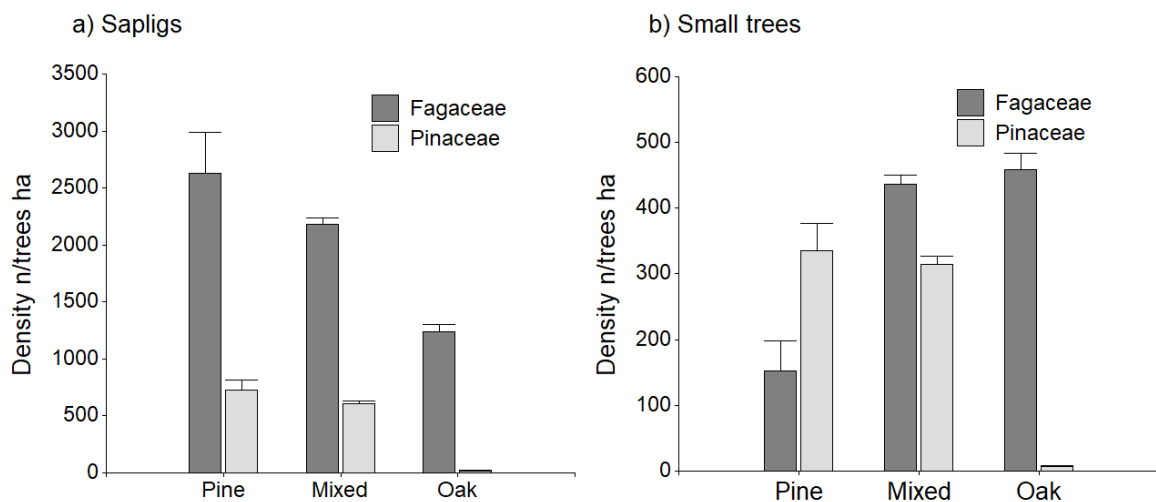


Figure 3. Density (individuals per ha) of saplings (a, left) and small trees (b, right) of Fagaceae and Pinaceae in the three forest types (pine, mixed, oak). Error bars indicate standard errors.

Table 1. Estimated coefficients (and corresponding standard errors) of a generalized linear mixed-effects model of the presence of saplings and small trees (binomial variable: yes, no) as a function of family (Pinaceae or Fagaceae), forest type (oak, mixed, pine), total plot basal area (BA), climate variables (mean annual temperature and annual precipitation), land tenure (private, public, social) and occurrence of several disturbance types (pests, wood extractions, wildfires, grazing). Conglomerate nested in state were included as random factors (see text). Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. Coefficient values are given relative to the reference level for each factor (Family='Fagaceae', Forest type='Oak', Land tenure='Private', no disturbance for all disturbance types). Significance codes: ., 0.1 > P > 0.05; *, 0.05 > P > 0.01; **, 0.01 > P > 0.001; *** P < 0.001.

	<i>Saplings</i>		<i>Small trees</i>	
	Coef.	S.E.	Coef.	S.E.
(Intercept)	-2.07 ± 0.90 *		-0.03 ± 0.69	
Family Pinaceae	-0.08 ± 0.99		2.00 ± 0.89 *	
Forest type Mixt	-0.30 ± 0.10 **		-0.18 ± 0.08 *	
Forest type Pine	-1.72 ± 0.16 ***		-2.30 ± 0.19 ***	
sqrt(Total BA)	0.04 ± 0.04		0.04 ± 0.03	
log(Mean temperature)	0.63 ± 0.24 **		0.11 ± 0.19	
log(Precipitation)	0.27 ± 0.14 *		0.02 ± 0.11	
Land tenure Public	-0.65 ± 0.45		-0.15 ± 0.41	
Land tenure Social	0.06 ± 0.09		-0.05 ± 0.07	
Wildfires	0.54 ± 0.10 ***		0.01 ± 0.07	
Grazing	-0.22 ± 0.09 **		-0.23 ± 0.06 ***	
Pests	0.09 ± 0.12		0.04 ± 0.09	
Wood extractions	0.19 ± 0.11 .		0.05 ± 0.08	
Family Pinaceae: Forest type Mixt	3.25 ± 0.18 ***		3.36 ± 0.22 ***	
Family Pinaceae: Forest type Pine	5.22 ± 0.26 ***		5.64 ± 0.31 ***	
Family Pinaceae: sqrt(Total BA)	0.04 ± 0.06		0.07 ± 0.05	
Family Pinaceae: log(Mean temperature)	-1.97 ± 0.29 ***		-2.63 ± 0.26 ***	
Family Pinaceae: log(Precipitation)	0.08 ± 0.17		0.09 ± 0.15	
Family Pinaceae: Land tenure Public	0.98 ± 0.65		0.42 ± 0.65	
Family Pinaceae: Land tenure Social	0.09 ± 0.12		0.24 ± 0.11 *	
Family Pinaceae: Wildfires	-0.57 ± 0.12 ***		-0.39 ± 0.10 ***	
Family Pinaceae: Grazing	0.24 ± 0.11 *		0.44 ± 0.10 ***	
Family Pinaceae: Pests	0.04 ± 0.16		0.22 ± 0.13	
Family Pinaceae: Wood extractions	0.22 ± 0.14		0.20 ± 0.12	

Factors affecting the presence of saplings and small trees of Pinaceae and Fagaceae

Consistent with the previous results, the generalized linear mixed-effects model indicated that the presence of Fagaceae and Pinaceae saplings was highest in their own forest types and that Fagaceae presence was higher in oak and mixed forests, whereas saplings of the two families were similarly present in pine forests (Table 1). Basal area had a slight positive effect on sapling presence for both families, although the effect was only significant for Pinaceae. Mean temperature had a positive effect on the presence of Fagaceae saplings but a strong negative effect on Pinaceae saplings (Fig. 4, Table 1). The effect of precipitation was positive and similarly strong for both families. Wildfires had a positive effect on the presence of Fagaceae saplings that was not observed for Pinaceae; whereas the opposite occurred for grazing effects, which only affected (negatively) the presence of Fagaceae saplings (Table 1).

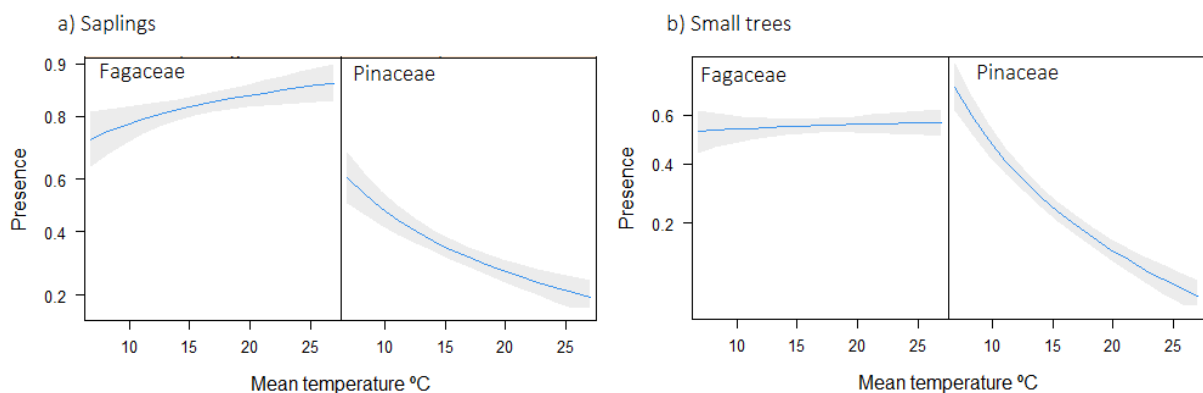


Figure 4. Effect of the interaction between family and mean annual temperature on the presence of Fagaceae vs. Pinaceae saplings (a) and small trees (b) in the forests of Mexico.

The overall patterns were similar when considering the regeneration of small trees, particularly regarding the effects of forest type, basal area, and wood extractions (Table 1). The effect of temperature was not significant for Fagaceae, whereas it was even more strongly negative for Pinaceae (Fig. 4). On the other hand, the effect of precipitation was not significant for small trees (Table 1). The presence of small Pinaceae trees was higher under social land tenure, whereas this effect was not observed for Fagaceae. Wildfires had a negative effect on the presence of Pinaceae small trees, whereas the effect was neutral for Fagaceae (Table 1). Grazing and pests had a positive effect on the presence of Pinaceae small

trees, whereas grazing was the only of these variables that affected Fagaceae, in this case reducing the presence of small trees (Table 1).

Factors affecting the abundance of saplings and small trees of Pinaceae and Fagaceae

Forest type had a significant effect on the general linear mixed-effects models carried out for the abundance of the saplings of the two families separately: the density of both Pinaceae and Fagaceae saplings was higher in mixed and pine forests than in oak forests (Table 2). Basal area contributed positively to the abundance of Pinaceae saplings but negatively to that of Fagaceae (Table 2).

Table 2. Estimated coefficients (and corresponding standard errors) of a general linear mixed-effects models of the abundance of Pinaceae and Fagaceae saplings and small trees (separate models for each combination) as a function of forest type (oak, mixt, pine), total plot basal area (BA), climate variables (mean annual temperature and annual precipitation), land tenure (private, public, social) and occurrence of several disturbance types (pests, wood extractions, wildfires, grazing). State was included as a random factor (see text). Model simplification was based on AIC. Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. Coefficient values are given relative to the reference level for each factor (Forest type='Oak', Land tenure='Private', no disturbance for all disturbance types). Significance codes: ., $0.1 > P > 0.05$; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$.

	<i>Saplings</i>				<i>Small trees</i>			
	<i>Pinaceae</i>		<i>Fagaceae</i>		<i>Pinaceae</i>		<i>Fagaceae</i>	
	Coef.	S.E.	Coef.	S.E.	Coef.	S.E.	Coef.	S.E.
(Intercept)	2.50 ± 0.66 ***		7.56 ± 0.50 ***		4.93 ± 0.66 ***		7.72 ± 0.34 ***	
Forest type Mixt	0.58 ± 0.15 ***		0.17 ± 0.05 ***		-	-	-	-
Forest type Pine	0.61 ± 0.17 ***		0.54 ± 0.11 ***		-	-	-	-
sqrt(Total BA)	0.07 ± 0.03 *		-0.07 ± 0.02 ***		0.11 ± 0.03 ***		-0.08 ± 0.02 ***	
log(Temperature)	-0.38 ± 0.17 *		-0.99 ± 0.13 ***		-0.65 ± 0.16 ***		-0.53 ± 0.11 ***	
log(Precipitation)	0.54 ± 0.09 ***		0.31 ± 0.07 ***		0.35 ± 0.09 ***		-	-
Land tenure			-	-	-	-		
Public	0.49 ± 0.32						-0.04 ± 0.25	
Land tenure			-	-				
Social	0.13 ± 0.06 *				-	-	0.10 ± 0.04 *	
Wildfires	-		0.30 ± 0.04 ***		-0.14 ± 0.06 *		0.12 ± 0.04 **	
Grazing	0.08 ± 0.05		-0.25 ± 0.04 ***		-	-	-0.10 ± 0.04 **	
Wood extractions	0.14 ± 0.06 *		-0.09 ± 0.05		-	-	-	-
R ² marginal	0.054		0.059		0.045		0.022	
R ² conditional	0.107		0.111		0.085		0.083	

Concerning climatic factors, temperature negatively affected the abundance of both families, although the effect was stronger for Fagaceae, while precipitation had always a positive effect (Table 2). Wood extractions increased the abundance of Pinaceae saplings only, whereas fires had a positive effect and grazing a negative effect on the abundance of Fagaceae saplings only (Table 2). Finally, the social tenure of the land had a positive effect on the abundance of Pinaceae saplings.

In the general linear mixed-effects models for the abundance of small trees the effect of forest type was not significant for either of the two families (Table 2). As in the case of the sapling models, basal area contributed positively to the abundance of small Pinaceae trees but negatively affected that of Fagaceae (Table 2). Temperature negatively affected the abundance of both families, while precipitation had a positive effect on the abundance of small Pinaceae trees only. Social tenure favoured the abundance of small Fagaceae trees but had no effect on the Pinaceae. Finally, as far as disturbances are concerned, fires favoured the abundance of small Fagaceae trees and had a negative effect on Pinaceae, while grazing negatively affected the abundance of small Fagaceae trees only (Table 2).

Discussion

Our results show that the regeneration of Pinaceae and Fagaceae in pure and mixed temperate Mexican forests is quite different. The regeneration of saplings and small trees of Fagaceae is more frequent in oak and mixed forests, although in pine forests the presence of saplings of Fagaceae is also appreciable. On the other hand, Pinaceae regeneration has a greater presence in pine forests and mixed forests, but very low presence in oak forests. The abundance pattern is similar, with more saplings and small trees of Pinaceae and Fagaceae in their own forest types and in mixed forests than in the other group's pure ones. These results indicate that, as expected, regeneration is largely determined by overstory composition. Several studies, however, indicate that this is not always the case in pine-oak Mexican forests, where high pine regeneration has been reported in stands previously dominated by *Quercus* (González-Espinosa et al. 1991; Ochoa-Gaona and González-Espinosa 2000; Ramirez-Marcial et al. 2001; Ramírez-Marcial 2003) or, on the contrary, as mixed coniferous forests have been replaced by oaks (Goforth and Minnich 2008).

Climatic events play an important role in the successional dynamics of pine-oak species in Mexico (Roncal-García et al. 2008; van Zonneveld et al. 2009; Figueroa-Rangel et al. 2012). According to our results, high temperatures benefit the presence of saplings and, to a much lesser extent, the presence of small trees of Fagaceae, but strongly reduces the presence of saplings and small trees of Pinaceae. In plots where there is regeneration, temperature negatively affects the abundance of saplings and small trees of both species. On the other hand, precipitation generally benefited the regeneration of both families. In northern Mexico, the highest peaks of pine and oak regeneration have been associated with unusually high periods of humidity and long fire-free periods (Meunier et al. 2014a). In recent years, a magnification in the frequency and intensity of droughts associated with climate change has been reported in central America (Margolis et al. 2017), which has promoted an alteration in the frequency of fires and the increase in forest pests that directly and indirectly affect the regeneration of pines and oaks (Fulé et al. 2000; Cerano-Paredes et al. 2011; Galicia et al. 2013; Morin and Liebhold 2015; Rubin-Aguirre et al. 2015).

Our results show that forest fires (as recorded in INFyS surveys) negatively affected the presence and abundance of saplings and small trees of Pinaceae relative to Fagaceae. In the second half of the 20th century there was a very drastic change of the fire regime in many Mexican temperate forests, which has caused long periods without fires, promoting a greater recruitment of coniferous species, as well as a large accumulation of igneous fuels (Bryan Lee and James H. Perkins; Minnich et al. 2000; Rodríguez-Trejo and Fulé 2003; Cortés Montaña et al. 2012). More recently, fire return intervals are being reduced due to a combination of natural and anthropogenic causes, increasing fire impacts on these forests and, in some cases, promoting changes in species dominance (Minnich et al. 2000). This has happened particularly in coniferous forests in the north of the country, where fires have driven a substitution of pine species (mainly *Pinus lambertiana* and *P. ponderosa*) by oaks such as *Quercus chrysolepis* or *Q. kelloggii* (Goforth and Minnich 2008). The predominance of oak species in post-fire stands can be explained by their sprouting capacity after disturbance (Fulé and Covington 1998; Aguilar et al. 2012; Stambaugh et al. 2017). In addition, *Quercus* species have deep root systems that help them prevent water stress, which may be advantageous in the dry post-fire conditions (Davis and Mooney 1986; Anderegg et al. 2015a). In contrast, relatively few Mexican pine species, particularly in temperate forests, have specific

mechanisms to cope with fires and establish themselves after a fire, such as a thick bark, serotine cones or resprouting capacity (Rodríguez-Trejo and Fulé 2003).

Besides wildfires, livestock grazing is the disturbance recorded in this study that has greater effects on the presence of Fagaceae and Pinaceae regeneration. The strong negative impact of grazing on the presence and abundance of seedlings and small trees of Fagaceae, which was not observed for Pinaceae, is likely explained by the lower palatability and generally higher tolerance to browsing of pines (Hernández et al. 2000). At the same time, differential human use of these two species groups, and the corresponding management practices, are also likely to explain the observed regeneration patterns. Acorn consumption, trampling and browsing of the young shoots causes a strong reduction in the establishment and growth of oaks (Quintana-Ascencio et al. 2004). The high importance of management and land use is consistent with the effect of land tenure in our results: the abundance of Pinaceae seedlings and small Fagaceae trees were favored under a social tenure. These patterns could be the result of traditional land use practices by the indigenous population and other inhabitants of the temperate forests of Mexico, which have resulted in an increase of pine trees in some areas (Heyerdahl and Alvarado 2003; García-Barrios and González-Espinosa 2004; Works and Hadley 2004). Itinerant agriculture, for instance, favors the conditions for pine establishment (deeper soil, more light), while the oaks that are established are frequently used as firewood or poles (FAO 2010b).

Factors related to stand structure and development also affected the regeneration of pine-oak forests in Mexico. Total basal area of the conglomerate had a slight positive effect on the presence of regeneration for both families, but the effect was only significant for Pinaceae. On the other hand, the abundance of Pinaceae was favored in high basal area stands, while the abundance of Fagaceae saplings and small trees was negatively affected by total basal area. These results are consistent with several studies reporting that colonization of broadleaf species is low in mature, high basal area forests dominated by Pinaceae (Camacho-Cruz et al. 2000; Ramirez-Marcial et al. 2001; Galindo-Jaimes et al. 2002; García-Barrios and González-Espinosa 2004; Ramírez-Marcial et al. 2006). Oak regeneration frequently requires the presence of open spaces upper the tree canopy (Stambaugh et al. 2002; López-Barrera et al. 2006; Pérez et al. 2013), which are dependent on specific disturbance regimes (González-

Espinosa et al. 1991; Galindo-Jaimes et al. 2002; Quintana-Ascencio et al. 2004; Meunier et al. 2014a).

Overall, our results show that in Mexican forests the regeneration of Fagaceae tends to dominate over that of Pinaceae, although this depends on the type of forest and the disturbance regime. In that regard, our results are limited by the quality of the disturbance information provided by the INFyS surveys, which base our analyses. The fact that Fagaceae regeneration seems to be favored, relative to Pinaceae, under warmer climates and in the presence of wildfires, suggests that ongoing climate change (Sáenz-Romero et al. 2010; del-Val and Sáenz-Romero 2017) could favor the predominance of oaks, particularly in drier areas (Melo et al. 2010; Meunier et al. 2014a). These changes are consistent with global patterns reported for global temperate forests (Alfaro Reyna et al. 2018) and with current growth trends in Mexican forests (Alfaro-Reyna et al., submitted) and, if confirmed, would have important consequences for the structure, diversity and functioning of Mexican pine-oak forests (Gómez-Mendoza and Arriaga 2007; Gómez-Mendoza et al. 2008; Galicia et al. 2013). This would also have an important socioeconomic impact, due to the key role of Mexican pine-oak forests as providers of ecosystem services (e.g., pines constitute 75% of all Mexican wood extractions; Segura 2000) and the fact that many local communities depend on forest products for their subsistence (FAO 2010a). Further research assessing mid-term temporal patterns is needed to confirm the trends reported in this study, as well as to provide more detailed understanding of the corresponding spatial patterns.

Capítulo 5

Conclusiones generales

En esta tesis se ha analizado la dinámica relativa de las especies de Pináceas y Fagáceas en bosques templados a nivel global y para el caso concreto de los bosques de pino-encino de México, utilizando datos bibliográficos y de inventarios forestales. A continuación, se presentan las conclusiones principales de cada capítulo de la tesis.

Capítulo I. Existe una sustitución de Pinaceae por Fagaceae en los bosques templados a escala global?

1. Existe una tendencia de cambio direccional de Pinaceae a Fagaceae en la mayoría de los bosques templados del mundo que han sido estudiados. Esta tendencia es especialmente acusada en Europa y el este de Asia, y mucho menos clara en el este de Norte América.
2. Estos cambios direccionales de Pinaceae a Fagaceae ocurrieron preferentemente en áreas donde la dinámica de la vegetación era impulsada por el estrés climático, la dinámica sucesional y, en menor medida, las perturbaciones antropogénicas. En cambio, en bosques bajo regímenes de perturbaciones naturales las transiciones de Fagaceae a Pinaceae fueron más comunes.
3. Diferentes historias de perturbaciones, así como diferencias en las floras regionales, probablemente determinan la dirección dominante de las transiciones de la vegetación en diferentes regiones templadas.
4. Es importante considerar que los resultados anteriores sintetizan la información publicada existente, y se basan en tan solo 51 estudios que no son necesariamente representativos a escala global.
5. De confirmarse, los resultados anteriores sugieren un progresivo aumento en la abundancia de los planifolios (Fagaceae) en detrimento de las coníferas (Pinaceae) en los bosques templados. Estos cambios podrían tener consecuencias importantes tanto para el funcionamiento de los ecosistemas afectados (diferentes rasgos

funcionales entre Pinaceae y Fagaceae) como para su resiliencia ante nuevos regímenes de perturbaciones en un contexto de cambio climático (e.g., diferente vulnerabilidad a sequías, incendios y plagas).

Capítulo II. Dinámica reciente de los bosques de pino-encino en México

6. No existe un patrón direccional claro en los cambios en la abundancia relativa de Pinaceae y Fagaceae en los bosques de pino-encino de México.
7. La dinámica reciente de crecimiento de Pinaceae y Fagaceae en México es afectada principalmente por la estructura del bosque, especialmente por el área basal y, en menor medida por el diámetro promedio de los árboles y la historia de perturbaciones (extracciones forestales, plagas, tenencia de la tierra). Estos efectos son similares para las dos familias consideradas.
8. El crecimiento de los bosques de pino-encino mexicanos responde también a los patrones espaciales de la temperatura promedio y a sus cambios temporales (anomalías recientes de temperatura). Estos efectos son muy distintos entre familias, con un efecto negativo muy acusado de la temperatura para Pinaceae y un efecto prácticamente neutro para Fagaceae.
9. Aunque los resultados anteriores se han de considerar con cautela, puesto que los dos inventarios considerados están separados por un periodo de tiempo relativamente corto (3 – 10 años), parece claro que las especies de Fagaceae están respondiendo más favorablemente a los aumentos de temperaturas actuales. En un contexto de calentamiento global, esto podría conducir a un aumento en la abundancia de las fagáceas en detrimento de las pináceas en los bosques de pino-encino mexicanos y, por tanto, a cambios sustanciales en la estructura, composición y función de estos bosques.

Capítulo III. Patrones de regeneración en los bosques de pino-encino mexicanos

10. Más del 50% de bosques de pino-encino mexicanos presentan regeneración de pináceas o fagáceas. La regeneración de cada una de las familias siempre es superior en los bosques dominados por adultos de la misma familia.

11. Tanto la presencia de regeneración (% de conglomerados muestreados con regeneración) como su abundancia (considerando solo los conglomerados con regeneración) es superior para Fagaceae que para Pinaceae en bosques mixtos donde coexisten individuos adultos de ambas familias. En bosques de encino sin presencia de pináceas adultas prácticamente no se encontró regeneración de Pinaceae, mientras que la regeneración de Fagaceae es muy abundante. Finalmente, en bosques de pino (sin presencia de fagáceas adultas) la presencia y abundancia de regeneración es en general superior para las pináceas (especialmente para individuos jóvenes relativamente grandes), pero ambas familias están bien representadas en el regenerado.
12. Los patrones espaciales de la regeneración se ven afectados por la estructura forestal (área basal), por el clima (temperatura y precipitación) y por la historia de perturbaciones y tenencia de la tierra. Las principales diferencias entre familias se observan para los efectos de la temperatura, la cual presenta un efecto muy negativo para la regeneración de Pinaceae (especialmente para su presencia) que no se observa o es mucho menos acusado para Fagaceae. Los incendios parecen favorecer la regeneración de las fagáceas en relación a las pináceas, mientras que el pastoreo tiene el efecto contrario.
13. La mayor regeneración de Fagaceae en la mayor parte de bosques de pino-encino mexicanos y, en particular, el hecho que ésta se vea favorecida en condiciones de elevadas temperaturas y presencia de incendios sugieren un aumento progresivo en la abundancia de Fagaceae en los bosques de pino-encino mexicanos.
14. Estos resultados refuerzan las conclusiones de los capítulos anteriores. En relación al capítulo III, aportan evidencia adicional de que la dinámica actual de los bosques de pino-encino mexicanos conducirá a un aumento de la abundancia de las fagáceas en detrimento de las pináceas a medio plazo, especialmente en un contexto de cambio climático. En relación al capítulo II, los resultados de este capítulo final indican que incluso en zonas donde nuestro análisis global no aportaba información concluyente, la dinámica reciente de los bosques parece favorecer el aumento de dominancia de las fagáceas.

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