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**“Proyecciones de hábitat climático y evaluación de la migración
asistida de coníferas en proceso de declinación en la Faja Volcánica
Transmexicana”**

TESIS

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Resumen general

El cambio climático generará un desacoplamiento entre las poblaciones forestales y el clima de los sitios que ocupan (hábitat climático) ya que éste se desplazará hacia mayores altitudes y/o latitudes, reaparecerá en otra localidad o simplemente desaparecerá. Incapaces de migrar a la velocidad necesaria para seguir el clima al cual están adaptadas, las poblaciones forestales quedarán sometidas a un clima más cálido y seco que gradualmente las debilitará y hará más susceptibles al ataque de plagas y enfermedades, especialmente escarabajos descortezadores. Con la finalidad de explorar alternativas encaminadas a re-acoplar las poblaciones con el clima para el que han evolucionado y discutir los desafíos de manejo forestal impuestos por el calentamiento global, en el presente trabajo se examinó el hábitat climático contemporáneo (período 1961-1990) que *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana* y *P. oocarpa* perderán, mantendrán y/o ganarán, particularmente en la región de la Faja Volcánica Transmexicana (FVTM). Para ello, se utilizaron datos de presencias y ausencias del Inventario Nacional Forestal y de Suelos, el módulo Random Forest de R, y datos climáticos a futuro del ensamble de 17 Modelos de Circulación General usando el escenario intermedio de Concentración de Gases de Efecto Invernadero (RCP 6.0 watts/m²). Los resultados sugieren que para la década centrada en el año 2060 el hábitat climático que se perderá (hasta 77%) será el localizado en el límite inferior altitudinal (*límite xérico*) de cada especie, ya que éste se desplazará entre 300 y 500 m hacia mayores altitudes. Las especies que sufrirán mayor pérdida son *P. hartwegii* y *A. religiosa*. Nuestros resultados sugieren la necesidad de la intervención humana para migrar altitudinalmente hacia arriba las poblaciones hasta 500 m para mantenerlas acopladas con el clima al que están adaptadas.

En la FVTM una de las coníferas que está en proceso de declinación debido al estrés por sequía es *Abies religiosa*. Como *P. pseudostrobus* se distribuye inmediatamente por debajo de *A. religiosa*, esta sería la especie candidata para ocupar los sitios que podrían ser creados por la declinación del oyamel. Por tanto, en un ensayo de campo establecido a 3000 m de altitud, en el borde de la Reserva de la Biosfera de la Mariposa Monarca (RBMM), Estado de México, se evaluó la viabilidad de la migración asistida de *P. pseudostrobus* hacia mayores altitudes y el efecto de la reducción de lluvia utilizando cuatro procedencias de *P. pseudostrobus* colectadas a 2300, 2400, 2700 y 2900 m de altitud. La respuesta (en incremento en altura y sobrevivencia) a la migración y a la exclusión de lluvia de las cuatro procedencias se evaluó mediante un modelo

mixto (Proc Mixed de SAS), y se ajustó una curva de respuesta a la distancia de transferencia climática (diferencia entre clima del sitio de plantación y clima de las procedencias). Los resultados muestran que, aunque la distancia de transferencia en temperatura fue de -1.4 a -3.3 °C y se excluyó el 30% de la precipitación (-200 mm), no se encontraron diferencias estadísticamente significativas en crecimiento y sobrevivencia entre procedencias o entre tratamientos (exclusión o no de lluvia). Esto sugiere que la migración asistida de *P.*

pseudostrobus hacia el borde de la RBMM, donde *A. religiosa* está en declive, es viable y puede presentar el beneficio adicional de desalentar el cambio de uso de suelo circundante al mantener una barrera de árboles saludables adaptados al clima del futuro.

Finalmente, se utilizaron datos de superficie afectada por brotes de descortezadores de 2009 a 2018, la altitud a la que ocurrieron los brotes, valores de AHI (annual heat-moisture index = índice de aridez) obtenidos mediante el programa ClimateNA, así como proyecciones del hábitat climático para *Abies religiosa* y *Pinus pseudostrobus* en la FVTM para determinar la altitud con mayor superficie afectada, la ocurrencia de episodios de sequía (aridez) antes o durante el brote, y si éstos ocurren en los sitios donde se proyecta que cada especie perderá hábitat climático. De acuerdo a los resultados, de las 4,091 ha tratadas para *A. religiosa*, ~40% ocurre entre los 3000 y 3100 m de altitud, donde se encuentran las masas mejor conservadas de oyamel, mientras que para *P. pseudostrobus* más del 54% de la superficie tratada (4,664 ha) se distribuye entre los 2200 y 2400 m, lo que coincide con su *límite xérico*. Respecto al AHI, para cada especie el año previo fue más árido que el año de la corta, lo que sugiere que hay un período de retraso (*lag*) entre el año de sequía y la expresión de los brotes masivos de descortezadores, que no necesariamente ocurren en los sitios donde *A. religiosa* y *P. pseudostrobus* perderán hábitat climático, sino que ocurren en el límite real actual del bosque. Los resultados hasta aquí encontrados sugieren la necesidad de incorporar la migración asistida en los programas de manejo y reforestación en México. Es probable que las medidas tradicionales de conservación *in situ* sean equivalentes a la inacción y, por lo tanto, pueden no ser suficientes para mantener la composición actual y la función de los bosques.

Palabras clave: cambio climático, estrés por sequía, límite xérico, plagas forestales, manejo forestal.

Abstract

Climate change could generate a decoupling between forest populations and the climate of the sites that they occupy today (climatic habitat), due to its displacement to higher altitudes and / or latitudes, its reappearance in another location or its simply disappearance. Unable to migrate at the speed needed to follow the climate to which they are adapted, forest populations will be subjected to a warmer and drier climate that will gradually weaken them and make them more susceptible to attacks by pests and diseases, especially bark beetles. In order to explore alternatives aimed at re-coupling populations with the climate for which they have evolved and to discuss the challenges of forest management imposed by global warming, we project the contemporary climate habitat (period 1961-1990) that *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana* and *P. oocarpa* will lose, maintain or add, especially at the Trans-Mexican Volcanic Belt (TMVB) region. With data of the presences and absences obtained from the Mexican National Forest and Soil Inventory, we fit a bioclimatic model by species using the Random Forests classification tree. Climate data from an ensemble of 17 General Circulation Models were run through the classification tree to project future distributions under RCP 6.0 watts/m² scenario. Results suggest that by the decade centered in year 2060 the climatic habitat that will be lost (up to 77%) is the one located in the lower altitudinal limit (*xeric* limit) of each species, since it will move between 300 and 500 m towards higher altitudes. *P. hartwegii* and *A. religiosa* will suffer the greatest loss. Our results suggest the need for human intervention to migrate the populations up to 500 m of altitude to keep them coupled with the climate to which they are adapted.

In the FVTM one of the conifers that is in the process of decline due to drought stress is *Abies religiosa*. As *P. pseudostrobus* is distributed immediately below in altitude than *A. religiosa*, the former would be the candidate specie to occupy the sites that could be created by the decline of oyamel. Therefore, in a field test established at 3000 m of altitude, at the border of the Monarch Butterfly Biosphere Reserve (MBBR), Mexico state, we evaluated the feasibility of *P. pseudostrobus* upward in altitude assisted migration and explored the effect of rain reduction (30 %) using four *P. pseudostrobus* provenances, collected at 2300, 2400, 2700 and 2900 m altitude. Adaptation was assessed using climate transfer functions. Analysis of variance (ANOVA) was performed to assess differences among populations and rain exclusion treatments. Results show that, although the transfer distance in temperature was

from -1.4 to -3.3 ° C and was excluded 30% of precipitation (-200 mm), no significant differences were found in growth and survival between provenances or between treatments (rain exclusion or not). This suggests that *P. pseudostrobus* assisted migration towards the MBBR border, where *A. religiosa* is in decline, is feasible and may have the additional benefit of discouraging surrounding land use change by maintaining a healthy tree barrier adapted to projected future climate.

Finally, we used data of the area affected by bark beetle outbreaks from 2009 to 2018, and the elevation at which outbreaks occurred. AHI (annual heat-moisture index = aridity index) values were obtained through the ClimateNA program, as well as projections of the climatic habitat for *Abies religiosa* and *Pinus pseudostrobus* in the TMVB to determine the altitude with the greatest affected area, the occurrence of drought episodes (aridity) before or during outbreak, and if these outbreaks occur in sites where is projected that each species will lose habitat climate. According to results, of the 4,091 ha treated for *A. religiosa*, ~40% occurs at elevation between 3000 and 3100 m, where distribute the best conserved stands of oyamel, while for *P. pseudostrobus* more than 54% of the treated area (4,664 ha) is distributed between 2,200 and 2,400 m, which coincides with its *xeric* limit. Regarding the AHI, for each species the previous year was more arid than the year of the clear-cut, which suggests that there is a *lag* period between the year of drought and the expression of massive outbreaks of bark beetle, but they not necessarily occur at sites where *A. religioosa* and *P. pseudostrobus* will lose climatic habitat, but instead occur at the actual forest boundary.

Results found suggest the need to incorporate assisted migration into management and reforestation programs in Mexico. Traditional *in situ* conservation measures are likely to amount to inaction and therefore may not be sufficient to maintain current forest composition and function.

Keywords: climatic change, drought stress, xeric limit, forest pest, forest management.

Introducción general

Cambio Climático se define como el “*cambio de clima atribuido directa o indirectamente a la actividad humana que altera la composición de la atmósfera global y que se suma a la variabilidad natural del clima observada durante períodos de tiempo comparables*” (Naciones Unidas 1992). En este sentido, el Panel Intergubernamental del Cambio Climático (IPCC) reconoce que el impacto de las actividades antropogénicas en el sistema climático es innegable y atribuible a los Gases de Efecto Invernadero (GEI), particularmente al CO₂ cuya concentración en la atmósfera alcanzó niveles sin precedentes en 2019: 410.5 ppm de las 278 ppm que había al inicio de la actividad industrial (WMO 2020a). Tal concentración ha aumentado la temperatura media global en superficies terrestre ± 1.1 °C (Hansen *et al.* 2019, WMO 2020b), y podría alcanzar los +1.5 °C en 2030 (IPCC 2018). Para algunas regiones del hemisferio norte también se proyecta una reducción en la precipitación media anual (Zhang *et al.* 2007), la cual puede ser de hasta 30% (IPCC 2013).

Como el clima es uno de los principales factores que controlan la distribución geográfica de la vegetación en todo el mundo (Woodward y Williams 1987, Davis y Shaw 2001), los modelos dinámicos de vegetación proyectan que el cambio climático generará un desacoplamiento adaptativo entre las comunidades vegetales y el clima de los sitios que ocupan, es decir, su hábitat climático (Rehfeldt *et al.* 2006, 2012). Tal desacoplamiento conducirá a una reducción en el hábitat climático debido a que éste se desplazará hacia mayores altitudes y (o) latitudes, reaparecerá en otra localidad o simplemente desaparecerá (Crookston *et al.* 2010, Gonzalez *et al.* 2010). Para mantenerse acopladas al clima al cual se adaptaron a través de un largo proceso evolutivo, las poblaciones de varias especies forestales han empezado a migrar hacia latitudes y/o altitudes más altas (Beckage *et al.* 2008, Kelly y Gulden 2008, Lenoir *et al.* 2008, Chen *et al.* 2011, Ettinger *et al.* 2011). Sin embargo, la velocidad de migración natural es mucho más lenta que la velocidad de migración requerida para mantenerse acopladas al clima que les es propicio (McLachlan *et al.* 2005, Corlett y Westcott 2013, Gray y Hamann 2013). Se estima que algunas poblaciones de árboles se están moviendo entre 6 y 11 veces más lento que la velocidad a la cual el clima cambia (Peñuelas *et al.* 2007, Lenoir *et al.* 2008).

Derivado del efecto conjugado del incremento proyectado en la temperatura y disminución en la precipitación, las poblaciones incapaces de migrar a la velocidad requerida quedarán sometidas a episodios de sequía que cada vez serán más frecuentes, calientes y severas (Sheffield y Wood 2008, Dai 2013, Cook *et al.* 2020). En el contexto del cambio climático se reconoce que estas sequías más calientes “hotter droughts” se convertirán en el factor de estrés fisiológico más importante que gradualmente debilitará a los árboles, e incluso puede resultar letal (He *et al.* 2014, Allen *et al.* 2015). Aunado a esto, se espera que condiciones más secas y cálidas promuevan los brotes de muchas plagas forestales, principalmente descortezadores (Raffa *et al.* 2008, Seidl *et al.* 2017, Jactel *et al.* 2019, Stephenson *et al.* 2019), a la vez que condiciones más húmedas y cálidas promoverán la ocurrencia de patógenos (Sturrock *et al.* 2011, Seidl *et al.* 2017, Wyka *et al.* 2018). Con una mayor disponibilidad de árboles estresados y debilitados por las sequías, es de esperarse que el problema de plagas y enfermedades forestales se intensificará, llegando a matar un mayor número de árboles por brote. En relación a lo anterior, alrededor del mundo ya han sido documentados varios casos de muerte forestal masiva (Allen *et al.* 2010, 2015, McDowell *et al.* 2011, Hartmann *et al.* 2018, Klein *et al.* 2019), especialmente en el *límite xérico* de la distribución natural de las poblaciones (límite inferior altitudinal, o margen sur en el hemisferio norte), donde las condiciones de sequía ya limitantes (Mátyás *et al.* 2009, Mátyás 2010), se ven agravadas por el cambio climático.

A pesar de las evidencias, hay una creencia extendida de que los árboles lograrán adaptarse a los cambios en el clima puesto que cuentan con los mecanismos de plasticidad fenotípica y de recuperación necesarios (Tardieu y Simonneau 1998, Moran *et al.* 2017). No obstante, estos mecanismos tienen un límite y pueden ser insuficientes para que las plantas se adapten a episodios de estrés prolongado (Mátyás *et al.* 2010, Alfaro *et al.* 2014, Allen *et al.* 2015), por lo que resulta necesario incorporar medidas de manejo que busquen reacoplar las poblaciones a los nuevos ambientes generados por el calentamiento global. Una de estas medidas es la migración asistida (Rehfeldt *et al.* 2002, Hewitt *et al.* 2011, Pedlar *et al.* 2012), la cual consiste en recolectar semillas y producir plántulas en viveros para posteriormente sembrarla en los sitios donde los modelos climáticos proyectan que ocurrirá su clima propicio en un futuro cercano (Marris 2009, Sáenz-Romero *et al.* 2016, Commander *et al.* 2018). En algunos

casos, la migración asistida significará un reemplazo de la población de la misma especie, pero en el *límite xérico* y más allá del límite superior de la distribución altitudinal natural, significará el reemplazo de especies (Commander *et al.* 2018, Silcock *et al.* 2019). Evaluar en campo la respuesta de los árboles a la migración asistida resulta de vital importancia para determinar qué tanto se deben mover las poblaciones forestales hacia mayores altitudes para que no mueran por heladas en el presente, pero que sobrevivan al calor y sequía del clima del futuro (O'Neill *et al.* 2008, 2014, Silcock *et al.* 2019; Sáenz-Romero *et al.* 2021).

México es uno de los países más biodiversos a nivel mundial (Ramamoorthy *et al.* 1993) que, entre otras cosas, concentra el mayor número de especies de pino que se distribuyen a lo largo de las regiones montañosas de gran elevación (Perry 1991, Styles 1993). Por reunir los volcanes más altos (Neyra-Jaúregui 2012) y concentrar importantes Áreas Naturales Protegidas (ANP) (Ramírez-Amezcuca *et al.* 2016), la Faja Volcánica Transmexicana (FVTM) es una región refugio para muchas de estas especies. Por tanto, resulta alarmante que derivado del incremento en la temperatura media anual y la disminución en la precipitación (Sáenz-Romero *et al.* 2010), para finales de siglo el bosque de coníferas presente en dicha región podría perder más del 90% de su hábitat climático (Rehfeldt *et al.* 2012), muy probablemente debido su desplazamiento hacia mayores altitudes (Gómez-Mendoza y Arriaga 2007, Gómez-Díaz *et al.* 2011, Sáenz-Romero *et al.* 2012a, 2015, Gutiérrez y Trejo 2014, Pérez-Miranda *et al.* 2014), desplazamiento que en 2060 podría ser de hasta 500 m hacia arriba (Gómez-Pineda *et al.* 2019).

Como las poblaciones forestales no pueden migrar a la velocidad requerida, en México empieza a reunirse la evidencia de que estas poblaciones muestran síntomas de estar en proceso de declinación (muerte de ramillas y defoliación severa de la copa) debido a las condiciones de sequía que prevalecen en los sitios que ocupan. Tal es el caso de las localizadas en el *límite xérico* de *Abies religiosa* (oyamel) dentro y fuera de la Reserva de la Biosfera de la Mariposa Monarca (RBMM) (Flores-Nieves *et al.* 2011), así como las de *Pinus pseudostrobus* en el área forestal de la Comunidad Indígena de Nuevo San Juan Parangaricutiro (Lopez-Toledo *et al.* 2017). Otros casos recientemente documentados por Sáenz-Romero *et al.* (2020) son los de *Pinus gregii* en Querétaro, *P. patula* en Puebla, *P.*

hartwegii en Jalisco, *P. duranguensis* en Chihuahua, *Quercus affinis* en Hidalgo y *Quercus spp.* en Colima, cuyas poblaciones aparentemente debilitadas por sequía, presentaron brotes inusuales de plagas (avispa agalladora, defoliadores y descortezadores) y enfermedades (tinta del castaño y mancha foliar), siendo los descortezadores los que han afectado una mayor superficie forestal¹.

Con base en lo anterior, en el capítulo uno del presente trabajo se proyecta el cambio a futuro en el hábitat climático contemporáneo de cinco especies de coníferas mexicanas económica y ecológicamente importantes que ocurren a lo largo de la región conocida como Faja Volcánica Transmexicana (FVTM), esto con la finalidad de discutir los desafíos de manejo forestal en las actividades comerciales y de conservación que serán impuestos por el cambio climático.

Como *P. pseudostrobus* se distribuye inmediatamente por debajo de *A. religiosa*, esta sería la especie candidata para ocupar los sitios que podrían ser creados por la declinación del oyamel. Por tanto, en el capítulo dos se evalúa la viabilidad de la migración asistida de *P.*

pseudostrobus hacia mayores altitudes y el efecto del estrés por sequía usando un tratamiento de exclusión de lluvia en un ensayo establecido en el borde de la Reserva de la Biósfera de la Mariposa Monarca, Estado de México. En el capítulo tres se utilizan datos de cortas de saneamiento a fin de analizar la posible relación entre la ocurrencia de plagas forestales con los sitios dónde los modelos climáticos proyectan que *P. pseudostrobus* y *A. religiosa* perderán hábitat climático en el futuro.

¹ Las citas completas de esta sección se presentan en el apartado de Bibliografía complementaria.

Hipótesis

- El hábitat climático de *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana* y *P. oocarpa* se desplazará hacia mayores altitudes en una superficie cada vez menor.
- Los individuos de *P. pseudostrobus* que provienen de sitios con un clima similar al sitio de plantación presentarán mayor crecimiento y sobrevivencia que aquellos que provienen de sitios con clima distinto.
- Los brotes de descortezadores en *P. pseudostrobus* y *A. religiosa* se presentan en el *límite xérico* de cada especie.

Objetivo General

Estimar la pérdida de hábitat climático de especies de coníferas, los efectos sobre las poblaciones tales como brote de plagas, y ensayar posibles escenarios de migración asistida, como una opción de manejo para mantener una cubierta forestal sana en un contexto de cambio climático.

Objetivos Específicos

1. Estimar el hábitat climático contemporáneo para *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana* y *P. oocarpa* y los posibles cambios que éste experimentarán para el clima del 2030, 2060 y 2090.
2. Evaluar en campo la respuesta en crecimiento y sobrevivencia de cuatro procedencias de *P. pseudostrobus* al migrarlas a mayores altitudes y someterlas a un tratamiento de exclusión de lluvia.
3. Determinar las áreas, así como la temporalidad en dónde ocurren los brotes de descortezadores y la pérdida de hábitat climático en *P. pseudostrobus* y *A. religiosa*.

Capítulo I

Suitable climatic habitat changes for Mexican conifers along altitudinal gradients under climatic change scenarios

Suitable climatic habitat changes for Mexican conifers along altitudinal gradients under climatic change scenarios

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Abstract. The high biodiversity of the Mexican montane forests is concentrated on the Trans-Mexican Volcanic Belt, where several Protected Natural Areas exist. Our study examines the projected changes in suitable climatic habitat for five conifer species that dominate these forests. The species are distributed sequentially in overlapping altitudinal bands: *Pinus hartwegii* at the upper timberline, followed by *Abies religiosa*, the overwintering host of the Monarch butterfly at the Monarch Butterfly Biosphere Reserve, *P. pseudostrobus*, the most important in economic terms, and *P. devoniana* and *P. oocarpa*, which are important for resin production and occupy low altitudes where montane conifers merge with tropical dry forests. We fit a bi-climatic model to presence-absence observations for each species using the Random Forests classification tree with ground plot data. The models are driven by normal climatic variables from 1961 to 1990, which represents the reference period for climate-induced vegetation changes. Climate data from an ensemble of 17 general circulation models were run through the classification tree to project current distributions under climates described by the RCP 6.0 watts/m² scenario for the decades centered on years 2030, 2060 and 2090. The results suggest that, by 2060, the climate niche of each species will occur at elevations that are between 300 to 500 m higher than at present. By 2060, habitat loss could amount to 46–77%, mostly affecting the lower limits of distribution. The two species at the highest elevation, *P. hartwegii* and *A. religiosa*, would suffer the greatest losses while, at the lower elevations, *P. oocarpa* would gain the most niche space. Our results suggest that conifers will require human assistance to migrate altitudinally upward in order to recouple populations with the climates to which they are adapted. Traditional in situ conservation measures are likely to be equivalent to inaction and will therefore be incapable of maintaining current forest compositions.

Key words: assisted migration; conifer species; drought stress; forest conservation; forest management; Random Forests; suitable climatic habitat; xeric limit.

INTRODUCTION

Mexico is one of the five countries with the greatest biodiversity worldwide (Ramamoorthy et al. 1993). It presents the largest number of pine species (Styles 1993), mainly distributed throughout the mountain ranges of

the country (Perry 1991). The Trans-Mexican Volcanic Belt (TMVB), a high-altitude plateau that contains the highest volcanic peaks of the country (timberline at 4000 m above sea level [m a.s.l.] with the highest peak at 5,675 m a.s.l., Neyra-Jáuregui 2012), is a region located in central Mexico, along an east-west geographic distribution axis (between 19° and 20° N; see Fig. 1), on which is concentrated a large number of endemic conifer species. The conifer species of main ecological and economic importance are distributed sequentially from high

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to low altitudes on the TMVB as follows: (1) the timberline species, *Pinus hartwegii* (3,000–4,000 m a.s.l.; Lauer 1978), (2) *Abies religiosa* (2,400–3,600 m a.s.l.), which comprises the dense forest where the Monarch butterfly (*Danaus plexipus*) overwinters at the Monarch Butterfly Biosphere Reserve (MBBR; Oberhauser and Peterson 2003, Sáenz-Romero et al. 2012a), (3) the most economically important species, *P. pseudostrobus* (2,200–2,900 m a.s.l.; Sáenz-Romero et al. 2012b), (d) *Pinus devoniana* (also known as *Pinus michoacana*), which develops a juvenile grass stage and provides some resistance to drought (1,600–2,450 m a.s.l.; Sáenz-Romero and Tapia-Olivares 2008), and (5) *Pinus oocarpa*, which inhabits the lowest altitudinal limit of the pine–oak forest, and becomes interspersed with the tropical dry forests (1,100–1,600 m a.s.l.; Sáenz-Romero et al. 2006). The latter two species are both very important for resin production (Leyva-Ovalle et al. 2013, Quiroz-Carranza and Magaña-Alejandro 2015). Moreover, the most important Mexican Protected Natural Areas (PNA) of high-altitude vegetation is found in the TMVB, covering the highest volcanoes (for elevations see Fig. 1; Neyra-Jáuregui 2012). Finally, this region contains one of the best examples of sustainable pine–oak forest management conducted by the Purépecha Ethnic group at Nuevo San Juan Parangaricutiro (NSJP) and Cherán, Michoacán

state, whose communal forest management model is considered ecologically and economically equitable (Bray et al. 2005, Orozco-Quintero and Davidson-Hunt 2010).

Despite the enormous conservational and economic importance of the TMVB, the region is threatened by many factors, one of the most prominent of which is the impact of climatic change. Concentrations of greenhouse-effect gases in the atmosphere reached unprecedented global levels in 2017 of above 405 ppm of CO₂ (WMO 2018), and are likely to produce an increase in the global mean annual temperature of 1.5°C by 2030 (IPCC 2018, Hansen et al. 2019). In many regions of the world, this temperature increase will be accompanied by a precipitation decrease of up to 30% (IPCC 2013). For Mexico, the reduction of precipitation has been estimated at an average of 9.0% by the decade centered on the year 2060 (Sáenz-Romero et al. 2010).

This combination of temperature increase and precipitation decrease will cause more frequent, more severe, and hotter droughts that will act to induce forest decline (Allen et al. 2015), since the plastic response of tree populations to a changing climate will eventually be exhausted (Alfaro 2014, Allen et al. 2015), particularly for the populations at the xeric limits of the species (lower altitudinal limit, or southern margin in the Northern Hemisphere; Mátyás 2010, Mátyás et al.

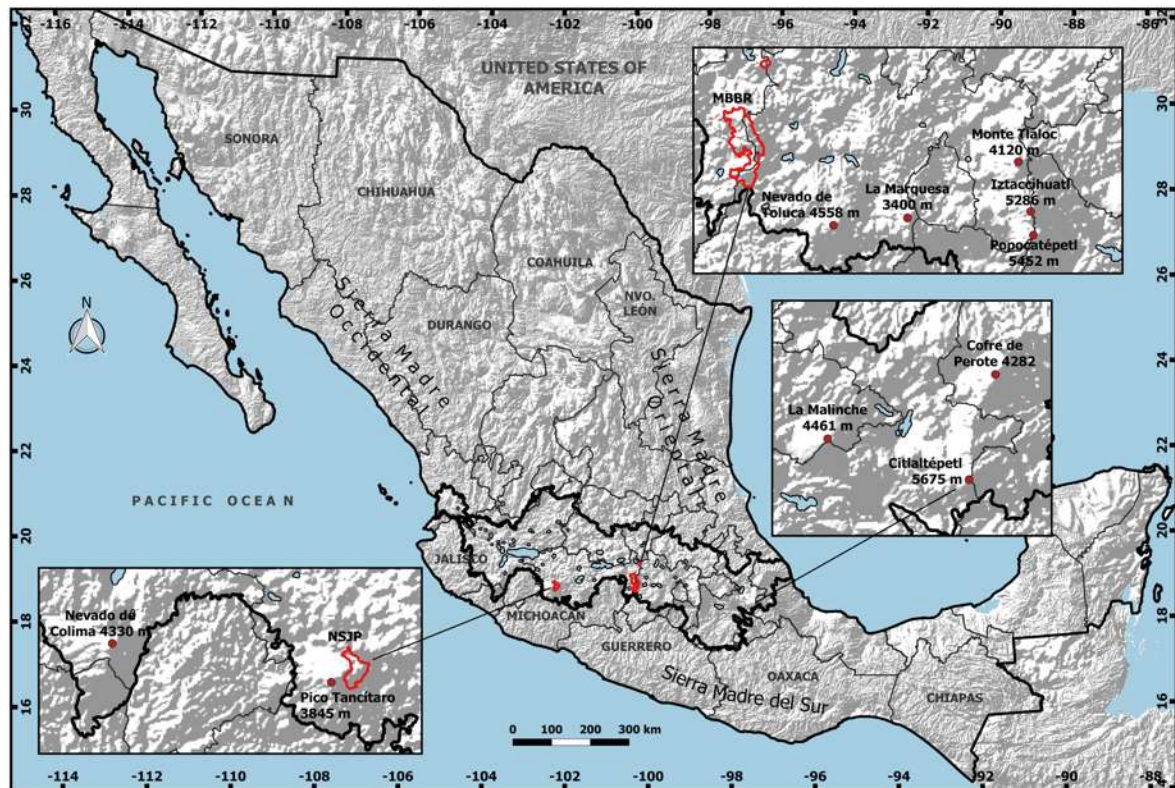


FIG. 1. Mexico political divisions, prominent geographical regions, and Trans-Mexican Volcanic Belt (TMVB; black contour), indicating the Monarch Butterfly Biosphere Reserve (MBBR; red contour) and the Native Indigenous Community of Nuevo San Juan Parangaricutiro (NSJP; red contour), and major volcanoes (red dots) with their altitudes (m above sea level).

2010). There is no doubt that forest decline is now an ongoing process in several parts of the world (Allen 2010). Some examples of this are *Populus tremuloides* in the Rocky Mountains, USA (Rehfeldt et al. 2009), *Cedrus atlantica* in the Moyen Atlas mountain range, Morocco (Mátyás 2010), and *Fagus sylvatica* in south-western Hungary (Mátyás et al. 2010).

In Mexico, *Abies religiosa* trees of the TMVB with symptoms of decline have been documented (Flores-Nieves et al. 2011; severe defoliation), along with the decline of *Pinus pseudostrabus* trees at the xeric limit of the species distribution (López-Toledo et al. 2017).

Vegetation models that consider climatic change in order to predict the geographic distribution of biomes suggest that the Mexican conifer forest will lose 92% of its suitable climatic habitat in the TMVB and 85% in the Sierra Madre by the end of the current century (Rehfeldt et al. 2012). Other projections made for several Mexican conifer species suggest that current habitats will not only be reduced, but will shift to higher altitudes, appear in other localities and even perhaps disappear altogether (Gómez-Mendoza and Arriaga 2007, Ledig et al. 2010, Gómez-Díaz et al. 2011, Sáenz-Romero et al. 2010, 2012a, 2015, Gutiérrez and Trejo 2014, Pérez-Miranda et al. 2014, Cruz-Cárdenas et al. 2016).

The problem is not only the reduction in area of suitable climatic habitat. Within the suitable climatic habitat projected to be maintained for the species as a whole, a decoupling will occur between forest tree populations and the climate to which they are genetically adapted. There is experimental evidence from provenance tests showing that several Mexican conifers have populations that are genetically differentiated for quantitative traits as an adaptation to the relatively narrow intervals of the environment occupied by the species as a whole. This is the case for the five conifer species of the present study: *Pinus hartwegii* (Loya-Rebollar et al. 2013), *Abies religiosa* (Ortiz-Bibian et al. 2017), *P. pseudostrabus* (Sáenz-Romero et al. 2012b), *P. devoniana* (Sáenz-Romero and Tapia-Olivares 2008), and *P. oocarpa* (Sáenz-Romero et al. 2006).

Aims of this research

There is no doubt that the suitable climatic habitat for each species will be displaced to higher altitudes in the TMVB (Sáenz-Romero et al. 2012a). Unfortunately, there is increasing evidence that the speed at which plant species can migrate to higher altitudes by natural means in response to the ongoing climatic change is much slower than will be necessary to maintain the coupling between the plant populations and their suitable climate (Peñuelas et al. 2007, Lenoir et al. 2008, Jump et al. 2009). This necessitates the establishment of programs of human assistance to re-couple these populations to the climatic habitat for which they have evolved. This assisted migration would consist of collecting seeds, producing seedlings in a nursery and conducting massive plantations at sites where the suitable climatic habitat of

the seed source is projected to occur in the near future (Rehfeldt et al. 2002, Tchebakova et al. 2005, Castellanos-Acuña et al. 2015, Sáenz-Romero et al. 2016). In some cases, assisted migration will involve replacing provenances of the same species; in others, for example, at the xeric limit and beyond the upper altitudinal limits of a given species, assisted migration will imply species replacement. The former replacement might be viewed as customary artificial reforestation programs; the latter, however, is the subject of great controversy, especially in ecologist and conservationist circles.

In this study, we determine contemporary and future climatic niches suitable for five conifer species that occur along the elevational gradients of the TMVB: *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrabus*, *P. devoniana*, and *P. oocarpa*. We examine the suitable climatic habitat lost, maintained and added for each species, and discuss the management challenges for both commercial forestry operations and biodiversity conservation that will be imposed by the projected impacts of climatic change.

In support of the previous excellent and pioneering climate niche modeling available for Mexican forest species, e.g., the research of (although this list is by no means exhaustive): Téllez-Valdés and Dávila-Aranda (2003), Téllez-Valdés et al. (2006), Gómez-Mendoza and Arriaga (2007), Gómez-Díaz et al. (2011), we aim to provide for five coniferous species of the TMVB: (1) more maps of the contemporary and future habitat distribution, in sufficient detail for future use in forest management decisions, (2) more accurate projections, given the statistical robustness provided by Random Forest when using species absence data points in addition to presence data, (3) updated projections using modern projected greenhouse-effect concentration scenarios, such as the RCP 6.0 watts/m² and an ensemble of global circulation models.

MATERIALS AND METHODS

Presence data input: Mexican Forest Inventory

We constructed our species presence database from field observations of *P. hartwegii* Lindl., *Abies religiosa* (Kunth) Schltdl. and Cham., *P. pseudostrabus* Lindl., *P. devoniana* Lindl., and *Pinus oocarpa* Schiede. The data were taken from a subset of 6,674 observations of the presence of conifers from the Mexican National Forest and Soil Inventory (MexFI), produced by the Mexican National Forestry Commission (CONAFOR 2004–2009). The data set of observations produced for each species with these procedures is listed in the results section; Table 1.

Absence data input

We sampled sites with absences of the species from a subset of the MexFI data with ~13,000 plots containing species other than conifers. To ensure that our sample of

TABLE 1. Number of observations, number of “forests,” expansion factor used on climatic limits, out-of-bag error, error of omission, and error of commission for each species.

Species	No. observations	No. forests	Hypervolume expansion factor (SD)	Out-of-bag error	Error of omission	Error of commission
<i>Pinus oocarpa</i>	1,118	10	1.25	0.056	0.004	0.091
<i>P. devoniana</i>	269	35	1.25	0.054	0.008	0.084
<i>P. pseudostrobus</i>	429	14	1.25	0.057	0.004	0.092
<i>Abies religiosa</i>	128	25	1.25	0.018	0.000	0.031
<i>P. hartwegii</i>	34	35	1.50	0.074	0.029	0.622

Note: Errors of fit are presented as proportions.

distant absence observations was representative of the vegetation of Mexico, we also used systematic sampling of point locations within the digitalized map of the Biotic Communities of North America (Rehfeldt et al. 2012). The technical procedures, described in detail in Rehfeldt et al. (2006) and also used by Ledig et al. (2010), involved the use of ARCMAP software to obtain a systematic sample of point locations from each polygon on the map and assign an elevation to each point from the digitized elevation model of GLOBE Task Team (1999).

Climate data input for the bioclimatic model

The climate of each species presence or absence data point was estimated by interrogating the spline climate model (built on the ANUSPLINE software; Hutchinson 2004) developed originally by Rehfeldt (2006) and Rehfeldt et al. (2006, 2018), and expanded for Mexico in Sáenz-Romero et al. (2010) for 1961–1990 normals. We use normals of this period to represent a reference climate from which global warming is occurring (Rehfeldt et al. 2018). A complete list of climatic variables is provided in Appendix S2.

Bioclimatic model

Our statistical models are built on the framework of Iverson and Prasad (1998) and closely parallel those of Rehfeldt et al. (2006). We use the Random Forests classification tree (Breiman 2001) to predict the presence–absence of *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana*, and *P. oocarpa* from climate variables. The model thus predicts the habitat realized for the contemporary climate, which is referred to as the climate profile (see Rehfeldt et al. 2006). The Random Forests algorithm, available in R (R Development Core Team 2004), constructs a set of regression or classification trees from an input data set. The trees in their aggregate are called “forest” (Liaw and Wiener 2002).

For classification trees, Breiman (2001) recommends that the number of observations within classes be approximately equal. To satisfy this recommendation, we used the sampling protocol of Rehfeldt et al. (2009) to draw the species data set from our database. In each data set,

40% of the observations were those for which the species was present, weighted by a factor of two. An additional 40% were drawn from the pool of observations lacking the species that occurred within a 32-variable hypervolume, the dimensions of which corresponded to the climatic limits for each species within the TMVB. Each dimension of the hypervolume was expanded somewhat (Table 1) such that most of the absence observations would be the most difficult to separate from the presence observations. The remaining 20% were selected from a pool of data points lacking the species and located outside this hypervolume. Multiple forests were constructed (Table 1) such that all of the observations within the hypervolume would be used in the analysis. Results are presented as averages across the forests.

Mapping realized contemporary 1961–1990 climatic habitat

Pixels of ~1 km² (30 arc seconds) resolution comprised the terrestrial portion of our geographic window, defined as the Trans-Mexican Volcanic Belt (TMVB; Gómez-Tuena et al. 2007). By using the digitalized elevations of GLOBE Task Team (1999), we estimated the climate of each pixel from the spline surfaces of Sáenz-Romero et al. (2010). The climate of each pixel was then run through the bioclimatic model using the R program (modules randomForest and yaImpute), with each tree of each forest providing a vote as to whether a given pixel fell within the realized climatic habitat of *Pinus oocarpa*, *P. devoniana*, *P. pseudostrobus*, and *Abies religiosa*; a pixel was assumed to have a suitable climate when receiving a majority (>0.5) of favorable votes; such threshold has been used to display suitable climatic habitat (Sáenz-Romero et al. 2010, 2012a, 2015). To compensate for the low number of observations for *P. hartwegii* and, therefore, a high probability of there being suitable habitat that is not occupied, a pixel was classified as having a suitable climate when it received a favorable vote of > 0.4.

Prediction of future suitable habitats

We projected the 1961–1990 climatic habitat into a future climate space for the decades centered on 2030, 2060, and 2090 using the climate grids (Rehfeldt et al.

2018) for an ensemble of 17 general circulation models, and the scenario 6.0 W/m² of the representative concentration pathway (RCP). We considered that ensemble to represent one of many climates and their impacts that should occur later in this century. Since our objective is to aid present forest management decision-making, we focus our discussion on 2060, viewing 2030 as being too soon to achieve any substantial result of alternative forest management, and 2090 as being too distant for projections to be reliable.

RESULTS

Bioclimatic model

The number of presence data points obtained from MexFI varied among species, ranging from 1,118 for *P. oocarpa* to only 34 for *P. hartwegii* (Table 1).

The 32-variable model produced a classification error (also known as out-of-bag error, OOB) across the different number of “forests” created for each species. As the variables were eliminated in a stepwise fashion according to their importance, this error fluctuated until stabilizing just prior to an exponential increase. The most parsimonious model was judged to be at the point where culling an additional variable resulted in a sudden increase in

the mean OOB error from across all “forests.” We chose a model with six variables for *P. oocarpa* and *A. religiosa*, seven each for *P. devoniana* and *P. pseudostrobus*, and 10 for *P. hartwegii*. The lowest classification error was for the six-variable model of *A. religiosa* (0.018), while the highest error was for the 10-variable model of *P. hartwegii* (0.074) (Table 1).

Error of commission; i.e., predicting the presence of a species when it is absent, was important only for *P. hartwegii* (0.622), which had the highest proportion of such errors (Table 1). Omission errors near zero (Table 1) are suggestive of overfitting, as zero error in biological data is implausible. Using the average prediction from multiple forests, however, compensates for the effects of overfitting when the models used.

The climatic variables of major importance used to generate the bioclimatic model of each species are listed on Table 2.

Mapping of the 1961–1990 climate profile

High precision of the bioclimatic models is demonstrated by superimposing the locations inhabited by each species on predicted distributions. Nearly all of the data points occur in grid cells for which the bioclimatic model predicts that climate is very likely to be suitable for each

TABLE 2. Acronyms, definition, and ranking of climatic variables of greatest relevance to the climate profile of each species.

Acronym	Climatic variable definition	Importance ranking				
		<i>P. oocarpa</i>	<i>P. devoniana</i>	<i>P. pseudostrobus</i>	<i>A. religiosa</i>	<i>P. hartwegii</i>
SUMP	summer precipitation; sum of precipitation Jul–Aug	1		7		6
MAPDD5	(MAP × DD5)/1,000		1			
MMAX	mean maximum temperature in the warmest month			1		1
MTWM	mean temperature in the warmest month	4	3		1	3
SPRP	spring precipitation; sum of precipitation Apr–May	2	6	2		2
TDIFF	MTWM – MTCM	5	2		5	9
GSPMTCM	(GSP × MTCM)/1000				2	
WINP	winter precipitation; sum of precipitation of Nov–Feb	3	7	3		7
PRATIO	GSP/MAP				3	
MAP	Mean annual precipitation (mm)		4			
MMIN	mean minimum temperature in the coldest month		5	4		
SDI	(GSDD5 × 0.5)/GSP				4	
DD5	degree-days > 5°C	6				4
GSDD5	degree-days > 5°C accumulated within the frost-free period					10
MAPMTCM	(MAP × MTCM)/1000			5		
MTCM	mean temperature in the coldest month					5
MTCMMAP	MTCM/MAP			6		
GSPMTCM	(GSP × MTCM)/1000				6	
MAT	mean annual temperature (°C)					8
GSP	growing season precipitation, Apr–Sep					

Note: 1 = most relevant, to 10 = least relevant.

species (probability $\geq 50\%$ for *P. oocarpa*, *P. devoniana*, *P. pseudostrobus*, and *Abies religiosa*, 40% for *P. hartwegii*). No data points reside in grid cells that receive votes $< 50\%$ or $< 40\%$ for these species, respectively. In the following section, we present the modeling and mapping results according to the altitudinal distribution of these species.

Of these five species, *P. oocarpa* and *P. devoniana* have the broadest suitable climatic habitat distribution in Mexico (Table 3). *Pinus oocarpa* extends similarly from the northwest of the Sierra Madre Occidental in southern Sonora, until reaching the northern and southern mountains of Chiapas (Appendix S3: Fig. S1). The suitable climate for *P. devoniana* occurs mainly in the Trans-Mexican Volcanic Belt (TMVB; Table 3, Appendix S3: Fig. S2). *Pinus pseudostrobus* has the second largest suitable area in the TMVB (Table 3), occurring at moderately high elevations and along the flanks of the volcanoes (Appendix S3: Fig. S3). *Abies religiosa* and *P. hartwegii* have the most restricted areas of suitable climatic habitat (Table 3; Appendix S3: Figs. S4 and S5, respectively). The narrowest distribution is for *P. hartwegii*, since its climate occurs in the upper part of the highest volcanoes of the TMVB, forming the timberline.

Future suitable habitat

Table 3 summarizes the lost, maintained, and added areas (expressed as percentage of the 1961–1990 reference period distribution) of suitable climatic habitat at both country and TMVB scales, for three future periods: the decades centered in the years 2030, 2060, and 2090. For all species, the results show that the area lost will far exceed that added and that this discrepancy will increase over time.

Countrywide and within the TMVB, by 2060, the species that is projected to lose the most suitable climatic habitat are *A. religiosa* ($>75\%$), *P. hartwegii* ($>68\%$), and

P. oocarpa ($>52\%$). *Pinus pseudostrobus* should lose 52% and *P. devoniana* is the species with the lowest loss ($<46\%$). On the other hand, the species that are projected to gain the most area, because their suitable climate appears in new localities, are *P. oocarpa* (11% countrywide and 25% in the TMVB), followed by *P. devoniana* (12% and 16%, respectively), and *P. pseudostrobus* (4% and 9%, respectively). *Pinus hartwegii* and *A. religiosa* are the species with the lowest quantity of new suitable areas ($<5\%$; Table 3).

As the results suggest, for all species, new areas with favorable climate added will advance toward the slopes and highest volcanoes of the TMVB (Figs. 2–6). Some of the new areas for *P. oocarpa* will be located at Tancítaro peak (Fig. 2F), the western edge of the MBBR (Fig. 2B), as well as in the lower parts of the natural protected area of La Marquesa (Fig. 2C). New suitable areas for *P. devoniana* are similar to those of *P. oocarpa* (see Fig. 3B, C, F). For *P. pseudostrobus*, the area added should be mainly in the upper parts of the TMVB volcanoes (Fig. 4A, C).

For *Abies religiosa*, a very worrisome issue is the projected dramatic reduction within the area of the MBBR, especially in the southwestern portion of the Reserve (Fig. 5F). New suitable areas should be added mainly toward the summits of the TMVB volcanoes at elevations exceeding 4000 m a.s.l. (Fig. 5B, E). The suitable climate of *Pinus hartwegii* currently located in the Sierra Madre Oriental (Fig. 6A), like Tancítaro peak (Fig. 6E) would disappear completely. Its suitable climate is projected to appear in the snow-capped mountains at elevations greater than 4,300 m a.s.l., such as the volcanoes Nevado de Colima (Fig. 6F), Nevado de Toluca, Popocatepetl, Iztaccihuatl (Fig. 6B), Pico de Orizaba, and Cofre de Perote (Fig. 6C).

Fig. 7 illustrates both the altitudinally separate and overlapping distributions of the five conifer species studied along altitudinal gradients of the TMVB, as well as the trend of net reduction of suitable climatic habitat as

TABLE 3. Countrywide and Trans-Mexican Volcanic Belt projected lost, maintained, and added suitable climatic areas for 2030, 2060, and 2090, in comparison to area predicted for 1961–1990.

Species	Current (km ²) 1961–1990	Future predicted area (percent change of 1961–1990)								
		Lost			Maintained			Added		
		2030	2060	2090	2030	2060	2090	2030	2060	2090
Countrywide										
<i>Pinus oocarpa</i>	228,669	-33	-52	-67	67	48	33	+9	+11	+12
<i>P. devoniana</i>	135,095	-31	-46	-58	69	54	42	+12	+12	+11
<i>P. pseudostrobus</i>	105,787	-66	-52	-68	34	48	32	+4	+4	+3
<i>Abies religiosa</i>	47,359	-62	-77	-88	38	23	12	+2	+2	+1
<i>P. hartwegii</i>	4,037	-57	-73	-87	43	27	13	+3	+4	+5
Trans-Mexican Volcanic Belt										
<i>Pinus oocarpa</i>	37,344	-32	-62	-73	68	38	27	+26	+25	+25
<i>P. devoniana</i>	41,470	-29	-43	-54	71	57	46	+13	+16	+16
<i>P. pseudostrobus</i>	40,072	-33	-52	-66	67	48	34	+7	+9	+7
<i>Abies religiosa</i>	33,695	-60	-75	-86	40	25	14	+1	+1	+1
<i>P. hartwegii</i>	3,255	-51	-68	-85	49	32	15	+3	+5	+6

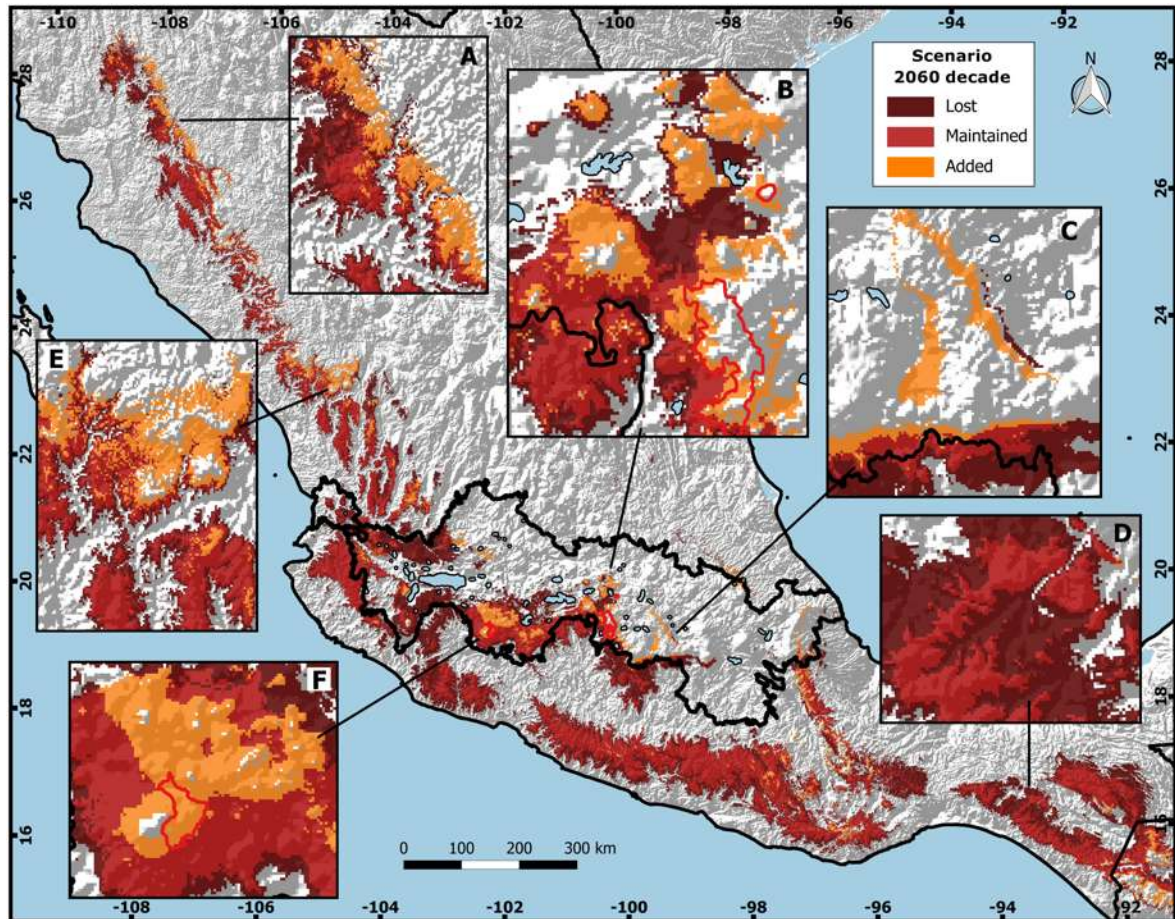


FIG. 2. Mapped prediction of the climatic habitat of *Pinus oocarpa* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel B shows the Monarch Butterfly Biosphere Reserve (red contour). Panel F shows the forest of the Native Indigenous Community of Nuevo San Juan Parangaricutiro (red dotted contour), Michoacán state.

these species shift toward higher altitudes. Note that the two species occupying the highest elevations, *Abies religiosa* and *P. hartwegii*, are those with the least suitable climatic habitat projected for the decade centered on 2060 (Fig. 7D, E). Moreover, for these two species, the upward shift would be the lowest, since the emergent habitat is limited along the flanks of the volcanoes.

The expected changes in the distribution of suitable habitat in the TMVB for the decades centered on the years 2030 and 2090, in addition to that of 2060, are available in Appendix S4 (Figs. S1–S5, one figure per species).

DISCUSSION

Fit of bioclimatic model and relevant climatic variables

As measured by the overall classification error, the fit of our bioclimatic model, using from six predictors for *A. religiosa* to 10 for *P. hartwegii*, is similar to those for

74 western U.S. species for which the same methods were applied (Crookston et al. 2010). For conifers of Mexico, the error was 4.5% for *Picea* spp. (Ledig et al. 2010), 4.7% for *Pinus chiapensis*, (Sáenz-Romero et al. 2010) and 4.6% for *Pinus leiophylla* (Sáenz-Romero et al. 2015). The prediction of the 1961–1990 distribution is in general agreement with maps developed based on field observations by Perry (1991) and Farjon and Styles (1997). In our analyses, like those of many western U.S. species (see Crookston et al. 2010), errors of omission were exceptionally low (<0.029), a result directly linked to the sampling protocol that weights the observations in which the species of interest was present by a factor of two (see Rehfeldt et al. 2009).

As is normal in climate niche modeling, the area where the 1961–1990 climate is predicted to be suitable for each species is greater than the actual distribution. This result is to be expected when habitat suitability is predicted on the basis of climate alone. Many factors other than

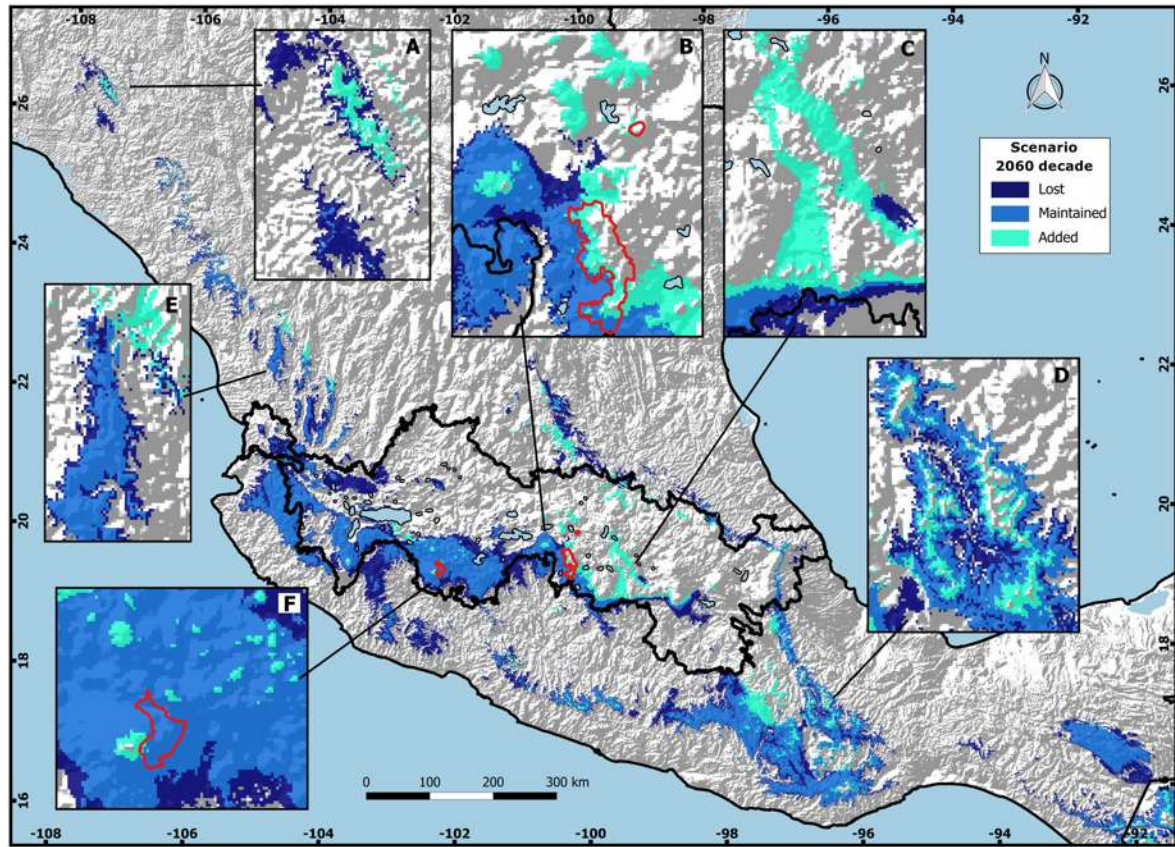


FIG. 3. Mapped prediction of the climatic habitat of *Pinus devoniana* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel B shows the Monarch Butterfly Biosphere Reserve (red contour). Panel F shows the forest of the Native Indigenous Community of Nuevo San Juan Parangaricutiro (red contour), Michoacán state.

climate may restrict where species actually occur (see Soberón and Peterson 2005, Pearson and Dawson 2003). In addition, using the majority of votes (>0.5) to predict presence or absence, prevents identification of locations where the climate may only approach suitability. Nevertheless, a portion of the classification error results from correctly predicting suitable niche space that is unoccupied as a result of other factors, such as limitations of species germplasm dispersion, competitive exclusion, human disturbances, soil conditions, among others (Rehfeldt et al. 2006).

Regarding the climatic variables of major importance used to generate the bioclimatic model of each species, the results suggest that those related to precipitation (summer, spring, and winter precipitation) are more relevant to those species that occur at low altitudes in the transition toward the dry tropical forest, such as *P. oocarpa*. For species that occur at higher altitudes (such as *P. hartwegii* and *A. religiosa*) the extreme temperatures of the warmest month (mean temperature of the warmest month, mean maximum temperature in the

warmest month) and/or the precipitation that occurs during the dry season (spring precipitation) or precipitation during the growing season (GSPMTCM, PRATIO) are the most important variables controlling species distribution (Table 2).

Shifting and loss of suitable climatic habitat

According to future projections, as the time slices considered become more distant in the future (decades centered on the years 2030, 2060, and 2090), the climatic habitat of each species should eventually reduce and move toward higher elevation sites, especially toward those located along the Trans-Mexican Volcanic Belt (TMVB; see Appendix S4). These results are in accordance with previous projections realized by Gómez-Mendoza and Arriaga (2007), Gómez-Díaz et al. (2011), Monterroso-Rivas et al. (2013), and Gutiérrez and Trejo (2014).

Of the five study species, those with the broadest climatic habitat, *P. oocarpa*, *P. devoniana*, and *P. pseudostrobus*, should lose less area since their suitable

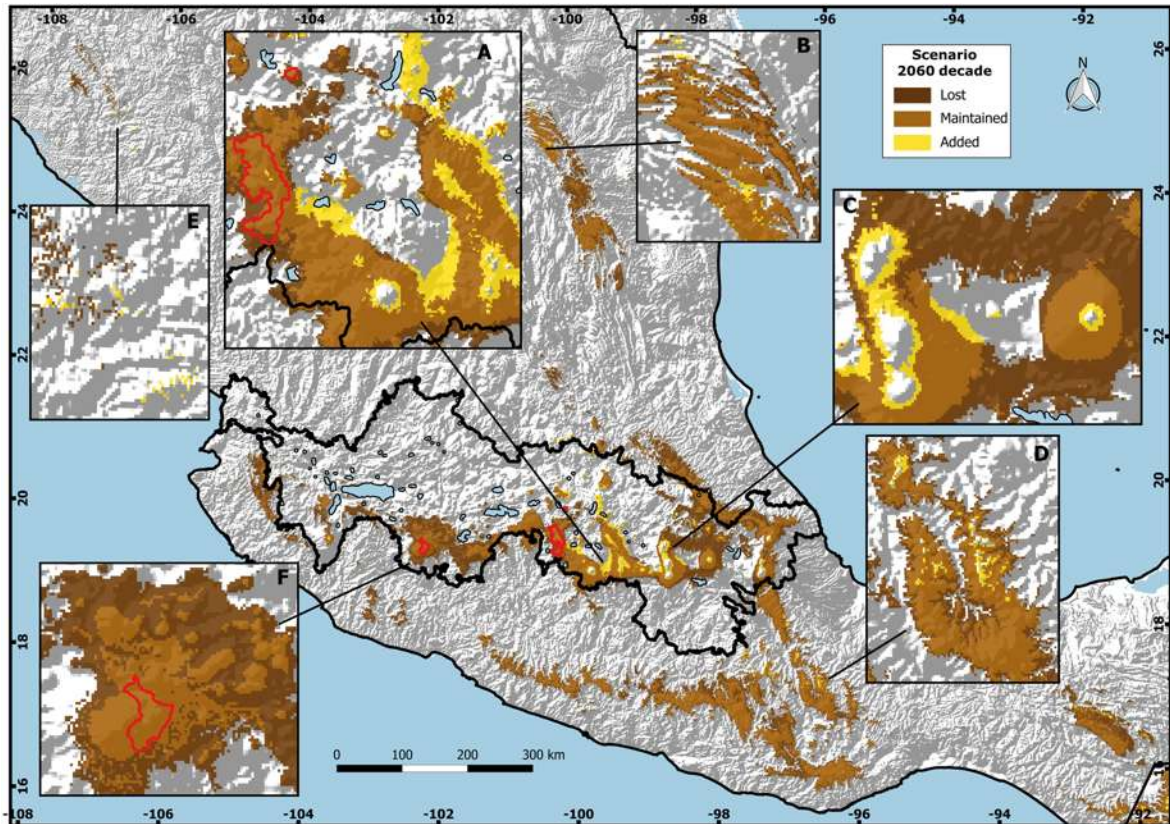


FIG. 4. Mapped prediction of the climatic habitat of *Pinus pseudostrubus* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel A shows the Monarch Butterfly Biosphere Reserve (red contour). Panel F shows the forest of the Native Indigenous Community of Nuevo San Juan Parangaricutiro (red contour), Michoacán state.

climate will shift to sites located at higher elevations (between 300 and 400 m higher compared to the present distribution), which would partially compensate for the current area lost. On the other hand, the species with the most restricted climatic habitat, *P. hartwegii* and *Abies religiosa* (the latter will shift 500 m higher), would have the highest proportion of range lost, since new suitable climatic habitat would be restricted to the highest parts of the mountains, which, due to the conicity of the mountain, will comprise an increasingly smaller area. This does not even consider the impoverished soils characteristic at altitudes above timberline, where the soils are mostly composed of volcanic ashes and stones (See Lauer 1978).

Due to altitudinal climate displacement, the contemporary climatic habitat most subject to loss is located at the lower limit of the present distribution of each species (see Fig. 7a–e), i.e., the xeric limit (sensu Mátyás 2010). At this interface, massive and sudden decline of forest populations has already been documented for several forest tree species (Rehfeldt et al. 2009, Allen 2010, Mátyás 2010, Mátyás et al. 2010) as

a result of temperature increases promoting increasingly frequent heat waves and droughts that exceed mechanisms of phenotypic plasticity and forest population recovery (Mátyás et al. 2010, Alfaro 2014, Allen et al. 2015). In Mexico, for example, within the forest area of the Native Indigenous Community of NSJP, populations of *P. pseudostrubus* that are located in the lower reaches of their altitudinal distribution frequently show poor health and low fecundity due to environmental stress and/or pest attacks derived from the higher temperatures of the dry season (López-Toledo et al. 2017). This is consistent with our models, which indicate that, by 2060, the climate of this area (NSJP, Michoacán) will be suitable for *P. oocarpa* (Fig. 2F) and *P. devoniana* (Fig. 3F), which are currently distributed at lower altitudes.

Indeed, the direct effects of moisture stress at the xeric limit seem especially critical at lower TMVB elevations where the pine-oak vegetation changes into the deciduous tropical dry forest, and consequently, the habitat at the xeric limits of *P. devoniana* and *P. oocarpa* seems particularly vulnerable to the increasingly arid climate.

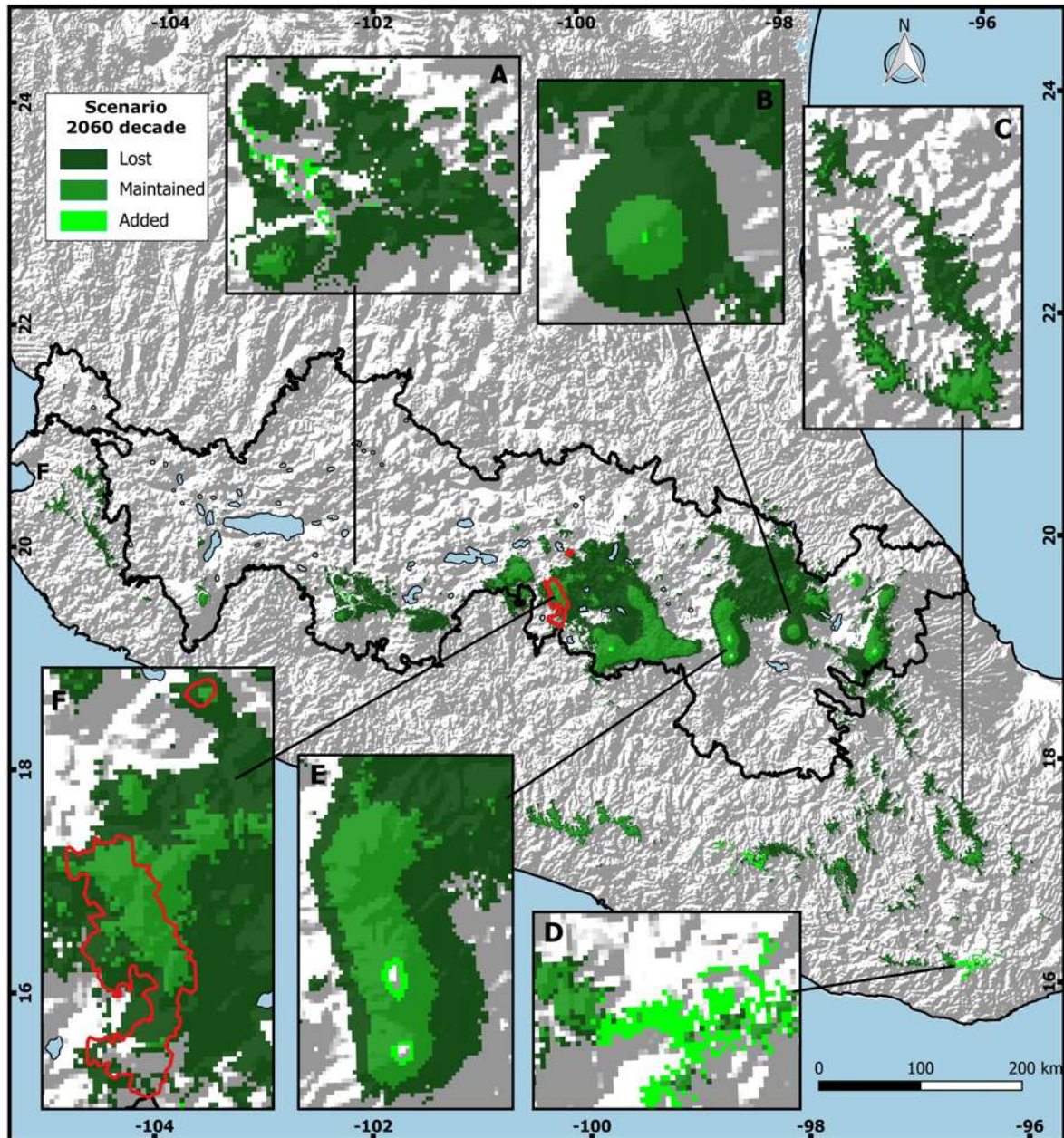


FIG. 5. Mapped prediction of the climatic habitat of *Abies religiosa* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt. Panel F shows the Monarch Butterfly Biosphere Reserve (red contour).

At higher elevations where conditions are less xeric, loss of habitat can be viewed as an interaction between competitive ability and environmental stresses. Loss of habitat of *A. religiosa* to *P. pseudostrobus*, for instance, may be determined more by competitive exclusion of *A. religiosa* by the faster growing *P. pseudostrobus* (C. Sáenz-Romero, *personal observation*). Accordingly, Avendaño et al. (2009) and Flores-Nieves et al. (2011) documented foliar biomass

reduction due to death of twigs and foliage in adult individuals from the lower part of the altitudinal distribution of *A. religiosa* on mount Tlaloc, where our model suggests that the species would lose climatic habitat (Fig. 5E) and which would eventually become suitable for *P. pseudostrobus* (Fig. 4C). Our projections for the Monarch Butterfly Biosphere Reserve (MBBR) are more optimistic than those of Sáenz-Romero et al. (2012a), likely because the

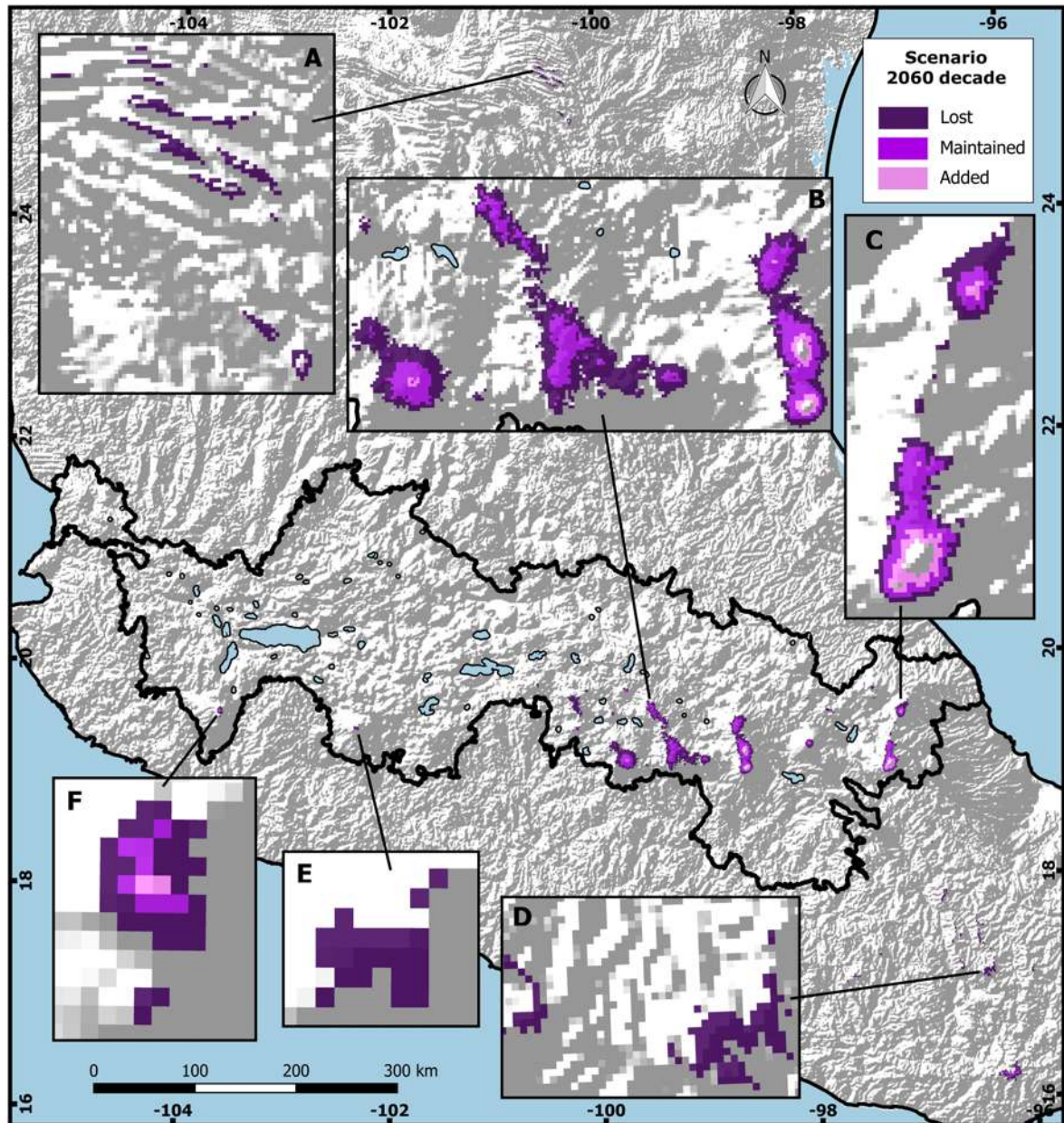


Fig. 6. Mapped prediction of the climatic habitat of *Pinus hartwegii* for the 2060 decade. Darkest toned grid cells represent the area lost from the contemporary climatic habitat, middle-toned grid cells represent the area of climatic habitat maintained, and the brightest toned grid cells represent the area of climatic habitat added. The black contour corresponds to the physiographic province of the Trans-Mexican Volcanic Belt.

projections of precipitation of the model ensemble used is more optimistic that the consensus among the three general circulation models used on Sáenz-Romero et al. 2012a, but nonetheless suggest that the persistent *Abies religiosa* habitat (Fig. 5F) would also be suited for the co-occurrence with *P. pseudostrobus* (Fig. 4A) and that much of the area projected to be lost would then be suited to *P. devoniana* (Fig. 3B) and *P. oocarpa* (Fig. 3B), which are currently absent within the MBBR.

Limits to altitudinal upward migration

Highest elevations within the MBBR are about 3,500 m a.s.l. This elevation coincides with the highest occurrence of extant actual *A. religiosa* populations in Mexico. With its climate niche shifting upward toward 4,000 m a.s.l. (Fig. 7d), *A. religiosa* must migrate upward to higher mountains outside the Reserve. Similarly, *P. hartwegii* already occupies sites of up to 4,000 m

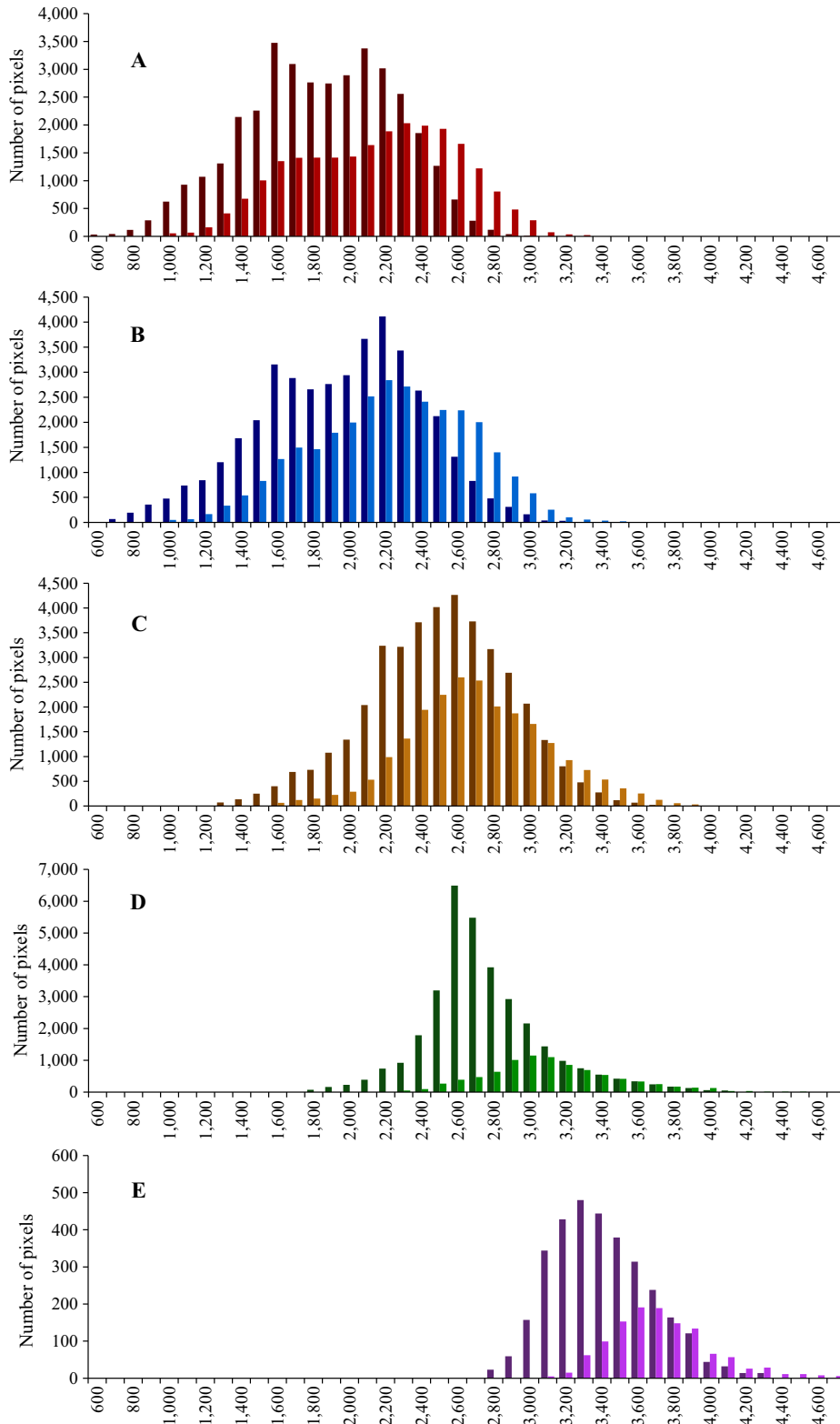


FIG. 7. Number of pixels that occur at each altitude along the Trans-Mexican Volcanic Belt in the reference period (1961–1990) climate (dark tones) and 2060 climatic habitat (light tones): (A) *P. oocarpa*; (B) *P. devoniana*; (C) *P. pseudostrobus*; (D) *A. religiosa*, and (E) *P. hartwegii*. Bar colors are the same for each species as those used in Figs. 2–6, and as in Appendix S3: Figs. S1–S5. Note that the interval values for the y-axis differ among species, but the x-axis uses the same scale throughout.

of altitude, the highest timberlines in Mexico. Beyond that point, the soils become limiting (Lauer 1978). Consequently, migration of *P. hartwegii* to sites of between 4,000 and 4,700 m a.s.l. in elevation, as suggested in Fig. 7e, presents serious biological challenges.

Discrepancy between the required migration speed and actual migration

As an apparent response to ongoing climatic change, forest plant populations are migrating to and colonizing altitudes higher than those they currently inhabit (Lenoir et al. 2008), although this is occurring at a speed less than that required to keep them coupled with their suitable climatic habitat (Peñuelas et al. 2007). For example, in western Europe the upward shift in species optimum elevation averages 29 m in altitude per decade. That represents an upward shift of 65 m for the time periods compared (mean year of surveys 1975 vs. 1993) when, in fact, a shift of 150 m (or 68 m per decade) would be required to compensate the increase in average temperature of about 1°C that already has occurred (Lenoir et al. 2008). Thus, the speed at which migration takes place is much slower than that required to keep up with the changing climatic conditions, since it is estimated that the required migration rate would be much higher than that observed in the post-glacial period (McLachlan et al. 2005). For example, Siberian populations of *Pinus sylvestris* would have to migrate at a rate of 110 km per decade in order to cope with the warming that is projected in the area toward the end of the century (Rehfeldt et al. 2002, Tchebakova et al. 2005). In the case of the five conifer species distributed in the TMVB, an upward migration of 300–400 m would be required to compensate for the change in climate expected by the year 2030 (Sáenz-Romero et al. 2010). This represents a required altitudinal migration speed of 55–73 m per decade.

The lag between the speed of the natural migration of populations and the speed at which climate change occurs requires human assistance in order to realign forest populations to sites where the climates for which they are adapted will occur. This is possible through assisted migration, assisted colonization, assisted relocation, or facilitated migration (Rehfeldt et al. 2002, Tchebakova et al. 2005, Aitken et al. 2008, Pedlar et al. 2012).

Alternative forest management needed for the xeric limit

Our results clearly indicate that ecological restoration efforts through assisted migration would have to be implemented at the low altitudinal limit (the xeric limit in some cases) of each species. For example, in the NSJP forest area, populations of *P. pseudostrobus* that are at their xeric limit and showing signs of decline, should be replaced by the assisted migration of individuals located at the upper altitudinal distribution limit of *P. devoniana*. In the MBBR, *Abies religiosa* must be replaced at its

xeric limit by individuals from the upper limit of *P. pseudostrobus*, and in turn, populations at the xeric limit of *P. pseudostrobus* must be replaced by populations from the upper limit of *P. devoniana*.

In order to maintain pure stands of *Abies religiosa*, their populations must immigrate to the new locations where their climatic habitat is projected to appear (Fig. 5D) or to the xeric limit of *P. hartwegii*, where habitat loss and contraction of their populations are already underway, while at the same time recruitment of individuals is occurring at altitudes of over 4,000 m a.s.l. (Astudillo-Sánchez et al. 2017). Field evidence indicates that the habitat loss of *P. hartwegii* is offset by its recent colonization of alpine grassland (Ramírez-Amezcuca et al. 2016).

Expected impacts on timber production

The previously described species replacement expected at the xeric limit presents silvicultural and conservation challenges. From the silvicultural perspective, for example, the replacement of the highly productive and fast-growing *P. pseudostrobus* species at its xeric limit by the slower growing, grass stage *P. devoniana*, at NSJP, Michoacán, is a justified measure based on our projections, but one that is difficult to accept from the perspective of commercial forestry in that region. The tradeoff that exists between drought resistance and growth rate is expressed clearly when comparing these two species. If a fast-growing species that is susceptible to drought stress is replaced with another more tolerant of drought, timber yield will have to be sacrificed (Sáenz-Romero et al. 2016). In other words, the decision will necessitate a strategy to deal with the economic losses due to the future impacts of climatic change: whether or not to accept future economic losses now in a climate projected to be warmer and drier, in exchange for the possibility of having healthy future forests established through assisted migration (Millar et al. 2007).

In addition to considering shifting provenances and species upward in altitude as part of a commercial management strategy, other practices such as commercial thinning to higher intensities than is currently practiced might be recommended. By lowering stand densities, such practices would reduce competition for water and vulnerability to forest fires as the climate becomes warmer and drier (Millar et al. 2007).

Implications for conservation in Protected Natural Areas

A second management dilemma involves conservation. It is very difficult to accept that a relatively successful Mexican program for conserving Monarch butterfly overwintering sites might be insufficient alone to preserve the dense *Abies religiosa* stands that serve as winter hosts for this butterfly, especially when the current conservation efforts include local community organization, field surveillance against illegal logging, and ecotourism development. Replacement of the low altitudinal limit of

Abies religiosa with pine species not currently present within the MBBR, such as *P. devoniana* and even *P. oocarpa*, is in opposition to the accepted paradigm of in situ conservation: i.e., that ecological restoration should be conducted only with local endemic species.

Assisted migration has been proposed as a tool for recovery of ecosystem services and not necessarily involving reconstruction of the ecosystem composition (Lunt et al. 2013, Williams and Dumroese 2013). Ecosystem composition cannot be maintained if species replacement is the appropriate management alternative. However, our projections indicate that if forest decline continues at the *A. religiosa* lower altitudinal limit, the actual managerial alternative might be decimated *A. religiosa* stands or even treeless tracts on the one hand or having a planted stand of a different conifer species (such as *P. pseudostrabus*) on the other hand. On the sites where suitable climatic habitat for *P. pseudostrabus* (a species currently present within the MBBR) persists, the priority should be maintaining this species, perhaps by selecting drought-resistant genotypes from the local populations. However, decay of *A. religiosa* will act to reduce forest diversity toward stands dominated by *P. pseudostrabus*, a species that is not preferred by Monarch butterflies when overwintering in the MBBR.

Although alternatives such as the two examples described above that include assisted migration at the lower altitudinal limit (or xeric limit) might be unattractive, they must be considered in view of the inevitable outcome of continued inaction. With such inaction, a large body of worldwide evidence on forest decline (Allen 2010, Mátyás 2010, Mátyás et al. 2010, Allen et al. 2015) suggests that species will be lost as degradation of the Mexican pine and conifer forest takes place, beginning at the corresponding xeric limit of each species.

Opportunities for ex situ conservation

The new suitable climatic habitat, displayed as added habitat on Figs. 2–6 and the total area of which per species is presented in Table 3, also represents an opportunity for ex situ conservation, given that the species is not currently present there. Translocation of genotypes from their natural contemporary distribution to a place currently not occupied naturally, but one that is projected to have a suitable climatic habitat under a given climatic change scenario, can be viewed as “assisted colonization,” sensu Ledig et al. (2010). However, most of the germplasm movement would be within the areas currently occupied by the species. In other words, most of the seed and seedling movement would be from the contemporary lower altitudinal limit to the mid-altitudinal range, and from the latter to the upper altitudinal limit, and only a small portion of transfers would exceed the contemporary upper altitudinal limit. This must be stressed, since a concern of some ecologists is the potential risk of species replacement (Ricciardi and Simberloff 2008, Hewitt et al. 2011, Seabrook et al. 2011).

Limitation of the study

The use of an ensemble of 17 global circulation models, aiming to represent an average of numerous models and thus to explore the range of possibilities, has the drawback of not individually exploring the projections yielded by each global circulation model, which sometimes present important differences, particularly due to differences in projections of precipitation patterns. Although this would be an interesting approach, it is beyond the stated aim of this work. A possible suggestion for follow-up work would therefore be to run the analysis for each individual global circulation model, and then to construct a map of the resulting consensus.

The present study focused on what we considered to be the most ecologically and economically important five conifer tree species along altitudinal gradients in the TMVB. However, in a megadiverse country such as Mexico, there are many more conifer and broadleaf species to be considered; for example, in terms of conservation, the very rare, fragmented and endangered *Pinus rzedowskii*; for commercial management and timber production, *Pinus montezumae*; for Christmas trees, *Pinus ayacahuite*, to mention only a few. There is therefore the need for further suitable climatic modeling addressing these other species.

CONCLUSIONS

The results suggest that, by 2060, the climate niche of each species will occur at elevations that are between 300 to 500 m higher than at present. By 2060, countrywide habitat loss could amount to 46% (*Pinus devoniana*) to 77% (*Abies religiosa*), mostly affecting the lower limits of distribution of each species. The two species at the highest elevation, *P. hartwegii* and *A. religiosa*, would suffer the greatest losses while, at the lower elevations, *P. oocarpa* would gain the most niche space (+25% of the contemporary distribution at the Trans-Mexican Volcanic Belt). Our results suggest that conifers will require human assistance to migrate altitudinally upward in order to recouple populations with the climates to which they are adapted. Traditional in situ conservation measures are likely to be equivalent to inaction and will therefore be incapable of maintaining current forest compositions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2041/full>

DATA AVAILABILITY

Data are available on Figshare: <https://doi.org/10.6084/m9.figshare.9827231.v3>

Capítulo II

***Pinus pseudostrobus* assisted migration trial with rain exclusion; maintaining Monarch
Butterfly Biosphere Reserve forest cover in a climate change environment**



Pinus pseudostrabus assisted migration trial with rain exclusion: maintaining Monarch Butterfly Biosphere Reserve forest cover in an environment affected by climate change

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Abstract

In the Trans-Mexican Volcanic Belt in central-western Mexico, drought stress causes the decline of two of the most ecologically and economically important conifers: *Abies religiosa* and *Pinus pseudostrabus*. Since *P. pseudostrabus* is distributed immediately below the lower elevation limit of *A. religiosa*, it would be a logical choice of species to fill gaps that may be created by the decline of *A. religiosa*. We assessed the feasibility of upward assisted migration and explored the effect of rain reduction using four *P. pseudostrabus* provenances in a rain exclusion field test at the border of the Monarch Butterfly Biosphere Reserve (MBBR) in Mexico. Our results show that, although populations were transferred between -1.4 and -3.3 °C mean annual temperature, and 30% of the precipitation (-200 mm) was excluded, no statistically significant differences were found among treatments or populations for height increment (overall average 1.52 m) or survival (overall average 87%). These findings suggest that it is feasible to migrate *P. pseudostrabus* upward, towards the MBBR border, which also coincides with the sites where *A. religiosa* is in decline. This may present the additional benefit of discouraging change in land use from forestry to potato production by maintaining a healthy barrier of trees. If assisted migration is not included in management and reforestation programs, climate change could induce significant mortality in the present *A. religiosa* forest, facilitating expansion of the agricultural frontier toward the MBBR.

Keywords Climatic change · Forest decline · Drought stress · Assisted migration · Rain exclusion

Introduction

One forest tree population response to climatic change is to shift distribution to higher latitudes or elevations, trying to follow the climate to which populations are adapted (Beckage et al. 2008; Kelly and Gulden 2008; Lenoir et al. 2008; Chen et al. 2011;

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Ettinger et al. 2011). However, tree natural migration rates are slower than that required to remain coupled to their suitable climate (McLachlan et al. 2005; Corlett and Westcott 2013; Gray and Hamann 2013; Shirk et al. 2018). Therefore, populations could be subject to more frequent, warmer and severe drought episodes (Sheffield and Wood 2008; Dai 2013) that could become the most important physical stress factor, and can even be lethal (McDowell et al. 2008, 2011; Ryan 2011; He et al. 2014; Allen et al. 2015). Although trees can employ phenotypic plasticity and recovery (Tardieu and Simonneau 1998; Moran et al. 2017), those mechanisms work on a limited range of climates (Leal-Sáenz et al. 2020; Rehfeldt et al. 2020), and consequently they could be exhausted and may not be able to adapt to prolonged or intense climate events (Mátyás et al. 2010; Alfaro et al. 2014). So, it is therefore very likely that climate change could induce local extinctions of forest populations due to drought stress (Rehfeldt et al. 2009; Allen et al. 2010; McDowell et al. 2011), especially at the xeric limit of the natural distribution of populations, where drought conditions are already limiting (Mátyás et al. 2009; Mátyás 2010).

Climate change projections for Mexico (Sáenz-Romero et al. 2010) suggest that coniferous forest will be one of the biomes most affected due to climate habitat shift towards higher elevations (Gómez-Mendoza and Arriaga 2007; Ledig et al. 2010; Gómez-Díaz et al. 2011; Sáenz-Romero et al. 2012a, 2015; Gutiérrez and Trejo 2014; Pérez-Miranda et al. 2014; Shirk et al. 2018; Gómez-Pineda et al. 2020). However, because of the slow rate of natural migration of trees relative to the movement of the climate zones (Peñuelas et al. 2007; Lenoir et al. 2008; Jump et al. 2009), there is increasing evidence of stress on forest populations. A strategy for mitigating the impacts of climatic change on forest populations is assisted migration, the intentional movement of populations toward colder environments in order to keep them coupled to the climate to which they are adapted (Rehfeldt et al. 2002, 2020; Aitken et al. 2008; Hewitt et al. 2011; Pedlar et al. 2012; Sáenz-Romero et al. 2016). However, assessment of field responses of populations to assisted migration is crucial to the determination of appropriate migration distance and thus to ensure the success of efforts to maintain a healthy forest cover in a climate change environment.

Pinus pseudostrobus and *Abies religiosa*, distributed in the Trans-Mexican Volcanic Belt (TMVB), are species of significant economic and ecological importance that already exhibit symptoms of drought stress (Sáenz-Romero et al. 2020). Monarch butterfly populations overwinter exclusively on *A. religiosa* in the Monarch Butterfly Biosphere Reserve (MBBR) (Sáenz-Romero et al. 2012a) and harvesting of *Pinus pseudostrobus* provides a significant economic opportunity for the Indigenous Community of Nuevo San Juan Parangaricutiro, Michoacán state (Lopez-Toledo et al. 2017). If the decline of *Abies* populations continues as a result of drought stresses (Sáenz-Romero et al. 2012a; Pérez-Miranda et al. 2014; Gómez-Pineda et al. 2020), it is likely that forests will be converted to agricultural crops at the expense of the protected natural forest area, thereby threatening local biodiversity, environmental services and the migratory phenomenon of the Monarch butterfly (Oberhauser and Peterson 2003; Ramírez et al. 2015). Since *P. pseudostrobus* is the species found immediately below the lower elevation limit of *A. religiosa*, it could be the logical choice of species to plant in locations vacated by *A. religiosa* at its xeric limit (lower elevation). Thus, it is important to evaluate the performance of *P. pseudostrobus* when migrated upward. To date, there are very few reports of provenance tests with rain exclusion treatments that assess the adaptive capacity of populations to projected future climate (Sánchez-Humanes and Espelta 2011; Ogaya et al. 2011; Horváth and Mátyás 2016). Therefore, we sought to test the feasibility of assisted migration of *P. pseudostrobus* to sites that may be vacated

by declining *A. religiosa* populations at their lower elevation limit, by testing four populations of *P. pseudostrabus* in a provenance field trial located at the lower distribution limit of *A. religiosa* in combination with a rain exclusion treatment.

Materials and methods

Study area and experimental design

Open pollinated *P. pseudostrabus* seeds were collected from natural stands at elevations of 2300, 2400, 2700 and 2900 m within the managed forest of the Indigenous Community of Nuevo San Juan Parangaricutiro (ICNSJP), Michoacán state (Fig. 1A). The seeds were sown in containers in January 2015 and grown in a shade house at Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán state (Lopez-Toledo et al. 2017). A provenance field trial was established in July 2016 in “El Cabrero” (19° 34' 34.3" N, 100° 11' 0.69" W), Ejido la Mesa, Estado de México, in a site located at 3000 m, immediately outside the Monarch Butterfly Biosphere Reserve (MBBR) (Fig. 1B), with seedlings that were 18 months-old and 30 cm tall when planted (Lopez-Toledo et al. 2017).

The experimental design consisted of treatments assigned randomly to each of 20 blocks; with rain exclusion (as a proxy for drought treatment) assigned to seven blocks, a shade treatment assigned to seven blocks and a control treatment assigned to six blocks. Within each block, seedlings were arranged in a 16-tree lattice containing four 4-tree row-plots (60 cm within rows, 90 cm between rows), such that each population was represented once within each row and each column. The term “population” is used here to refer to a group of open-pollinated individuals represented in the test site by their seedlings, while “provenance” refers to the geographic origin of a population.

Rain exclusion

In April 2017, nine months after the trial was established, three treatments were applied: (1) 30% rain exclusion (Fig. 2a), (2) shade (Fig. 2b), and (3) control (Fig. 2c). Rain exclusion was achieved by installing five rows of gutters in each block – 3 rows between seedling rows and two rows outside the seedling rows. Gutters consisted of PVC pipe 3 m in length × 0.3 m in diameter that had been cut lengthwise. It was assumed that the gutters excluded rain by 30%, since they covered 30% of the soil surface of each block. Shade treatment was achieved by placing the gutters upside-down, allowing rain to fall to the ground while generating only the effect of the shade. This treatment aimed to account for the shade effect generated by the gutters, without excluding rain. No gutters were installed in the control treatment.

To prevent the water collected by the gutters from reaching the trees, 20 and 40 cm projections of the gutters were left at the upper and lower end of the drought treatment block, respectively. Moreover, at the upper end of each treatment block, drainage ditches 5.5 m in length × 40 cm in width and 40 cm in depth were dug at a distance of 1.5 m from the upper edge of the block (relative to the terrain slope) with the purpose of capturing seepage runoff that originated upslope and preventing it from reaching the blocks.

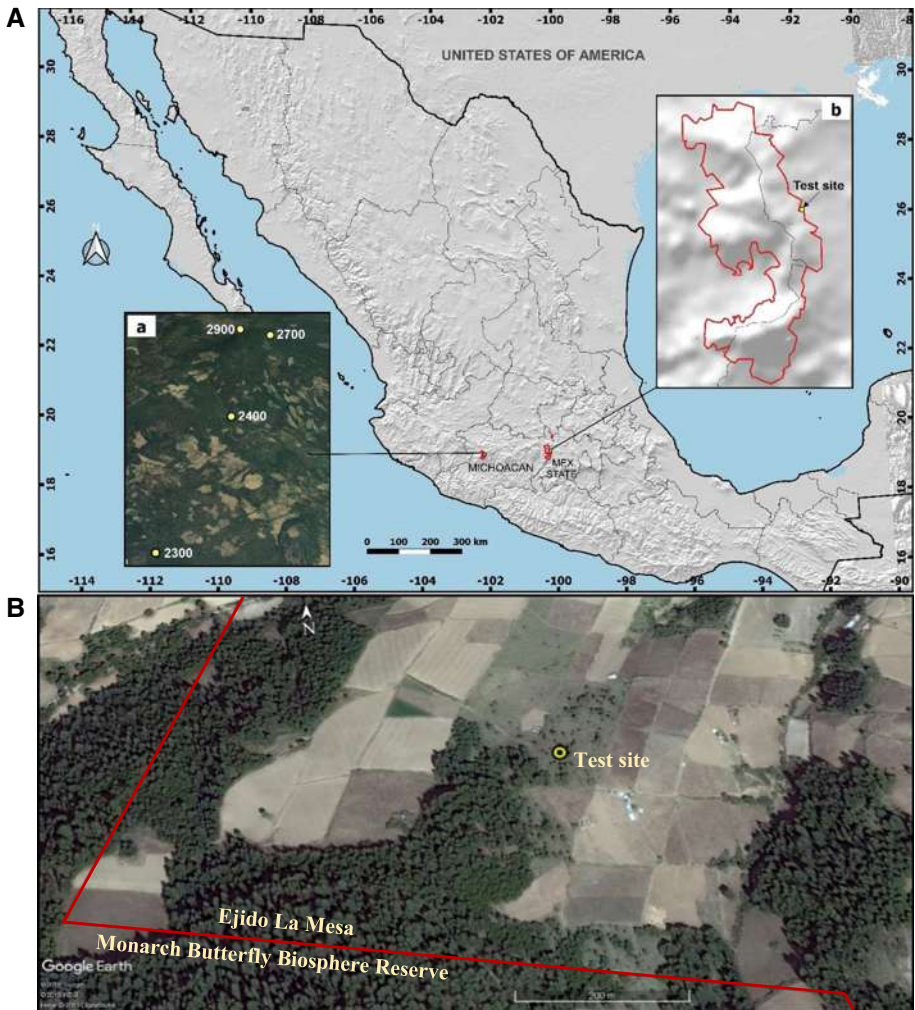


Fig. 1 Geographic location of: **A** *Pinus pseudostrobus* provenances (inset a) and the Monarch Butterfly Biosphere Reserve (MBBR) (inset b). **B** Test site “El Cabrero”, in Ejido La Mesa, in the Buffer Zone limit of the MBBR (red line). Note the field crop (potatoes) located on the edge of this Buffer Zone

Field measurements

Temperatures at 40 cm above ground level were monitored every hour using a data logger (Hobo® H01-001-01 Onset Computer Corporation, USA). Precipitation was quantified monthly from June 2017 using the rainwater collected with a funnel 17 cm in diameter placed in the neck of a 20-L bottle that was buried to ground level at the trial site. Monthly precipitation at the site during the 12 months prior to establishment of the devices was estimated by extrapolation using the linear relationship between the values recorded at the test site and those from the nearby automated meteorological station located in “Llano de las Papas” (Chincua station CIGA-UNAM, inside the MBBR, Sierra Chincua; 19° 39′

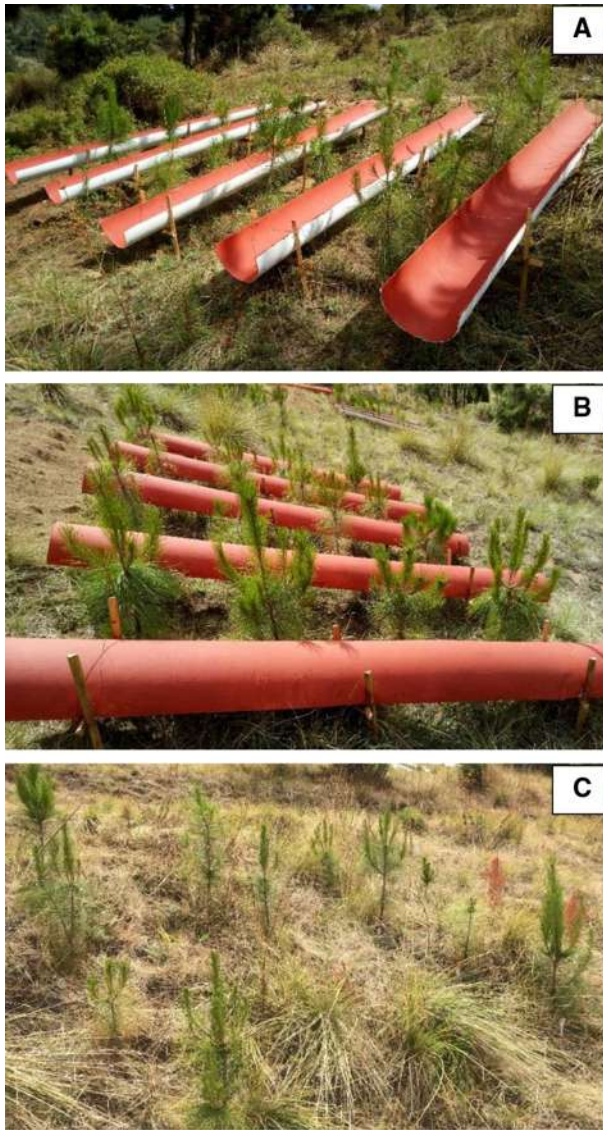


Fig. 2 Provenance trial using four populations of *Pinus pseudostrobus* subjected to: **a** 30% rain exclusion, **b** shade or **c** control. (Color figure online)

41.76°N, 100° 16' 5.52"W; 3150 m a.s.l.). Missing monthly precipitation values were estimated using linear regression, with an R^2 value of 0.9605, $p < 0.0001$.

Historical temperature and precipitation values for the four provenances of *P. pseudostrobus* were obtained for the period 1961–1990 (reference period) from spline climate models at a resolution of $\sim 1 \text{ km}^2$ (30 arc-seconds) available at the URL: <http://charcoal.cnre.vt.edu/climate/customData/> (Crookston and Rehfeldt 2019; splines based on Sáenz-Romero et al. 2010). This period was selected as the reference period because climatic

conditions were exerting selection pressures at that time on establishment of the seedlings that are now the adults that comprise the *P. pseudostrobus* population tested in this experiment (Sáenz-Romero et al. 2015).

Height increment and survival were evaluated every two months for the 2.5 years over which the field experiment was conducted.

Statistical analysis

Transfer functions relating population climate transfer distance (site climate minus population climate) to population height increment and survival were fitted using a quadratic function in order to assess local adaptation (according to Castellanos-Acuña et al. 2015). In order to assess differences among populations when transferred to a higher elevation (assisted migration) and the impact of partial rain exclusion on height increment and survival (tree alive = 1, tree dead = 0), an analysis of variance (ANOVA) was performed using the Procedure MIXED (for height increment) and Procedure GLIMMIX (for survival), of the statistical program SAS [Statistical Analysis System (SAS 2004)], with the following statistical model:

$$Y_{ijkl} = \mu + T_i + P_j + B_k(T_i) + P_j * T_i + P_j * B_k(T_i) + e_{ijkl}$$

where Y_{ijkl} = value of the $ijkl$ th observation; μ = general mean; T_i = effect of the i th treatment; P_j = effect of the j th population; $B_k(T_i)$ = effect of the k th block nested in the i th treatment; $P_j * T_i$ = effect of the interaction of the j th population with the i th treatment; $P_j * B_k(T_i)$ = effect of the interaction of the j th population with the k th block nested in the i th treatment; e_{ijkl} = error. Treatment (exclusion, shade and control) was considered a fixed effect, while population and blocks were considered random effects.

Results

Mean annual temperature (MAT) recorded at the test site during 2017 and 2018 averaged 11.7 °C, while provenance MAT during the reference period (1961–1990) was 15.0, 14.7, 13.8 and 13.1 °C for the 2300, 2400, 2700 and 2900 m populations, respectively. All MAT transfer distances were therefore negative, ranging from –3.3 °C to –1.4 °C.

Mean annual precipitation (MAP) at the test site averaged 1336 mm during the reference period, while provenance MAP was 1156 mm, 1120 mm, 1104 mm and 1128 mm for the populations from 2300, 2400, 2700 and 2900 m, respectively. Considering that 30% (*ca.* 401 mm) of the precipitation at the test site was excluded (assuming there was not significant infiltration water from outside the rain exclusion blocks, due to the peripheral drainage ditches), the amount of precipitation received by the seedlings in the exclusion treatment was only 935 mm (Table 1). That implies the *P. pseudostrobus* populations the rain exclusion treatment received approximately 200 m less precipitation annually, compared with the average MAP experienced at the seed sources (Table 1). Therefore, the effective MAP transfer distance (MAP_{td}) for the exclusion treatment ranged from –169 mm for the 2700 m population to –221 mm for the 2300 m population, while the MAP_{td} control and shade treatments was 180 mm for the 2300 m population to 232 mm for the 2700 m population (Table 1; Fig. 3).

Table 1 Mean annual temperature (MAT) and mean annual precipitation (MAP) of *P. pseudostrobus* provenances (Prov.) during the reference period (1961–1990)

Prov	Elev. (m)	MAT (°C)	MAP (mm)	MAT_td (°C)	MAP_td (mm)	Height Increment (m)			Survival (%)				
						Ex	Sh. & Co	Ex	Sh	Co	Ex	Sh	Co
P. 2300	2300	15.0	1156	-3.3	-221	-221	180	1.59	1.56	1.37	85	100	83
P. 2400	2400	14.7	1120	-3.0	-185	-185	216	1.65	1.48	1.46	93	79	83
P. 2700	2700	13.8	1104	-2.1	-169	-169	232	1.61	1.54	1.47	90	83	81
P. 2900	2900	13.1	1128	-1.4	-193	-193	208	1.48	1.50	1.39	87	100	83
<i>Provenance test site</i>													
<i>“El Cabrero”</i>													
Rain Ex	3000	11.7	935										
Without Rain Ex	3000	11.7	1336										

Elevation (Elev.), MAT and MAP transfer distances (_td), height increment and survival per population and per treatment: rain exclusion (Ex.), shade (Sh.) and control (Co.)

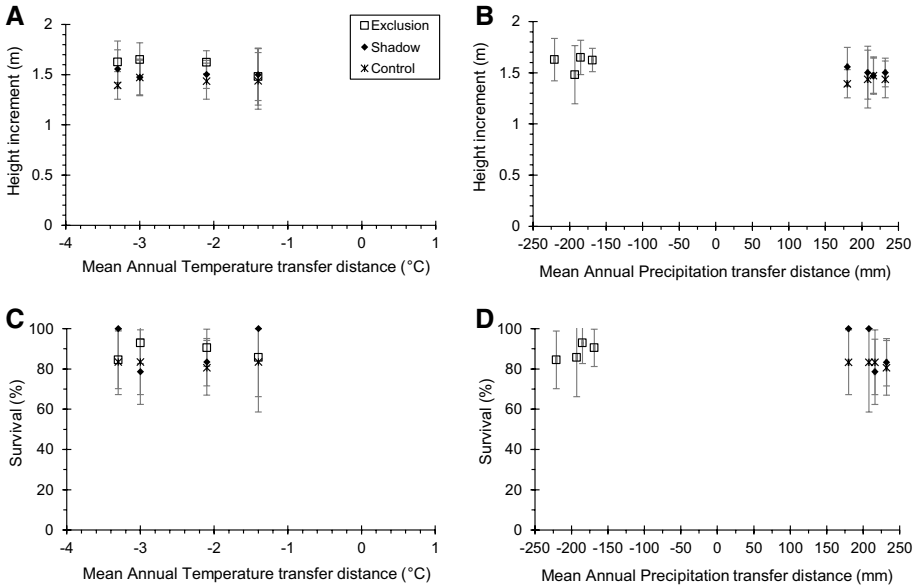


Fig. 3 Least square means by population height increment (a, b) and survival (c, d) by treatment (rain exclusion, shade and control) versus climatic transfer distances for mean annual temperature (°C) (a, c) and mean annual precipitation (mm) (b, d). Vertical bars indicate 95% confidence intervals

The 2300 m population under the control treatment had the lowest seedling height increment at 1.37 m, while the 2400 m population under the exclusion treatment had the highest, at 1.65 m. With respect to survival, the 2400 m population under the shade treatment presented the lowest survival, at 79%, while the 2300 and 2900 m asl populations under shade treatment presented the highest, at 100% (Table 1, Fig. 3).

Despite moderately large temperature and precipitation climatic transfer distances, ANOVA showed no significant differences among treatments, populations, or their interaction, for either response variable (tree height increment or survival; Table 2). Height of seedlings of all four populations were greater in the exclusion and shade treatments than in

Table 2 Analysis of variance showing the extent to which variation among populations, treatments and blocks affect tree height increment and survival of *Pinus pseudostrabus*

Source of variation	Tree height increment		Survival	
	Variance	P value	Variance	P value
<i>Fixed effects</i>				
Treatment	–	0.5440	–	0.4121
<i>Random effects</i>				
Population	0	1	0	1
Block (Treatment)	520.7	0.0065	0.047	0.4327
Pop*Treatment	0	1	0	1
Pop*Block (Treatment)	0	1	0.281	0.2570
Error	1260.3	–	–	–

the control, although differences were not statistically significant. Perhaps such difference might become significant at later ages.

Analyzing the combined effect of temperature and precipitation among provenances and the test site, we found that the aridity index (square root of degree days above 5 °C divided by the mean annual precipitation) of the provenances (*ca.* 0.051) was practically the same as that of the test site with rain exclusion treatment (aridity index value = 0.053), while the shade and control treatments presented a climate that is wetter and colder (index = 0.037) (Fig. 4—where higher values = more aridity). The similarity of seed source and test site aridity index values in the rain exclusion treatment is likely due to the decrease in precipitation (due to rain exclusion) being offset by the decrease of temperature due to the upward elevation transfer from warmer and drier *P. pseudostrubus* seed sources to a colder and wetter test site. Such differences of climate between seed sources and tests site are more evident in the warm and dry season (April–May; Fig. 5).

Discussion

Although previous results from common garden tests under optimal growing conditions indicate that populations of *P. pseudostrubus* are genetically different when separated by ~300 m in elevation (Sáenz-Romero et al. 2012b), such differentiation was not expressed in our field test, suggesting that phenotypic plasticity plays an important role in the species' adaptation. Alternatively, the short duration of the trial may not have allowed expression of differentiation among populations, or even the expression of a negative effect of rain exclusion. Furthermore, the northern aspect and 15% slope at the test site is likely to have diminished the risk of frost relative to other sites at similar elevations (Holland and Steyn 1975; Dearborn and Danby 2017).

We found no negative impacts on populations transferred up to 700 m upward in elevation (equivalent to a -3.3 °C MAT transfer) for the *P. pseudostrubus* population originating at 2300 m. This finding was unanticipated, since previous estimations suggested

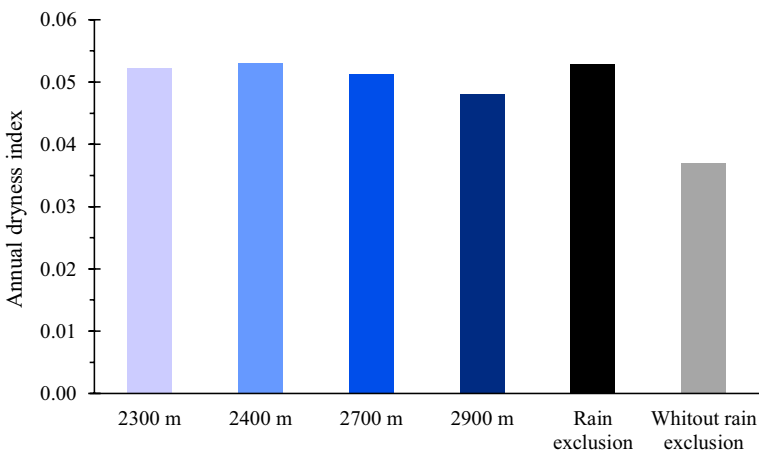


Fig. 4 Annual dryness index of *P. pseudostrubus* provenances (P; blue bars) during the reference period (1961–1990) and at the test site during 2017 and 2018 with (exclusion—black) and without (shade and control—gray) rain exclusion. (Color figure online)

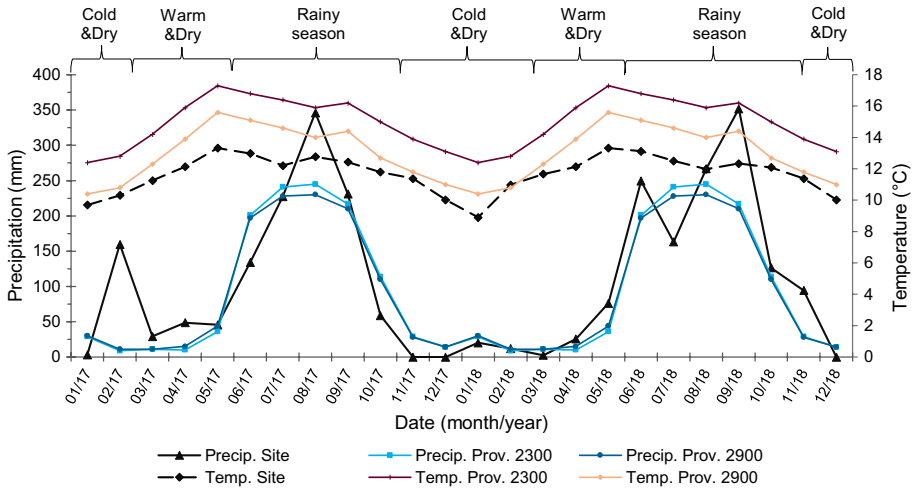


Fig. 5 Monthly average precipitation (dark and light blue lines) and monthly average temperature (red and orange lines) for the upper (2900 m) and lower (2300 m) *P. pseudostrobus* provenances during the reference period (1961–1990) and at the test site during 2017–2018 (black dashed line = temperature; black solid line = precipitation). Note that the actual amount of precipitation received by seedlings in the drought treatment would have been 30% less than the quantities shown here

an upward elevational transfer of *P. pseudostrobus* populations of 300 m (equivalent to a -1.5 °C MAT transfer) by 2030 would be needed to maintain populations in their climates of origin (Sáenz-Romero et al. 2010, 2012b). Likewise, a previous common garden reciprocal transplant experiment suggested that an upward shift of *P. pseudostrobus* populations should not exceed 400 m (Castellanos-Acuña et al. 2015).

In terms of climate transfer distance, movement of the populations to a colder and wetter environment than that of their origin possibly acted to buffer the effect of rain exclusion by decreasing evapotranspiration, which may account for the lack of negative impacts on the growth and survival of the migrated populations. This is consistent with some regional climate change projections that suggest that, with warmer weather and increased precipitation (Zhang et al. 2007; Gonzalez et al. 2010; Ettinger et al. 2011), the negative effects of climate change, such as drought and heat stress, on vegetation health may be mitigated. For example, some papers already report the upward expansion and diversification of certain biomes at high latitudes and elevations where ecosystems are experiencing rapid warming, increased precipitation and extensions of the growing season (Walther et al. 2005; Parolo and Rossi 2008; Telwala et al. 2013). However, a contrary situation can arise when increased temperatures are accompanied by unchanged or decreased precipitation, which acts to increase tree stress due to increased soil water deficit combined with increased evapotranspiration demand (Breshears et al. 2013; Dai 2013; Eamus et al. 2013).

Thus, moving this species to elevations higher than its present natural distribution might be a wise climatic change adaptation strategy since it exploits a new habitat that is increasingly less suitable to *A. religiosa* but more suited to *P. pseudostrobus* (Gómez-Pineda et al. 2020). Such transfer of genotypes needs to be done considering the patterning of genetic differentiation among populations along environmental gradients, and the projected local adaptive optima under future climate conditions (Leal-Sáenz et al. 2020).

In an environment that is increasingly dry and hot, physiological mechanisms will fail and the trees will gradually weaken (Mátyás et al. 2010). Weakened trees are then more susceptible to attack by pests and diseases (Raffa et al. 2008; Sturrock et al. 2011), which can lead to massive mortality (Allen et al. 2010), in some cases due to hydraulic failure (cavitation) (Choat et al. 2012; Sáenz-Romero et al. 2017) or a lack of carbon as result of drought stress (McDowell et al. 2008, 2011). In the case of *Abies religiosa*, it is becoming clear that one expression of the impacts of the environmental stress caused by a March–May warmer, is the lack of seedling recruitment by natural regeneration at the lower altitudinal range of its distribution (Guzmán-Aguilar et al. 2020; Romahn-Hernández et al. 2020).

Although natural migration of tree distributions to higher elevations in response to anthropogenic climate change has been documented, the speed of this phenomenon appears insufficient to keep the populations coupled with the climate to which tree populations are adapted (Peñuelas et al. 2007; Beckage et al. 2008; Kelly and Gulden 2008; Lenoir et al. 2008; Chen et al. 2011). This may be the case for *P. pseudostrubus* populations, which will require human intervention in the form of upward elevational transfer in order to remain in their climate niche.

Since the test site was located at the low elevation distribution limit of *Abies religiosa*, where the species is in the process of decline (Flores-Nieves et al. 2011), assisted migration with *P. pseudostrubus* could serve the double purpose of moving *P. pseudostrubus* populations to climates where they will be better adapted while also serving to fill the gaps created by declining *A. religiosa* populations. Furthermore, Ortiz-Bibian et al. (2017), recommend that sites between 2650 and 3000 m should no longer be reforested with *A. religiosa* since, in 40–70 years, the established trees could find themselves in climates that pose a challenge to their survival (Sáenz-Romero et al. 2012a; Gómez-Pineda 2020). Planting *P. pseudostrubus* in gaps created by declining *A. religiosa* would have the additional benefit of discouraging the expansion of agricultural incursion (such as potato production) into the Monarch Butterfly Biosphere Reserve (as illustrated in Fig. 1b). If assisted migration is not included in management and reforestation programs, climate change could induce significant mortality as genetic variability becomes eventually exhausted as a support for phenotypic plasticity and natural selection (Mátyás et al. 2010).

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Author contributions CSR and RLC conceived the project. LLT provided the seedlings. EGP, CSR, ABG and RLC conducted the experiment. GON contributed to the discussion of the results and revised the English writing. All co-authors revised the manuscript. EGP and CSR led the writing.

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Compliance with ethical standards

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Capítulo III

Mortalidad de *Abies religiosa* y *Pinus pseudostrobus* por ataque de descortezadores en la Faja Volcánica Transmexicana y su relación con el cambio climático

Mortalidad de *Abies religiosa* y *Pinus pseudostrobus* por ataque de descortezadores en la Faja Volcánica Transmexicana y su relación con el cambio climático

Introducción

Los ecosistemas forestales cubren poco más del 30% de la superficie terrestre y son fundamentales para la provisión de bienes y servicios, conservar la biodiversidad, regular el ciclo del agua y el carbono, entre otros servicios ambientales (FAO y UNEP 2020). Sin embargo, el cambio climático de origen antrópico ha puesto en peligro los bosques a través de múltiples factores estresantes (Seidl *et al.* 2017, McDowell *et al.* 2020). Varios autores coinciden en señalar que los eventos de “sequías más calientes” (hotter droughts - episodios de sequías en las que temperaturas inusualmente altas exacerbaban los efectos de la baja precipitación - Allen *et al.* 2015) serán el factor de estrés físico más importante (He *et al.* 2014, Allen *et al.* 2015). No obstante, existen otros agentes de estrés tales como: insectos (Stephenson *et al.* 2019), patógenos (Sturrock *et al.* 2011), fuego (Hood *et al.* 2018), vientos inusualmente fuertes (Rich *et al.* 2007) y relámpagos (Yanoviak *et al.* 2020), que también inducen a la mortalidad de árboles. Si bien estos agentes han existido en ausencia de cambio climático, su capacidad para afectar los bosques se ve amplificada en presencia de sequías más calientes (McDowell *et al.* 2020).

En el caso de insectos herbívoros, se espera que bajo condiciones más cálidas y secas tengan más generaciones al año, como consecuencia de una mayor fecundidad y supervivencia, lo que provocará más brotes y la expansión de su rango de distribución histórico (Raffa *et al.* 2008, Seidl *et al.* 2017, Jactel *et al.* 2019, Stephenson *et al.* 2019). Condiciones más cálidas y húmedas también promoverán la ocurrencia de patógenos (Sturrock *et al.* 2011, Seidl *et al.* 2017, Wyka *et al.* 2018). Paralelamente, los árboles hospedantes debilitados por sequías calientes serán más susceptibles a los ataques de insectos y patógenos, puesto que sus mecanismos de defensa se verán reducidos (McDowell *et al.* 2008, 2011, Gessler *et al.* 2018). Por ejemplo, en algunas coníferas la disminución en la disponibilidad de carbohidratos y el potencial hídrico bajo durante la sequía pueden limitar la producción de resina y la generación de presión hidráulica en los conductos (Netherer *et al.* 2015, Hammond *et al.* 2019), ambos necesarios para resistir los ataques de descortezadores. Debido al efecto conjugado de estrés

por sequía y al subsecuente brote de plagas y (o) enfermedades, varios casos de muerte forestal han sido documentados alrededor del mundo (Allen *et al.* 2010, 2015, McDowell *et al.* 2011, Klein *et al.* 2019, Hartmann *et al.* 2018), especialmente en el *límite xérico* de la distribución natural de las poblaciones (límite inferior altitudinal, o margen sur en el hemisferio norte), donde las condiciones de sequía de por sí ya limitantes (Mátyás *et al.* 2009, Mátyás 2010) se ven agravadas por el calentamiento global.

En México, uno de los primeros casos que sugieren la relación entre el clima y plagas forestales es el ocurrido dentro de la Reserva de la Biosfera de la Mariposa Monarca (RBMM) donde el brote del descortezador *Scolytus mundus* afectó un gran número de árboles de *Abies religiosa* después de una importante sequía ocurrida de 2007-2008 (Manzo-Delgado *et al.* 2013). En el área forestal de la Comunidad Indígena de Nuevo San Juan Parangaricutiro (NSJP) el aumento en las temperaturas máximas también impulsó un brote de descortezadores, principalmente del género *Hylastes*, que mayormente afectaron las poblaciones de *P. pseudostrobus* localizadas en la parte baja de su distribución altitudinal (Rubín-Aguirre *et al.* 2015). Recientemente Sáenz-Romero *et al.* (2020) documentaron casos de plagas y enfermedades inusuales promovidos por eventos de sequía: descortezadores (*Dendroctonus frontalis*) en *Pinus gregii*, avispa agalladora (*Andricus quercuslaurinus*) en *Quercus affinis*, mancha foliar (*Lophodermium sp.* y *Ocoaxo sp.*) en *Pinus patula*, tinta del castaño (*Phytophthora cinnamomien*) en *Quercus spp.*, y defoliadores (*Neodiprion autumnalis*) en *Pinus duranguensis*. En otro caso reciente, árboles de *Pinus hartwegii* en el Nevado de Colima, Jalisco, aparentemente debilitados por un mayor estrés por sequía en los meses de marzo a principios de mayo, están padeciendo infestaciones frecuentes de *Dendroctonus adjunctus* (observación personal, Figura 1a, 1b). A nivel nacional, se estima que los descortezadores son los que han afectado una mayor superficie forestal en los últimos diez años (Sáenz-Romero *et al.* 2020), y se espera que los brotes de plagas forestales sigan en aumento en varios estados de la república (Sosa-Díaz *et al.* 2018).

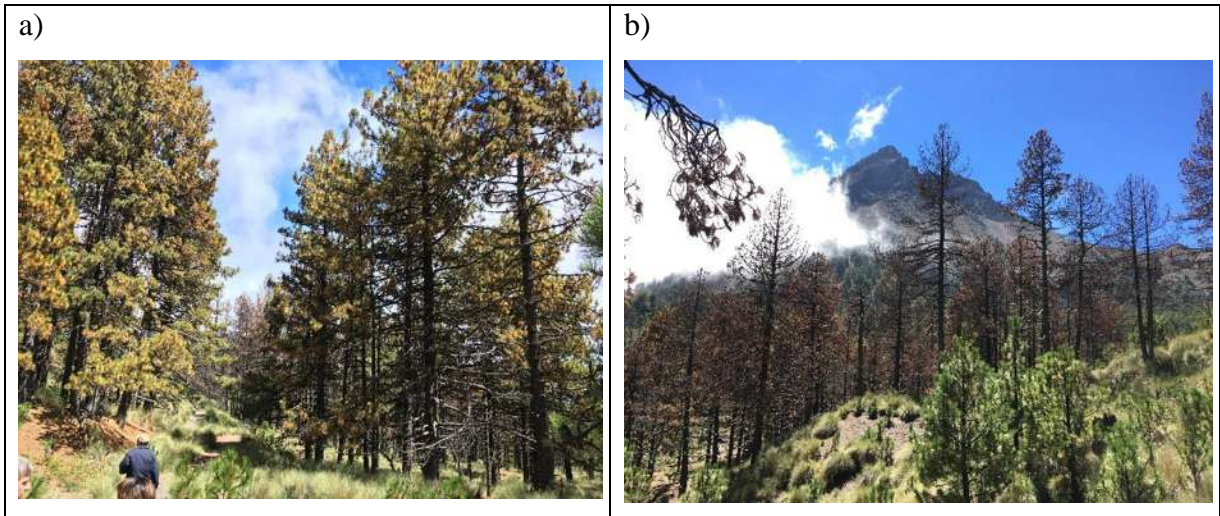


Fig. 1. Evidencias de brotes inusualmente numerosos e intensos de ataque de descortezador en rodales de *Pinus hartwegii*, Nevado de Colima, Jal. (a) Árboles con follaje amarillento, debilitados por el ataque de descortezador. (b) Árboles ya muertos por un ataque de descortezador. (Fotos: C Sáenz-Romero, octubre 2018).

Con base en lo anterior, a fin de determinar si en México la ocurrencia de plagas forestales está siendo impulsada por el incremento en la aridez derivada del efecto conjugado del incremento de temperatura y disminución de precipitación (Sáenz-Romero *et al.* 2010), en este capítulo se utilizan los datos de cortas de saneamiento y las proyecciones de hábitat climático para las poblaciones de *A. religiosa* y *P. pseudostrobus* de la Faja Volcánica Transmexicana (FVTM). La hipótesis a probar es que los brotes de descortezadores ocurren en el *límite xérico* (límite inferior) de la distribución altitudinal de cada especie ya que es donde perderán su hábitat climático.

Materiales y métodos

Área y especies de estudio

El área de estudio es la Faja Volcánica Transmexicana (FVTM), una región situada en el centro de México, a lo largo de un eje de distribución geográfica Este-Oeste (entre 19° y 20° Latitud N). En ésta se concentran los picos volcánicos más altos del país como el Citlaltepetl o Pico de Orizaba que alcanza los 5675 msnm (Neyra-Jaúregui 2012 - Ver Fig. 1 del capítulo 1), así como importantes Áreas Naturales Protegidas (ANP) (Ramírez-Amezcuca *et al.* 2016). En esta región, las poblaciones de *A. religiosa*, que forman el denso bosque donde la mariposa Monarca pasa el invierno dentro de la Reserva de la Biósfera de la Mariposa Monarca, se

distribuye entre los 2500 y 3600 m de altitud (Sáenz-Romero *et al.* 2012a), mientras que las poblaciones de *P. pseudostrobus*, que brindan una importante fuente de ingreso económico para gran parte de las comunidades indígenas de la Meseta Purépecha de Michoacán, se distribuyen desde los 2100 hasta los 2900 m (Sáenz-Romero *et al.* 2012b).

Cortas de saneamiento

La información de las notificaciones emitidas por la Comisión Nacional Forestal (CONAFOR) y la Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) para realizar cortas de saneamiento en las poblaciones de *A. religiosa* y *P. pseudostrobus* de la FVTM, fueron proporcionados por el Ing. Oscar Trejo Ramírez, jefe del Laboratorio de Análisis y Referencia en Sanidad Forestal, Dirección General de Gestión Forestal y de Suelos, SEMARNAT. Las notificaciones son emitidas de manera posterior al aviso de presencia de plagas, aviso que se da por parte del propietario del predio y un prestador de servicios técnicos forestales. El prestador debe realizar el Informe Fitosanitario Técnico, documento en el cual se especifica la superficie y volumen afectados, así como la georreferenciación de los brotes. Este informe es verificado por la CONAFOR, quien emite la notificación (ver Ley General de Desarrollo Forestal Sustentable) que obliga a los propietarios de los predios a realizar los trabajos de saneamiento en un periodo específico de tiempo en función de la superficie y volumen afectados. De acuerdo con la NOM-019-SEMARNAT-2006, los árboles afectados por descortezadores, deben ser derribados, troceados y en el material resultante se debe aplicar insecticidas autorizados.

En la base de datos, que abarca de 2009 a 2018, se realizó la limpieza de datos comenzando por eliminar las coordenadas duplicadas (la base original incluye la coordenada de cada vértice por sitio, pero dada la cercanía entre vértices, las coordenadas resultaron duplicadas en algunos casos). Posteriormente, con la coordenada “central” por predio (sitio) se realizó la unificación del sistema de coordenadas; de UTM y Geográficas con notación sexagesimal y Datum WGS84 o NAD27 se convirtieron a coordenadas Geográficas con notación decimal y Datum WGS84. Los valores de latitud y longitud fueron usados para obtener la altitud (msnm) de cada predio a partir del modelo de elevación digital de GLOBE Task Team (1999). En el

análisis no se consideraron los predios con valores de altitud fuera del rango de distribución altitudinal de cada especie.

Cortas de saneamiento y hábitat climático

Las capas (*grids*) que muestran el hábitat climático contemporáneo (periodo 1960-1990) que *A. religiosa* y *P. pseudostrobus* perderán, mantendrán y ganarán para 2060, fueron las elaboradas por Gómez-Pineda *et al.* (2019). Sin embargo, en los modelos de nichos climáticos el área propicia usualmente es mayor que el área realmente ocupada por cada especie ya que ésta se proyecta con base en el clima, sin considerar otros factores limitantes que restringen su distribución; competencia, dispersión, barreras geográficas, etc. (ver Soberón y Peterson 2005, Pearson y Dowson 2003). Por lo anterior, a fin de representar la superficie realmente cubierta de vegetación forestal, usando la carta de Formaciones Forestales elaborada por la Comisión Nacional Forestal (CONAFOR 2018) se realizó el recorte del hábitat climático proyectado para cada especie.

Para *A. religiosa*, la formación forestal considerada para el recorte de su hábitat climático fue el Bosque de Oyamel (BA), que incluye la vegetación secundaria arbórea y arbustiva (VSA/BA y VSa/BA, respectivamente). Para *P. pseudostrobus* las formaciones forestales fueron Bosque de Pino (BP) y Bosque de Pino-Encino (BPQ), las cuales también incluyen la vegetación secundaria arbórea (VSA/BP, VSA/BPQ) y arbustiva (VSa/BP, VSa/BPQ) correspondiente. Los sitios donde se realizaron cortas de saneamiento (representados como puntos) se sobrepusieron a las capas recortadas a fin de determinar si los brotes de descortezadores ocurren en el *límite xérico* (límite inferior) de la distribución altitudinal de cada especie, es decir, donde se proyecta que perderán hábitat climático. El recorte de las capas, la representación cartográfica del hábitat climático ocupado por cada especie y la sobreposición de los puntos de cortas se realizó utilizando una combinación de los Sistemas de Información Geográfica de QGIS Desktop v3.10.1 (disponible en <https://www.qgis.org/es/site/>) y ArcGis Desktop v10.3.

Superficie tratada vs. altitud y AHI

Los datos de altitud se agruparon por especie en rangos de 100 m y se graficaron contra la superficie cortada en cada intervalo altitudinal para determinar si la mayor superficie tratada ocurre a elevaciones menores. De igual manera, se graficó el año de corta contra la superficie tratada para determinar el año de mayor afectación.

Del programa ClimateNA, versión 6.3 disponible en <http://climatena.ca/> (Wang *et al.* 2016), se obtuvieron los valores de AHI (annual heat-moisture index = índice de aridez) para el año de mayor afectación (corta), así como para el año previo (antes de que surgieran los brotes de plagas). AHI se seleccionó ya que expresa el equilibrio entre la temperatura y la precipitación, que a su vez son consideradas dos de las variables bioclimáticas de gran importancia en la distribución de las poblaciones forestales (Rehfeldt *et al.* 2006, O'Neill *et al.* 2014). La superficie tratada se graficó contra intervalos de AHI para analizar si ocurrieron episodios de sequía (aridez) antes o durante el surgimiento de plagas que afectaron una mayor superficie durante determinado año.

Resultados y discusión

De 2009 a 2018 se emitieron un total de 209 notificaciones de saneamiento de *Abies religiosa*. De éstas, 8 no fueron consideradas para el análisis pues estaban fuera del rango de distribución altitudinal de la especie. Las 201 notificaciones consideradas representaron una superficie tratada de 4,091 ha. Para *Pinus pseudostrobus* las notificaciones de saneamiento otorgadas fueron 1053, sin embargo, 104 estaban fuera del rango por lo que sólo se consideraron 949 notificaciones con una superficie tratada de 4,664 ha. Para ambas especies, los estados más afectados fueron Estado de México y Michoacán (Figuras 2 y 3).

Cortas de saneamiento y hábitat climático

La sobreposición de las cortas (puntos) con el recorte del hábitat climático ocupado por poblaciones de cada especie muestra que los brotes de descortezadores no necesariamente ocurren dentro de los sitios donde se proyecta que *A. religiosa* (Figura 2) y *P. pseudostrobus* (Figura 3) perderán su hábitat para la década centrada en 2060. De hecho, la mayoría las cortas de saneamiento caen dentro del área donde los modelos climáticos proyectan que ambas especies mantendrán su hábitat climático.

Aparentemente las cortas de saneamiento están más relacionadas con lo que se podría identificar como el borde (límite) actual del bosque. Por ejemplo; *Abies* dentro de la RBMM (Figura 2A). Otro factor que podría estar relacionado es la orientación de la ladera. Por ejemplo, las cortas de *P. pseudostrobus* se concentran en la cara sur del área de protección de flora y fauna Pico de Tancítaro (Figura 3A). Las cortas de saneamiento también parecen concentrarse en lo que parece ser el límite actual del bosque (Figura 3B), e incluso hay puntos que caen donde aparentemente no hay bosque, lo cual puede deberse a errores de las coordenadas consignadas, o a manchones muy pequeños que no están presentes en los mapas consultados.

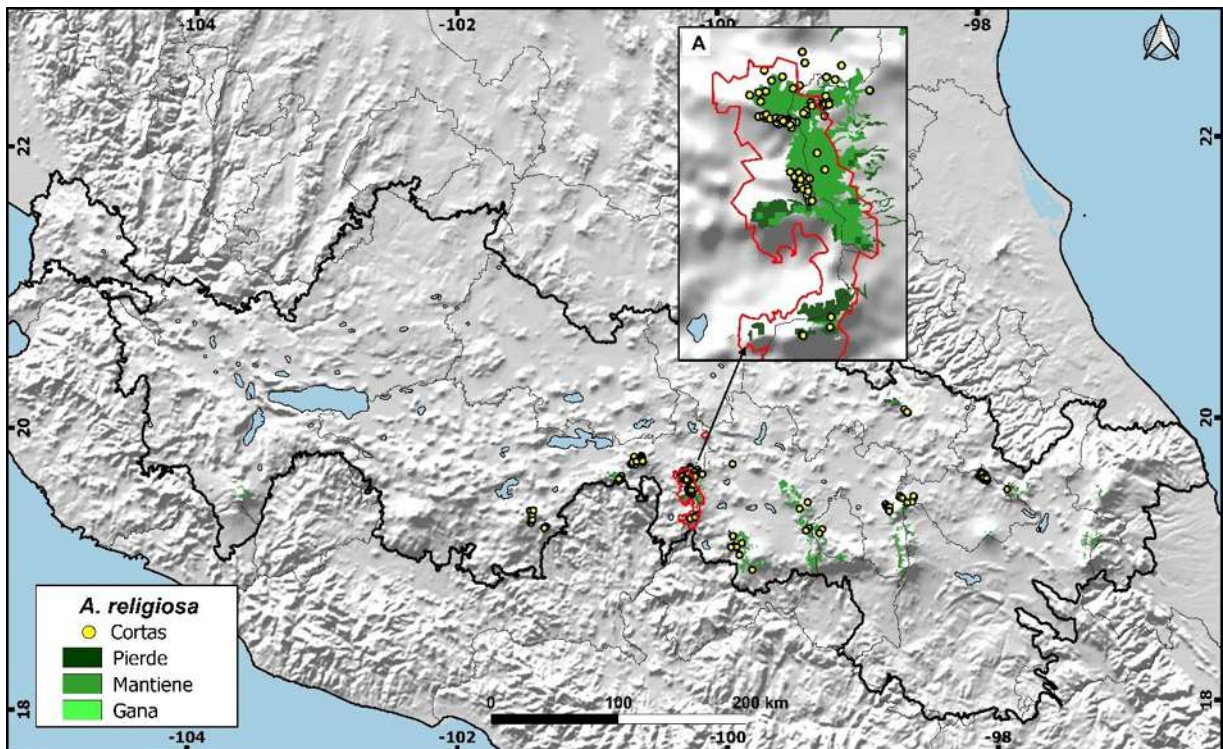


Fig. 2. Hábitat climático con bosque de Oyamel que se perderá, mantendrá y ganará para 2060. Los puntos amarillos son las cortas de saneamiento realizadas de 2009 a 2018. A) En rojo se muestra el área de la Reserva de la Biosfera de la Mariposa Monarca.

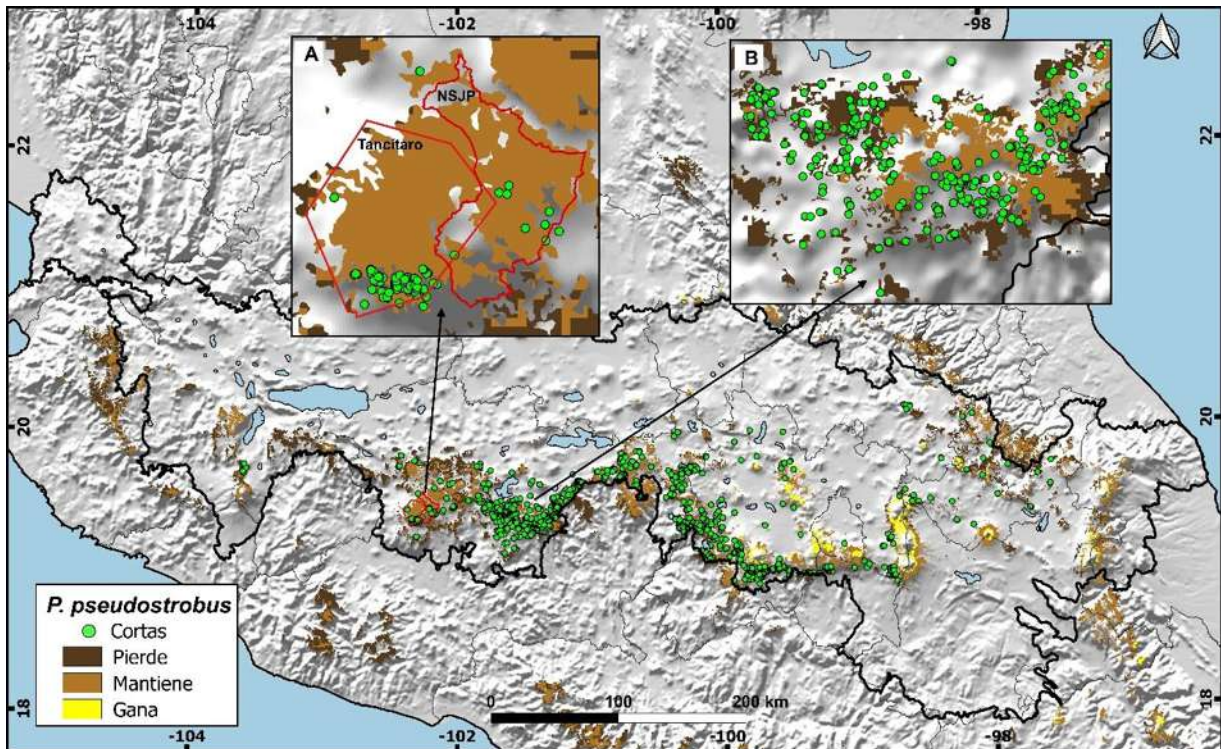


Fig. 3. Hábitat climático con bosque de *P. pseudostrobus* que se perderá, mantendrá y ganará para 2060. Los puntos verdes son las cortas de saneamiento realizadas de 2009 a 2018. A) Área de Protección de Flora y Fauna Pico de Tancitaro y área forestal de la Comunidad Indígena de Nuevo San Juan Parangaricutiro (NSJP). B) concentración de cortas de saneamiento en lo que parece ser el límite actual del bosque.

Superficie tratada vs. altitud

De las 4,091 ha tratadas para *A. religiosa*, aproximadamente 40% del total (1,596 ha) ocurre en el intervalo altitudinal de 3000-3100 msnm (Figura 4), es decir, donde se encuentran las masas puras y relativamente mejor conservadas de oyamel. Estos resultados son contrarios a nuestra hipótesis de que las cortas de saneamiento se concentrarían en la parte baja de la distribución altitudinal; sin embargo, son similares a los reportados por Leautaud y López-García (2017), quienes encontraron que la mayor afectación por descortezadores en la Sierra Chincua, dentro de la RBMM, se dio en la zona núcleo donde hay mayor densidad de individuos, posiblemente debido a las restricciones de manejo, en comparación con la zona de amortiguamiento, con menor densidad de árboles debido al manejo forestal. A su vez, Negrón *et al.* (2009) encontraron una relación positiva entre la muerte de *Pinus ponderosa* por ataque

de descortezadores y la densidad de los árboles, aunque la relación fue negativa con la altitud y el diámetro del árbol. A su vez, Stephenson *et al.* (2019) señalan que los insectos pueden actuar de dos maneras; atacan a los árboles más estresados fisiológicamente o, matan los árboles dentro de una clase de tamaño particular, independientemente de su estrés, por lo que hay selección de hospedero. Entonces, posiblemente para *Abies* los brotes de descortezadores se dan donde ocurren las masas puras con individuos más grandes. Además, 3000 m podría ser el límite actual de la distribución real de esta especie en la zona estudiada, ya que en altitudes menores las poblaciones en gran medida han sido reemplazadas por cultivos agrícolas (Ramírez *et al.* 2015), especialmente papa.

Para *P. pseudostrobus* el rango dentro del cual ocurre más de 54% (2,527 ha) de la superficie tratada va de los 2200 a los 2400 msnm (Figura 5). Este intervalo coincide con el límite altitudinal inferior de la distribución natural de *P. pseudostrobus* en la región de Nuevo San Juan Parangaricutiro, Michoacán, donde las poblaciones localizadas a 2200 m de altitud han sido las más afectadas por brotes de descortezadores (Rubín-Aguirre *et al.* 2015). Si se considera que en la misma región las poblaciones de *P. pseudostrobus* localizadas a los 2300 m de altitud comienzan a presentar síntomas de debilitamiento debido a las condiciones de sequía que prevalecen en los sitios (López-Toledo *et al.* 2017), es de esperarse que haya un incremento en la ocurrencia de brotes de descortezadores y, por tanto, en la superficie afectada en lo que se ha sido llamado el *límite xérico* (Mátyás *et al.* 2009).

La relación entre el número de notificaciones de saneamiento (cortas) y la superficie tratada no es proporcional para ninguna de las especies evaluadas.

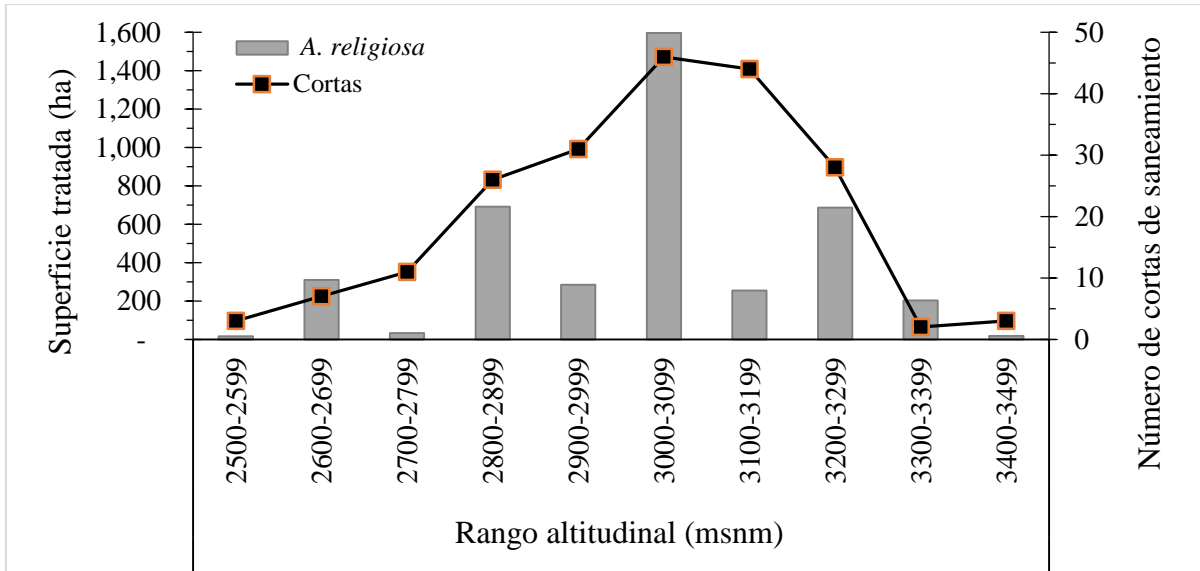


Fig. 4. Superficie tratada (barras) y número de cortas de saneamiento (línea) por intervalo altitudinal de *A. religiosa*

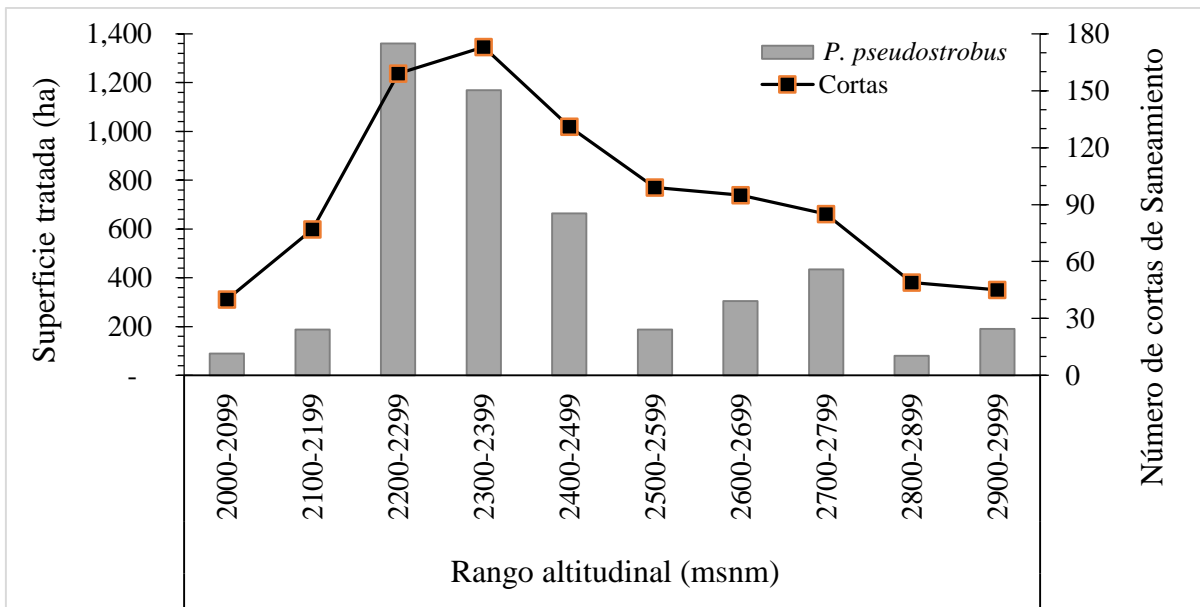


Fig. 5. Superficie tratada (barras) y número de cortas de saneamiento (línea) por intervalo altitudinal de *P. pseudostrobus*

Superficie tratada vs. AHI

Para *A. religiosa* el año más afectado fue 2014 (Fig. 6a) mientras que para *P. pseudostrobus* fue 2012 (Fig. 7a) con una superficie tratada de 1444 ha (35 % del total) y 1316 ha (28 %),

respectivamente. El índice de aridez se dividió en intervalos de 5 para cada especie tanto para el año de más superficie tratada como para el año previo al brote de las plagas. Los resultados sugieren que el año previo fue más árido que el año de la corta para cada una de las especies, y de estas, *P. pseudostrobus* presenta valores de aridez más altos (Fig. 7b) que *Abies* (Fig. 6b). Estos resultados coinciden con lo encontrado por Pinzón *et al.* (2018) quien reportó que los brotes de descortezadores en el Bosque Templado de Nuevo León aumentaron considerablemente en 2012 después de la sequía que tuvo lugar en 2011. Esto muy probablemente debido a que hay un período de retraso (*lag*) entre el año de sequía y los brotes masivos de descortezador, tal como lo demostró Sangüesa-Barreda *et al.* (2015), quienes encontraron que dos años antes de la muerte de árboles plagados por descortezadores hay una reducción en la producción resina en los ductos debido a la ocurrencia de sequías, concluyendo que la interacción de estos dos factores estresantes; sequías y descortezadores, juega un papel decisivo en el desencadenamiento de altas tasas de mortalidad forestal. De esta manera, en el caso de *A. religiosa* y *P. pseudostrobus* el ataque por descortezadores, que aparentemente ocurre un año después de la sequía, podría deberse al debilitamiento de los mecanismos de defensa después de episodios de sequía (Fig. 6 y Fig. 7).

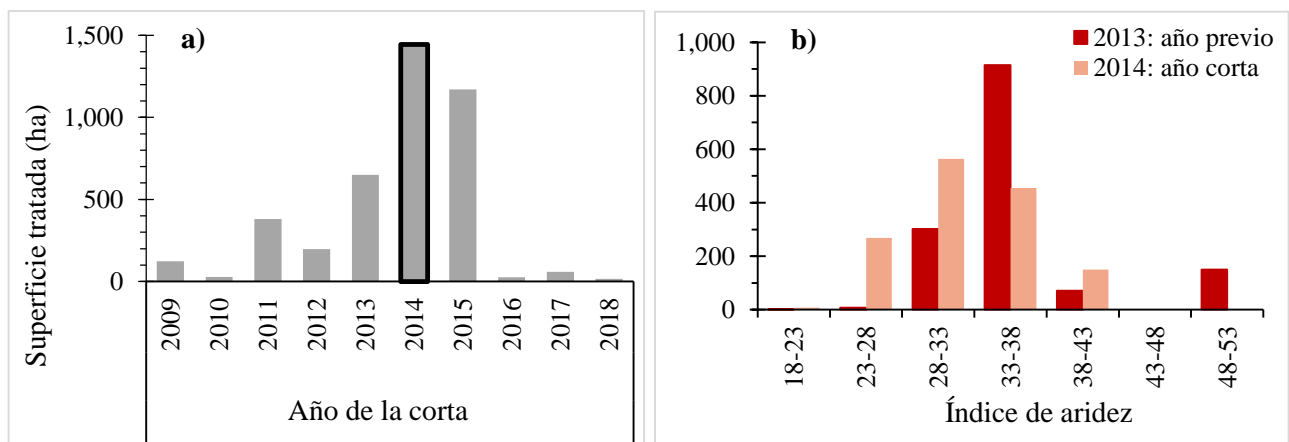


Fig. 6. Superficie tratada para *A. religiosa* a) por año de corta de 2009 a 2018 y, b) del año de más superficie tratada (año corta) y año previo, y su relación con el índice de aridez (AHI; valores más elevados indican mayor aridez).

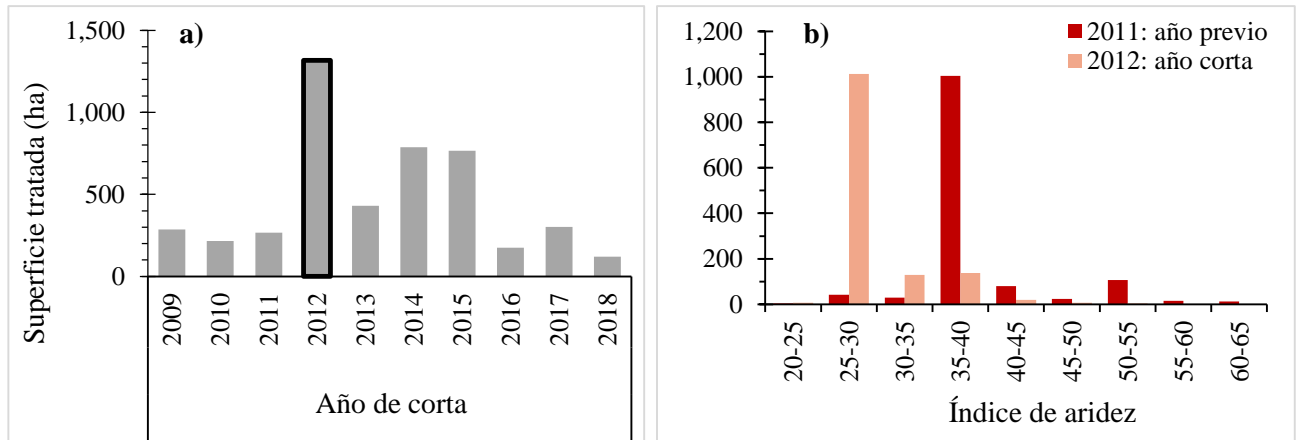


Fig. 7. Superficie tratada para *P. pseudostrobus* a) por año de corta de 2009 a 2018 y, b) del año de más superficie tratada (año corta) y año previo, y su relación con el índice de aridez (AHI; valores más elevados indican mayor aridez).

Conclusiones

Los resultados obtenidos muestran que de 2009 a 2018 en la región conocida como Faja Volcánica Transmexicana (FVTM), los brotes de descortezadores no necesariamente ocurrieron en el *límite xérico* o límite inferior de la distribución altitudinal donde los modelos climáticos proyectan que habrá pérdida de hábitat climático. En el caso de *A. religiosa*, aproximadamente el 40% de la superficie tratada (4,091 ha en donde se prescribieron y realizaron cortas de saneamiento) por la presencia de descortezadores ocurre en el intervalo altitudinal de 3000 y 3100 m, lo que coincide con el intervalo intermedio de la distribución altitudinal de la especie, donde se presentan las masas puras de esta especie, relativamente bien conservadas y que forman parte de la franja altitudinal de los sitios de estancia invernal de la mariposa Monarca. Esto sugiere que el escarabajo descortezador prefiere sitios con árboles de mayor tamaño y/o mayor densidad del arbolado. Sin embargo, esto requiere de una investigación más detallada que sustente o descarte esta hipótesis. Respecto a las poblaciones de *P. pseudostrobus*, 54% de la superficie tratada con cortas de saneamiento (4,664 ha), sí se localizó en el *límite xérico* (altitudinal inferior) de su distribución, entre los 2000 y 2400 m. Para esta especie la exposición de la ladera parece tener un papel determinante en la ocurrencia de los brotes ya que se encontró una mayor concentración de cortas de saneamiento (representados como puntos en los mapas) en sitios

con exposición sur. De igual manera, se requiere una investigación más detallada que pueda confirmar lo mencionado.

El año con mayor superficie afectada para *A. religiosa* fue 2014 y para *P. pseudostrobus* fue 2012. En ambos casos, el año previo presentó valores de índice de aridez (AHI) más elevados, lo que sugiere un período de retraso (*lag*) entre el año donde ocurre la sequía (año previo) y el año donde se presentan los brotes masivos de descortezador (año de mayor superficie afectada).

Considerando que en lugares como México, una gran porción de la superficie forestal del país pertenece y está bajo manejo de las comunidades que viven y dependen directamente de los bosques, en futuras investigaciones sería importante determinar, además de la influencia del clima, selección de hospedero y exposición de la ladera, la capacidad de respuesta de los actores sociales (ejidos, comunidades, pequeños propietarios, entre otros) para prevenir, controlar y manejar estas plagas forestales. Se requiere analizar, por ejemplo, su grado de organización social, capacidad de respuesta, capacitación técnica, gobernanza, entre otros aspectos. Esto es deseable no sólo para comprender el efecto combinado del clima y sociedad sobre los brotes de descortezadores, sino para identificar las implicaciones que esto pudiera tener en la implementación de acciones de manejo comunitario que ayuden a prevenir, controlar y mitigar los impactos más perjudiciales de este tipo de plagas forestales y a la vez contribuyan al desarrollo sustentable de las comunidades que dependen de ellos.

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Discusión general

Las proyecciones de hábitat climático muestran que, de las cinco especies, aquellas con el hábitat climático más amplio; *P. oocarpa*, *P. devoniana* y *P. pseudostrobus*, perderán menos área propicia ya que su clima se moverá hacia sitios ubicados a elevaciones más altas (entre 300 y 400 m hacia arriba), lo que compensaría parcialmente el área perdida. Por otro lado, las especies con el hábitat climático más restringido; *P. hartwegii* y *Abies religiosa* (esta última se moverá hasta 500 m hacia arriba), perderán más área propicia, ya que su clima estará restringido a los picos más altos de las montañas, especialmente en aquellos ubicados a lo largo de la Franja Volcánica Transmexicana (FVTM), los cuáles debido a su conicidad representan una superficie más pequeña con el aumento en altitud (ver Figuras 2 a 6 y Tabla 3 del capítulo I). En general, estos resultados concuerdan con proyecciones previas realizadas por Gómez-Mendoza y Arriaga (2007), Gómez-Díaz *et al.* (2011), Monterroso-Rivas *et al.* (2013), Gutierrez y Terejo (2014).

Debido a que el clima propicio de las cinco especies se desplazará altitudinalmente hacia arriba, el hábitat climático sujeto a perderse se encuentra en el límite inferior de la distribución actual de cada especie (ver Figuras 7a a 7e del capítulo I), es decir, su *límite xérico* (sensu Mátyás *et al.* 2009), por lo que éstas deberán migrar sus poblaciones altitudinalmente hacia arriba para seguir acopladas el clima al cual están adaptadas, tal como ya lo están haciendo (por medios naturales) otras poblaciones forestales (Beckage *et al.* 2008, Kelly y Gulden 2008, Lenoir *et al.* 2008). Sin embargo, es importante destacar que tal velocidad de migración natural resulta insuficiente para mantener un acoplamiento a su hábitat climático (McLachlan *et al.* 2005, Corlett y Westcott, 2013). Por ejemplo, en Europa occidental, el desplazamiento promedio hacia arriba en la elevación óptima de varias especies forestales es de 29 m/década, lo que representa una velocidad de migración altitudinal de 65 m para los dos periodos comparados (1905 a 1985 y 1986 a 2005), cuando en realidad se requeriría un desplazamiento de 150 m (o 68 m/década) para compensar el aumento de 1°C ya ocurrido (Lenoir *et al.* 2008). En el caso de las cinco especies de coníferas evaluadas, una migración altitudinal de 300 a 400 m compensaría la pérdida de su hábitat climático debido al incremento de temperatura y disminución de precipitación proyectado (Sáenz-Romero *et al.* 2010), no obstante, se requiere una velocidad de migración de entre 55 y 73 m por década.

Nuestros resultados indican claramente que los esfuerzos encaminados a adaptar las poblaciones a los nuevos ambientes creados por el cambio climático requieren estrategias de manejo como lo es, por ejemplo, la migración asistida. En ésta se busca mover intencionalmente las poblaciones de una especie (tanto dentro del área de su distribución actual natural como fuera de su área de distribución histórica), hacia sitios donde las proyecciones predicen que habrá su hábitat climático apropiado (Pedlar *et al.* 2012, Commander *et al.* 2018). Para las cinco coníferas evaluadas, la migración asistida debería implementarse especialmente en su *límite xérico* reemplazando las poblaciones del límite altitudinal inferior de una especie por las poblaciones del límite altitudinal superior de la especie que se distribuye inmediatamente a menor altitud. Por ejemplo, en el área forestal de la Comunidad Indígena de Nuevo San Juan Parangaricutiro (NSJP), las poblaciones de *P. pseudostrobus* que se encuentran en su *límite xérico* y que muestran signos de declinación (Lopez-Toledo *et al.* 2017) y ataque de descortezadores (Rubín-Aguirre *et al.* 2015), deben ser reemplazadas por la migración asistida de individuos ubicados en el límite altitudinal superior de *P. devoniana* (= *P. michoacana*). En la Reserva de la Biósfera de la Mariposa Monarca (RBMM), *A. religiosa* debe ser reemplazada en su *límite xérico* por individuos del límite altitudinal superior de *P. pseudostrobus*, y a su vez, las poblaciones en el *límite xérico* de *P. pseudostrobus* deben ser reemplazadas por poblaciones del límite altitudinal superior de *P. devoniana*, ya que el clima de los sitios será más propicio para dichas especies (Ver Fig. 5F, 4A y 3B del capítulo I).

La migración asistida de *P. pseudostrobus* hacia el borde de la RBMM, que además coincide con el límite altitudinal donde las poblaciones de oyamel están exhibiendo síntomas de declinación (Flores-Nieves *et al.* 2011), es viable en el sentido de que los resultados obtenidos en el Capítulo II del presente trabajo muestran que no hubo efectos negativos sobre el crecimiento y supervivencia en ninguna de las cuatro poblaciones de *P. pseudostrobus* migradas altitudinalmente hacia arriba. De reforestarse exitosamente el borde inferior de la RBMM (actualmente amenazada por la acelerada expansión de la frontera agrícola; ver Fig. 1 del Capítulo I), con germoplasma de *P. pseudostrobus*, se podría mantener una barrera de árboles sanos que desaliente la expansión de la frontera agrícola hacia el interior de la Reserva

de la Biósfera. Otros casos donde se demuestran la viabilidad de la migración asistida son los llevados a cabo usando 140 poblaciones de *Pinus contorta* (O'Neill *et al.* 2008), 264 de *Pseudotsuga menziesii* así como 129 de *Picea glauca* y *P. engelmannii* (O'Neill *et al.* 2014), todas provenientes de Canadá y Estados Unidos de América, pero establecidos en sitios localizados principalmente en el interior de la provincia canadiense de Columbia Británica en un ensayo a gran escala denominado AMAT - *Assisted Migration Adaptation Trial* (Marris 2009). Recientemente Silcock *et al.* (2019) documentó más de 1000 casos de migraciones asistidas que involucran 376 taxa en Australia, los cuales abarcan prácticamente todos los estados y territorios australianos, concentrándose en regiones con un alto número de especies amenazadas que incluyen desde pastos hasta árboles.

Aunque la migración asistida ha sido criticada al considerar el reemplazo de algunas especies de la composición natural de las comunidades vegetales (Mueller y Hellmann 2008) e ignorar las interacciones bióticas (Bucharova 2017), esta debe ser considerada en los futuros programas de manejo y reforestación que se lleven a cabo en México, especialmente para el caso de las coníferas, puesto que son especies susceptibles al calentamiento global (Sáenz-Romero *et al.* 2019). De no incluirse, las posibilidades genéticas y ecológicas de adaptación eventualmente se agotarán y la selección climática (Mátyás *et al.* 2010) dará lugar a bosques con árboles debilitados y estresados que serán más susceptibles al ataque de insectos (Netherer *et al.* 2015, Hammond *et al.* 2019), especialmente después de que ocurre un año seco como se muestra en el Capítulo III. En este contexto, es de esperarse que la inacción conduzca a la muerte masiva de las poblaciones de coníferas que ocurren en la FVTM, muy probablemente comenzando en el *límite xérico* de cada especie.

Conclusión general

Nuestros resultados sugieren que la pérdida de hábitat climático para *Pinus hartwegii*, *Abies religiosa*, *P. pseudostrobus*, *P. devoniana* y *P. oocarpa*, que se distribuyen a lo largo de un gradiente altitudinal en la región conocida como Faja Volcánica Transmexicana (FVTM), podría ser de hasta 77% de la superficie actual. Esta pérdida se dará ya que su hábitat ocurrirá en elevaciones entre 300 y 500 m más altas, afectando principalmente a las poblaciones localizadas en el límite inferior de la distribución altitudinal de cada especie (*límite xérico*). Para seguir su hábitat climático, estas especies tendrían que migrar sus poblaciones altitudinalmente hacia arriba a una velocidad de 55-73 m/década, lo cual es mucho más rápido que la velocidad de migración natural observada. Por tanto, se requiere de la intervención humana para reacoplar dichas poblaciones mediante la migración asistida. Un ensayo de lo anterior resultó ser viable en el caso de cuatro poblaciones de *P. pseudostrobus* plantadas a mayores elevaciones en el borde inferior de la Reserva de la Biosfera de la Mariposa Monarca, donde las poblaciones de *A. religiosas* están en proceso de declinación. La migración de *P. pseudostrobus* que se realice en el presente puede representar el beneficio adicional de desalentar el cambio de uso de bosque a producción de agrícola (papa), frenando la expansión agrícola hacia el interior de la Reserva de la Biósfera al mantener una barrera de árboles saludables adaptados al clima del futuro.

Los resultados hasta aquí encontrados sugieren que de no incluirse la migración asistida en los programas de manejo y reforestación que se lleven a cabo en México, las poblaciones forestales, principalmente las del *límite xérico*, quedaran sometidas a un estrés fisiológico por condiciones más secas y calientes que gradualmente las debilitará y hará más susceptibles al ataque de plagas que, al contar con árboles debilitados, afectarán una mayor superficie a nivel nacional. En este contexto, es probable que las medidas tradicionales de conservación *in situ* sean insuficientes, equivalentes a la inacción y, por lo tanto, no podrán mantener la composición actual y la provisión de los servicios ecosistémicos de los bosques.

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