Is there potential in elevational assisted migration for the endangered *Magnolia vovidesii*?

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ABSTRACT

Faced with global climate change, biodiversity management and conservation strategies must consider both the current and potential distribution of tree species in response to rising temperatures. Assisted migration is a climate change mitigation strategy to overcome the uncoupling between species populations and the climate. However, limited field information exists regarding the responses of tree species to such movement along elevation gradients. We analysed the performance of *Magnolia vovidesii* saplings planted along an elevation gradient (1250–2517 m a.s.l.) in Mexico. This is a native cloud forest tree species that is endangered throughout its restricted distribution. Saplings were planted in nine forest sites, one site at the same elevation as the *M. vovidesii* population seed source, five sites at higher elevation and with lower temperatures, testing the potential for assisted population migration, as well as three sites at lower elevation in order to mimic the effects of increased temperature. In each site, 30 saplings were planted under the forest canopy and their survival and relative growth rate in height (RGR_h) recorded over three years. Sapling survival ranged from 53 % to 97 % and survival increased with elevation, followed by a decrease at the two highest elevations studied. RGR_h also increased with elevation, followed by a decrease at the highest sites. Saplings displayed higher RGR_h at intermediate levels of canopy cover. Our results indicate that the transfer of *M. vovidesii* saplings up to ~2300 m a.s.l, which is 600 m above the elevation limit of its current reported distribution, has potential as a conservation strategy to mitigate climate change effects.

1. Introduction

Due to deforestation and over-extraction, several tree species undergo population bottlenecks and are subjected to local extinction risk (Lande, 1993; Millet, Tran, Vien Ngoc, Tran Thi, & Prat, 2013; Oostermeijer, Luijten, & Den Nijs, 2003). Rivers, Shaw, Beech, and Jones (2015) estimated that approximately 9600 tree species are threatened with extinction worldwide. In addition to forest loss and degradation, recent studies indicate that the persistence of many tropical tree species is under high risk due to increasing temperatures associated with global climate change, particularly in tropical montane forests (Feeley, Hurtado, Saatchi, Silman, & Clark, 2013). Tropical Montane Cloud Forests (TMCF) are under extreme threat because of deforestation, fragmentation, illegal selective logging and climate change (Feeley et al., 2013; Scatena, Bruijnzeel, Bubb, & Das, 2010; Toledo-Aceves, Meave, González-Espinosa, & Ramírez-Marcial, 2011). These forests develop in areas frequently covered in clouds or mist and, due to these particular climatic conditions, they are frequently isolated and restricted in area (Scatena et al., 2010; Vázquez-Garcia, 1995). As a

consequence of climate change, suitable climate areas for TMCF have been predicted to decline by 68 % by 2080 in Mexico, threatening the persistence of endemic species (Ponce-Reyes et al., 2012). The negative impacts of climate change could be exacerbated by current environmental land use changes (Rojas-Soto, Sosa, & Ornelas, 2012). In the latest evaluation, 60 % of TMCF tree species in Mexico are reported to be under some category of threat according to the IUCN criteria (González-Espinosa et al., 2011). The development of strategies to promote the management and conservation of TMCF tree species considering the effects of climate change is therefore urgently required (Rojas-Soto et al., 2012; Vargas-Rodriguez, Platt, Vázquez-García, & Boquin, 2010).

In view of the scenarios for TMCF, conservation efforts should consider potential shifts in the distribution of tree species; recent evaluations report upward migration of tree species to higher elevations and range retractions for many TMCF species associated with increasing temperatures (Duque, Stevenson, & Feeley, 2015; Feeley et al., 2011, 2013; Rehm, 2014). Thus, biodiversity management and conservation strategies for TMCF must consider the current as well as potential

distribution of tree species to higher elevations (Feeley et al., 2013; Lutz, Powell, & Silman, 2013) or to disjunct sites of high habitat suitability at higher latitudes, but unreachable by the tree species within the scope of a few decades, due to intrinsic dispersal limitations (Shalisko, Vázquez-García, Villalobos-Arámbula, & Muñiz-Castro, 2018). Given the potential for increased climatic mismatch between the locations in which species are naturally found and their 'ideal' environments, mitigation measures for climate change include the assisted migration of tree species to higher latitudes or elevations (Hoegh-Guldberg et al., 2008; Seddon, 2010; Thomas, 2011). However, there is insufficient information about the response of tropical tree species to translocation to higher elevations (Castellanos-Acuña, Lindig-Cisneros, & Sáenz-Romero, 2015; García-Hernández, Toledo-Aceves, López-Barrera, Sosa, & Paz, 2019). Since tree regeneration is a critical phase in tree population dynamics, increased understanding of the requirements for early establishment of vulnerable tree species is necessary to improve the outcomes of such interventions.

While there are concerns about assisted migration outside the historic distribution of species in terms of the potential risks to the recipient flora, this approach is considered a necessary response to anthropogenic impacts in some cases (Seddon, 2010). Most TMCF tree species are at high risk from climate change because they have reduced distributions, often occupy climatic conditions that are projected to disappear within the current range of the species, and migration routes in TMCF landscapes have become increasingly inaccessible due to human activities acting as barriers (Lutz et al., 2013; Ponce-Reyes et al., 2012). As a result of these conditions, endemic TMCF species are among the best potential targets for assisted migration. This is the case of *Magnolia vovidesii* A. Vázquez, Domínguez-Yescas & L. Carvajal, a tree species of very restricted distribution and small populations, as is the case for the majority of species of the genus *Magnolia* worldwide; 131 of the 245 taxa described in the family Magnoliaceae are threatened with extinction in the wild according to the IUCN Red List categories and criteria (critically endangered, endangered and vulnerable) (Cicuzza, Newton, & Oldfield, 2007). *Magnolia vovidesii* is confined to around three relict populations in TMCF areas in Veracruz, Mexico (Rivers, Beech, Murphy, & Oldfield, 2016; Vázquez-García et al., 2013). A 54–76 % reduction of the current TMCF area is estimated by 2050, according to predictions modelled under A2 and B2 climate change scenarios for eastern and southern Mexico (Rojas-Soto et al., 2012). Moreover, in central Veracruz, TMCF fragmentation is severe and with a continuous decline in the area and quality of its habitat through conversion to pasturelands, coffee plantations and human settlements (CONABIO, 2010). As a result of habitat destruction, *M. vovidessi* is reported as endangered according to the IUCN criteria (Rivers et al., 2016).

Evaluation of *M. vovidesii* sapling performance along an elevation gradient, including sites outside its reported distribution, could serve to determine the potential of assisted migration to contribute to conservation efforts of this species and to assess its likely response to the increased temperature trends projected by global warming model studies. If a climatic optimum exists for a population, growth and survival can be expected to decrease with deterioration of the climate from this optimum in either direction (Rehfeldt et al., 2003). Factors that affect plant performance change along gradients of elevation. Some, such as temperature, vary in strong association with elevation, but other factors, such as moisture or soil nutrients, are not generally elevation specific (Körner, 2007). However, there is limited information regarding the effect of variation in the microenvironment on tree sapling performance along gradients of elevation (García-Hernández et al., 2019; Rehm & Feeley, 2013, 2015; Song et al., 2016). In this study, we experimentally address the following questions: What is the probability of successful early establishment of *M. vovidesii* along an elevation gradient beyond its known distribution? What is the influence of microenvironmental variation on the survival and growth rates of *M. vovidesii* saplings?

2. Methods

2.1. Species

Magnolia vovidesii (Magnoliaceae) is a deciduous tree with gigantic leaves, and is $15 - 25$ m in height and $0.05 - 0.09$ m in diameter at breast height (dbh; at height 1.3 m). The trees flower when they are 7–10 years old (Vázquez-García et al., 2013). Until recently, *Magnolia vovidesii* was described and segregated from *M. dealbata* Zucc. and the majority of studies addressing or citing *M. dealbata* correspond to *M. vovidesii*. *Magnolia vovidesii* distribution is restricted to three locations in the centre of Veracruz, Mexico within an elevation range of between 1600 and 1700 m a.s.l. (Vázquez-García et al., 2013). However, a lower boundary ($1400 - 1500$ m a.s.l.) is supported for *M. vovidesii* based on records from Xico and Ixhuacán de los Reyes, Veracruz; R. Ortega O. & G. Pattison V083077 (XAL) and L. Gutiérrez-Carvajal XAL0114618 (XAL). Sánchez-Velásquez and Pineda-López del R (2006) estimated a density of 300 individuals (> 1.3 m height) per hectare in a grassland and 1,137 individuals per hectare in a secondary cloud forest, with a population size structure of inverse J type in Ixhuacán de los Reyes, Veracruz, Mexico. The main threats to the populations of this species include habitat destruction and unplanned timber harvesting (Cicuzza et al., 2007). *Magnolia vovidesii* is used for fence posts, rural construction, firewood, the flowers and bark are used for traditional medicine, and as an ornamental (Gutierrez & Vovides, 1997). Cytotoxic, antimicrobial and antifungal properties have been recently described for *M. dealbata* (Alonso-Castro et al., 2014; Ramírez-Reyes et al., 2015; Tiwari, Roy, & Tiwari, 2015) and the material used in some studies stems from the localities in which *M. vovidesii* was recently described.

For the purposes of the field experiment, seeds from each of 10 *M. vovidesii* individuals were collected (dbh > 7 cm). Fruits were collected in October 2013 in Coyopolan, Ixhuacán de los Reyes, Veracruz, Mexico (19° 22′ 05.33″ N and 97° 04′ 35.71″ W; 1626 m a.s.l.). Seeds were sown within five days after collection and displayed high germination (final germination $= 90.8 \pm 1.1$ %; mean time to germination $= 39.4$ days; Toledo-Aceves, 2017). Seedlings were transplanted into polythene bags (30×16 cm) with a mixture of forest soil and fine gravel (tepezil) (3:1) in a nursery under 30 % shade mesh and with watering twice a week at the Instituto de Ecología A.C., Xalapa, Veracruz, until transplantation in the field.

2.2. Study area

The field experiment was carried out along an elevation gradient from 1250 to 2517 m a.s.l., in central Veracruz, Mexico (Fig. 1). The historic mean annual temperature from 1420 to 3280 m a.s.l. in the studied elevation gradient ranges from $16 - 18$ to $8 - 10$ °C, and mean annual precipitation ranges between 1800 and 2000 mm (Vidriales-Chan, García-Coll, Martínez, Gerez, & Muñiz-Castro, 2012). Nine forest sites were selected. Each site had a forest fragment area > 1 ha, absence of cattle grazing inside the forest for at least five years, $\leq 40°$ slope and owners willing to participate in the long-term project (Table 1). Site 4 was at a similar elevation to the *M. vovidesii* population seed source, while the three lowest sites were below, and the five highest sites were above. The three sites of highest elevation were located above the TMCF in the region and corresponded to forests currently dominated by conifers. Based on the sampling described in the following section, the dominant tree species at each site were as follows: Site 1: *Eryobotria japonica* (exotic), *Syzygium jambos* (exotic), *Cinnamomum effusum*, Site 2: *Myrsine coriacea*, *Liquidambar styraciflua*, *Trema micrantha*, Site 3: *Quercus lancifolia*, *Q. xalapensis*, *Clethra macrophylla*, Site 4: *L. styraciflua*, *Hedyosmum mexicanum*, *C. macrophylla*, Site 5: *L. styraciflua*, *H. mexicanum*, Site 6: *L. styraciflua*, *C. macrophylla*, Site 7: *Cupressus* sp., *Miconia* sp., Site 8: *Pinus* sp., *Weinmannia pinnata*, Site 9: *Q. corrugata*, *Pinus patula*, *P. ayacahuite*, *W. pinnata*. *Magnolia vovidesii* is present at none of the study sites and it was not possible to include the site where
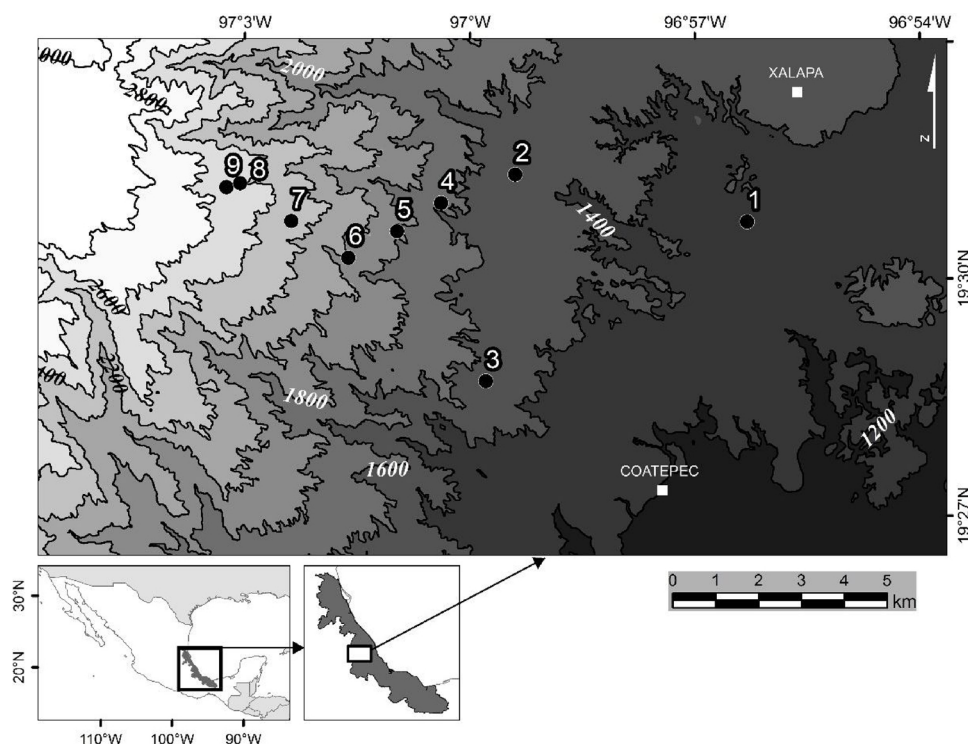
Fig. 1. Location of forest sites along an elevation gradient (1250–2517 m a.s.l.) in Veracruz, Mexico.

the seeds were collected due to the lack of disposition of the landowners in this case.

2.3. Field experimental design

One plot (50 × 50 m) was established in each forest site. To assess forest structure and tree composition, one transect (50 × 10 m) was delimited along the middle of the plot and the diameter at 1.3 m height (dbh) of all trees > 5 cm dbh was measured. The forest structure characteristics are shown in Table 1. To characterize the microclimate, a sensor was placed in the canopy of one tree (above human reach to reduce risk of theft) located in the centre of each plot in order to record air temperature (iButton Thermochron). Volumetric soil water content was quantified with a soil moisture probe (10HS soil moisture sensor) and data-logger (HOBO, Onset Computer Corporation, USA) buried at soil depth $20-30$ cm in the centre of each plot. Soil water content was recorded only during the first year after planting (2015–2016) and air humidity was recorded only during the second year (2016–2017), due to technical issues with various ibuttons and data loggers in the following year. To characterise the soil, soil samples were collected from $0-10$ cm depth (where the greatest concentration of nutrients occurs, in particular those of the most limiting nutrients for plants, such as phosphorus; Jobbágy & Jackson, 2001). Six samples were collected around each plot and mixed into one compound sample for laboratory analysis. The soil samples were stored at 4 °C for less than a week before the following laboratory analysis: pH, soil bulk density, total Carbon (C), Nitrogen (N) and Phosphorus (P). Total C (Ct) and N (Nt) were determined with the Dumas method (CHN analyser, model 2400, Perkin Elmer ®), total P (Pt) was determined with perchloric acid: nitric acid digestion (1:2), and the P content was determined by the vanadomolybdate method with a spectrophotometer (Spectronic 21d, Milton Roy ®) (Table 1 and Appendix A).

In each forest plot, 30 saplings (18-month-old) were planted (270 saplings in total) ~5 m apart, at the beginning of the rainy season (June) in 2015. Sapling height was 19.81 ± 0.60 cm (mean ± S.E.) at planting time. The planting holes were excavated to approximately 20

cm in depth. To reduce competition with grass and herbaceous vegetation, manual weeding within a 1 m radius around the plants was carried out prior to planting and after 3, 6 and 12 months. Sapling survival of all plants was recorded at 2, 4, 6, 8, 12, 18, 24 and 36 months after planting. Sapling height was measured immediately after planting and at 12, 24 and 36 months. Relative growth rates in height were calculated as follows: $RGR_h = (\ln H_2 - \ln H_1) / t_2 - t_1$, where H is plant height; t is time, and the initial and final measurements are denoted by subscripts 1 and 2 respectively (Hunt, 1982).

Since one of the most influential factors in the early establishment of trees in tropical humid forests is the availability of light (Whitmore, 1996), 10 saplings were selected at random in each plot to measure the canopy cover, as a surrogate for solar radiation reaching the sapling. Canopy cover was measured with hemispherical photographs above each of the 10 saplings selected per site for growth measurements one year after transplanting. The camera (Canon Eos rebel XSi) with a fisheye lens was located at 1.3 m from the ground with a tripod, levelled and orientated northwards. Photographs were analysed with the program Gap Light Analyzer (Version 2.0.).

2.4. Statistical analysis

To estimate sapling survival rates, we used the Kaplan–Meier survival test at 2, 4, 6, 8, 10, 12, 18, 24 and 36 months after planting in the nine different elevations (Crawley, 2002). The shape of the curves for the cumulative proportion of sapling death over time was compared between elevations with a survival function using the log-rank statistic and pairwise comparisons (Kaplan Meier procedure). A generalized linear model was fitted with the logit link function (binomial family) to evaluate the effect of elevation on sapling survival at 36 months. The quadratic term was included to fit the responses of the saplings to elevation.

To evaluate the influence of environmental variables on sapling growth rates (RGR_h), a general linear model was fitted, considering saplings as the experimental units (Cottingham, Lennon, & Brown, 2005). Correlations were calculated between elevation and

Table 1
Characteristics of nine forest sites along an elevation gradient in Veracruz, Mexico. Mean ± 1 SE. Temp. mean = mean temperature, Temp. min. = minimum temperature, Temp. max. = maximum temperature.

Site	Elevation (m a.s.l.)	Basal area (m²/ha)	Maximum tree height (m)	Canopy cover (%)	Temp. mean (°C)	Temp. min. (°C)	Temp. max. (°C)	Air humidity (%)	Soil humidity (mm³/mm³)	Soil total C (%)	Soil total N (%)	Soil total P (%)
1	1250	17.4	12.2 ± 1.39	95.44 ± 0.56	17.75 ± 0.06	7.0	33.6	87.69 ± 0.44	0.28 ± 5.9 e-04	5.8	0.66	0.03
2	1526	31.6	21.60 ± 1.44	95.01 ± 0.74	16.37 ± 0.05	2.5	31.6	89.97 ± 0.41	0.36 ± 5.9 e-04	9.81	0.95	0.05
3	1573	7.7	23.20 ± 1.83	86.88 ± 0.95	17.07 ± 0.04	4.0	33.0	85.02 ± 0.53	0.34 ± 7.7 e-04	16.90	1.33	0.07
4	1680	45.2	26.60 ± 0.87	96.44 ± 0.57	15.61 ± 0.04	2.5	31.5	91.28 ± 0.39	0.31 ± 5.8 e-04	13.24	1.17	0.07
5	1853	14.8	25.20 ± 0.66	95.47 ± 0.95	15.09 ± 0.05	4	27.5	88.88 ± 0.69	0.33 ± 3.9 e-04	16.34	1.14	0.03
6	1995	16.5	25.40 ± 1.03	95.96 ± 0.47	14.38 ± 0.05	2.0	31.5	85.18 ± 0.54	0.42 ± 2.8 e-04	18.63	1.10	0.02
7	2290	15.2	13.80 ± 0.74	94.71 ± 1.24	12.74 ± 0.05	−1.5	28.5	86.72 ± 0.72	0.23 ± 1.1 e-03	22.44	1.91	0.05
8	2498	16.0	19.00 ± 2.63	87.75 ± 2.34	11.07 ± 0.05	−2.0	28.5	89.12 ± 0.45	0.32 ± 2.6 e-04	27.57	2.38	0.05
9	2517	43.6	24.78 ± 1.35	93.14 ± 2.37	10.67 ± 0.04	−2.0	27.5	90.31 ± 0.43	0.25 ± 7.1 e-04	18.06	1.36	0.03

temperature, canopy cover and soil nutrients. Humidity was not included due to incomplete data. Temperature was excluded from the model because it was correlated with elevation (see results). Soil Ct and Nt were correlated with elevation and soil Pt was not correlated with elevation (see results). No significant correlation was found between elevation and canopy cover. For the initial complete model, elevation, canopy cover and soil Pt were included as covariables. The contribution of each covariable was assessed by deleting variables from the full model one at a time and comparing the depleted models with the full model using a test based on the Akaike Information Criterion (AIC). The quadratic term (elevation^2) was included for RGR_h based on the AIC. The best model was selected based on a low AIC (Appendix B). Initially, the interaction between elevation and canopy cover was included but, due to the low contribution to the explained variance and in order to reduce the complexity of the model, this interaction was excluded. Statistical analyses were carried out in R (R Development Core Team, 2019).

3. Results

3.1. Microenvironment along the elevation gradient

Mean temperature decreased with increasing elevation (r = -0.992, $P < 0.001$) and, during the first and third years, temperatures below zero were recorded in the three sites of highest elevation (Table 1). During the first year, mean air humidity was > 85 % all along the gradient and mean soil water content in the sites ranged between 0.25 and 0.42 % (Table 1). Mean canopy cover was also high in all sites, ranging from 86.88 to 96.44 % (Table 1). Soil Ct and Nt increased with increasing elevation (r = 0.859, P = 0.003, and r = 0.778, P = 0.014, respectively), while soil Pt was not correlated with elevation ($P > 0.05$) and presented wide variation among sites (Table 1).

3.2. Sapling performance along the elevation gradient

After three years, sapling survival varied along the gradient from 55.17 to 96.67 %. The shape of the curves differed among elevation sites (Log-Rank = 146.44, $d.f.$ = 8, $P < 0.001$) and an overall trend was observed in which saplings died faster in the two sites at higher elevation than at the lower elevations (Fig. 2; Appendix C). Probability of sapling survival at 36 months was affected by elevation; survival increased with elevation up to the site at 2290 m a.s.l., then decreased at the two highest elevations evaluated in this study (Intercept: *Coefficient* = -0.0571, t = -1.163, P = 0.246; Elevation: *Coefficient* = 0.0018, t = 3.429, P = 0.001; Elevation^2: *Coefficient* = -5.288e-07, t = -3.913, $P < 0.001$).

Three years after transplanting, mean sapling height was 74.19 ± 3.61 cm and the tallest individual reached 278 cm. RGR_h was affected by elevation, displaying a trend in which an initial increase at intermediate elevation was followed by a decrease at the highest site (Table 2; Fig. 3). Canopy cover had a negative effect on RGR_h. Soil Pt had no effect on RGR_h and was therefore excluded from the model based on the AIC.

4. Discussion

The use of transfer distances has been the subject of previous study (e.g. Castellanos-Acuña et al., 2015; Rehfeldt, Ying, Spittlehouse, & Hamilton, 1999), but its application in restoration and conservation practices is incipient, especially in tropical forests. Overall, the assessment of *M. vovidesii* sapling performance along the studied elevation gradient proved to be informative for estimating the effects of varying temperature on tree survival and growth and for developing conservation guidelines intended to overcome the poor establishment of planted trees. The higher probability of successful early establishment of *M. vovidesii* at intermediate elevation, including in sites above the
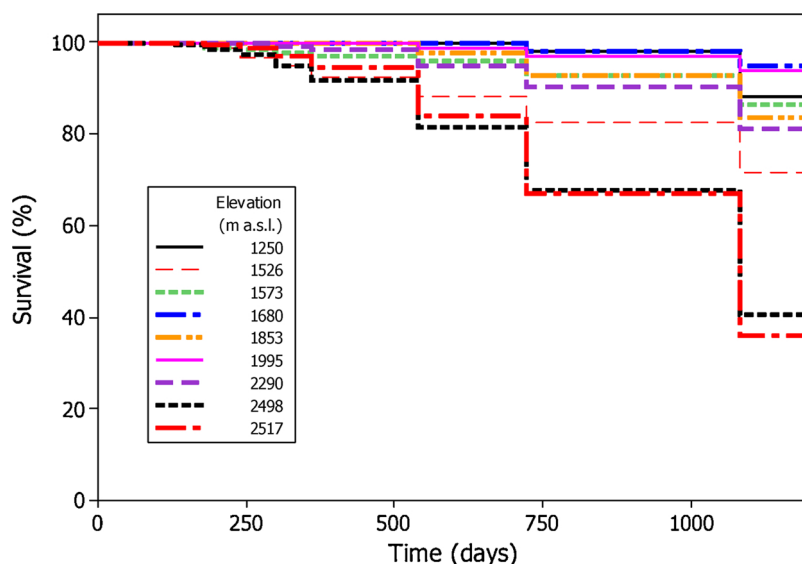
Fig. 2. Survival of *Magnolia vovidesii* saplings over a period of 36 months after planting along an elevation gradient (1250–2517 m a.s.l.) in Veracruz, Mexico. 95 % confidence intervals were excluded for clarity.

Table 2

General linear model parameters for the effects of elevation and canopy cover on the relative growth rate in height (RGR$_h$) of *Magnolia vovidesii* saplings. Coefficient ± SE, *t*-student (*t*) and *P* = probability of rejecting null hypothesis. N = 90, Error degrees of freedom = 83 (due to 3 missing data). RGR$_h$ (F = 15.86, $DF = 83$, $P < 0.001$).

RGR$_h$

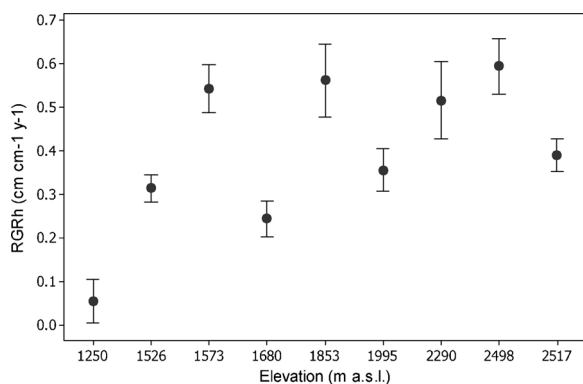|	*Coefficient*	*t*	*P*
Intercept	$-3.753\text{e-}02 \pm 4.949\text{e-}02$	-0.758	0.450
Elevation	$1.890\text{e-}04 \pm 4.612\text{e-}05$	4.097	< 0.001
Canopy	$-1.292\text{e-}03 \pm 3.450\text{e-}04$	-3.744	< 0.001
Elevation^2	$-4.435\text{e-}08 \pm 1.193\text{-}08$	-3.716	< 0.001

Fig. 3. Relative growth rate in height (RGR$_h$; mean ± S.E.; n: 10) of *Magnolia vovidesii* saplings planted under the forest canopy along an elevation gradient (1250–2517 m a.s.l.) in Veracruz, Mexico.

known distribution of this species, indicates that it could benefit from assisted migration to sites at higher elevation. Due to the lack of information of the realized and fundamental niche of *M. vovidesii*, as well as probable differences in its current and historical distribution, it is not possible to determine whether the results could be due to a present relictual distribution of a once more widely distributed species. According to scenarios for TMCF in Mexico (Ponce-Reyes et al., 2012; Rojas-Soto et al., 2012), it is possible that the known distribution of *M. vovidesii* already presents a mismatch with the climatic optimal distribution of this species as a result of rising temperatures associated

with climate change. According to ecological niche models under A2 and B2 climate change scenarios, an upward migration of TMCF to a higher elevation of ca. 200 m from the currently known 1600 m a.s.l. is predicted by the year 2050 in the studied region (Rojas-Soto et al., 2012). Given that survival above 2400 m a.s.l. presented an important decline, based on our results, moving *M. vovidesii* up to ~ 600 m above its known upper limit of distribution could be a conservation strategy that remains within the acclimation limits of the species. The freezing temperatures registered in the highest sites could be associated with survival decrease, while other factors that influence sapling performance could include the incidence of herbivory and pathogens, although these were not measured. Our results concur with the findings of Castellanos-Acuña et al. (2015) for three Mexican pine species, in which significant decrease in growth occurred when the transfer was greater than $400 - 650$ m of upward elevation shift, a much wider range in comparison to the ± 100 m maximum transfer distance recommended for *Pinus oocarpa* (Sáenz-Romero, Guzmán-Reyna, & Rehfeldt, 2006).

Previous transplantation field experiments have reported a growth decline in tree seedlings and adults at higher elevation that is associated with colder temperatures (Castellanos-Acuña et al., 2015; Leites, Robinson, Rehfeldt, Marshall, & Crookston, 2012), while other studies have found lower growth rates associated with increased temperatures in adult trees of tropical species (Brienen et al., 2015; Feeley, Wright, Supardi, Kassim, & Davies, 2007) and in cloud forest tree seedlings (García-Hernández et al., 2019). The reduced growth rates we found at lower sites could be the result of the increase in respiration that occurs at higher temperature (Slot & Winter, 2018). The high levels of air humidity recorded at the study sites (> 85 %) could have limited the ability of the seedlings to transpire at the lower sites. While plants can transpire to dissipate heat at higher temperature, the efficacy of transpiration is reduced by decreases in the leaf-atmosphere vapour pressure gradients at high relative humidity (Perez & Feeley, 2018). *Magnolia vovidesii* saplings displayed higher growth rates at intermediate elevation, probably due to the shorter transfer distance and higher similarity in the climatic conditions to the population seed source, while lower RGR$_h$ occurred at the lowest and at the highest elevation forest sites. The slower RGR$_h$ at the two highest sites could have been caused by the lower rates of carbon assimilation that occur at lower temperatures (Moser et al., 2011) and/or due to a lower availability of nutrients not measured at the higher elevations (Vázquez-García & Givnish, 1998), while the slower RGR$_h$ at the lowest elevation suggests

that the plants might have been stressed by the higher temperature at these sites.

Despite the heterogeneity among forest sites due to past management history, location and topography, overall elevation and canopy openness had strong influence on sapling performance while soil Pt did not contribute to explaining the variation found in the growth of *M. vovidesii* saplings. The high survival we found under the high canopy cover, and high growth rates recorded, concur with the proposed classification of this species as intermediate shade tolerant (Sánchez-Velásquez & Pineda-López del R, 2010; Toledo-Aceves, López-Barrera, & Vázquez-Reyes, 2017). The lower RGR_h with increasing canopy cover was probably due to the high canopy cover present at all of the forest sites (> 86 %) because low light availability in the forest understory can limit tree sapling growth (Valladares, Laanisto, Niinemets, & Zavala, 2016). Previous studies have reported lower survival and growth of *M. vovidesii* seedlings (previously treated as *M. dealbata*) planted in an open pastureland compared to saplings under the canopy of plantations of *Pinus maximinoi* and *Liquidambar macrophylla* (Ramírez-Bamonde, Sánchez-Velásquez, & Andrade-Torres, 2005); however, this is the first study to report *M. vovidesii* performance under the high canopy cover of TMCF and some conifer forests. In a meta-analysis, Zhu, Lu, and Zhang (2014) report an important increase in the regeneration density of shade tolerant species in gaps compared to under closed forest canopy, while Montgomery and Chazdon (2002) also report that shade tolerant species can benefit from the increased light in secondary forest and plantations under low light availability (0.2–6.2 % of full light). Overall, our results support the notion that intermediate levels of canopy cover could favour *M. vovidesii* sapling survival and could provide an environment in which this species could establish (with the aid of weeding) in locations beyond its known elevation range. Tree attributes can also change during ontogeny, for example some trees can change from being very shade tolerant at the seedling stage to having much faster growth when older (Poorter, Bongers, Sterck, & Wöll, 2005), in which case their demands for other resources such as soil nutrients could increase. Long-term evaluations are therefore recommended.

Our results show that the use of 18-month-old saplings and initial competition control represented an effective technique that allows circumvention of the most vulnerable phase of the seedlings before transplanting. This is promising given that early seedling establishment represents a bottleneck in tree population dynamics (Swaine, 1996). Despite the reduced population size of *M. vovidesii* and the limited number of tree seed sources used in this experiment, we found adequate sapling performance during the first three years after planting. The germination and seedling growth under controlled conditions, found in preliminary studies carried out with the same seeds as were used for this experiment, were also high and there was no evidence of poor performance (Toledo-Aceves, 2017; Toledo-Aceves et al., 2017). Assessment of within- and between-population genetic variability and its influence on seedling establishment under varied conditions is also recommended. Seed source selection for restoration plans is more important under climate change since it must account for current and future climate conditions (Richardson et al., 2014). Given the differential distribution patterns among related taxa; for example, in the three different sections of Neotropical Magnolia (*Macrophylla*, *Magnolia* and *Talauma*), which display different latitudinal and elevational spans, degrees of diversification, and are distributed in areas with varied social contexts, species-specific studies would be required in order to provide appropriate recommendations with which to target conservation alternatives (Vázquez-García et al., 2016).

In order to ascertain the feasibility of assisted migration to establish viable populations, long-term monitoring of introduced populations is also necessary to determine not only survival success but also the probability of reaching reproductive maturity, as well as whether individuals will be capable of producing the next generation. Interactions such as herbivory, pollination and dispersal require further investigation because, even if seedling establishment were successful via assisted migration, we still require information regarding the interactions of these saplings with associated biota. There is some debate concerning the benefits of assisted migration, such as its contribution to reducing the risk of species extinction, as well as the possible disadvantages, such as the possibility of invasion by translocated species and the lack of evidence about the effects of biotic interactions (Bucharova, 2017; Hewitt et al., 2011; McLachlan, Hellmann, & Schwartz, 2007). Nevertheless, evaluation of assisted migration of threatened tree species in the field is necessary in order to improve our understanding of the probability of success associated with this strategy.

Finally, although this study does not reflect on the cultural and socioeconomic contexts in which *M. vovidesi* is found, it should be emphasized that the loss of habitat and reduction of TMCF tree species populations in Mexico is the result of multiple factors, including agricultural expansion, illegal logging and a lack of information and programs to support sustainable management of the TMCF (CONABIO, 2010; González-Espinosa et al., 2011; Ortiz-Colín, Toledo-Aceves, López-Barrera, & Gerez-Fernández, 2017). Thus, assessment of the main drivers of change and initiatives that include multiple approaches are required, including the modification of policies that indirectly promote land use change, environmental education, promotion of local participation in biodiversity conservation and strengthening of conservation through sustainable use. These options are by no means easily implemented, but they are urgently required (Newton, 2008; Toledo-Aceves et al., 2011).

5. Conclusions

Our work supports the transplantation of *M. vovidesii* saplings to elevations equal to and higher than that of the population seed source as a viable conservation strategy to assist the early establishment of this endangered species throughout a heterogeneous forest matrix. Our results suggest that saplings of *M. vovidesii* could be transferred up to ~ 600 m higher than the reported current upper distribution limit of the species, as this range seems to be within its acclimation limits. Along the gradient of elevation studied, planting *M. vovidesii* saplings under intermediate levels of forest canopy could favour their performance. While longer term evaluations are recommended, this assessment of sapling establishment in response to different climatic conditions associated with an elevation gradient served to evaluate the potential of assisted migration in climate change mitigation efforts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Soil characteristics of nine forest sites along an elevation gradient in Veracruz, Mexico

Site	Elevation (m a.s.l.)	pH	Soil density (g /cm^2)	Silt (%)	Lime (%)	Sand (%)	C/N	P-Bray	Ca	Mg
1	1250	4.53	0.90	64.30	24.70	10.92	8.79	55.18	0.79	0.27
2	1526	4.66	0.82	32.30	28.70	38.92	10.33	94.47	6.67	1.94
3	1573	4.17	0.43	18.30	26.70	54.92	12.71	98.75	7.10	2.33
4	1680	5.44	0.47	18.30	22.72	58.92	11.32	98.25	11.40	2.22
5	1853	4.47	0.60	19.80	30.00	50.20	14.35	20.58	0.23	0.14
6	1995	4.24	0.32	23.80	32.00	44.20	16.88	17.86	0.53	0.41
7	2290	4.20	0.38	23.80	36.00	40.20	11.75	20.68	2.70	0.39
8	2498	3.60	0.42	21.80	30.00	48.20	11.60	73.01	3.73	0.46
9	2517	4.36	0.41	23.80	32.00	44.20	13.24	16.12	4.32	0.73

Litter characteristics of nine forest sites along an elevation gradient in Veracruz, Mexico.

Site	Elevation (m a.s.l.)	N (%)	C (%)	C/N (%)	P mg/Kg
1	1250	1.11	12.41	11.18	160.99
2	1526	1.45	16.22	11.19	255.68
3	1573	1.74	26.62	15.30	243.06
4	1680	1.62	19.44	12.00	268.31
5	1853	1.98	24.64	12.45	131.61
6	1995	1.24	21.83	17.61	65.48
7	2290	2.76	30.59	11.08	141.53
8	2498	2.72	31.53	11.59	118.37
9	2517	2.45	27.85	11.36	131.61

Appendix B. Models fitted to assess the effects of environmental variables on relative growth rate in height (RGR$_h$) of *Magnolia vovidesii*. R^2 indicates the explained variance for each model, AIC = Akaike Information Criterion, Df = degrees of freedom

Model	R^2	AIC	Df
RGR$_h$ = Intercept + Elevation + Canopy cover + Phosphorus Mean + Elevation:Canopy cover + Elevation^2	0.4176	− 463.49	81
RGR$_h$ = Intercept + Elevation + Canopy cover + Elevation:Canopy cover + Elevation^2	0.4176	− 465.49	82
RGR$_h$ = Intercept + Elevation + Canopy cover + Elevation^2	0.3644	− 459.88	83
RGR$_h$ = Intercept + Elevation + Canopy cover	0.2586	− 448.49	84

Appendix C. Pairwise comparisons (Log Rank, Mantel-Cox) of survival curves of *Magnolia vovidesii* saplings between elevations. Significant differences ($P < 0.05$) are shown in bold

Elevation (m a.s.l.)	1526 χ^2	1526 P	1573 χ^2	1573 P	1680 χ^2	1680 P	1853 χ^2	1853 P	1995 χ^2	1995 P	2290 χ^2	2290 P	2498 χ^2	2498 P	2517 χ^2	2517 P
1250	12.96	**< 0.001**	1.98	0.16	0.692	0.405	1.41	0.24	0.147	0.701	3.46	0.06	38.28	**< 0.001**	36.6	**< 0.001**
1526			5.62	**0.02**	17.11	**< 0.001**	6.83	**0.01**	14.84	**< 0.001**	3.85	0.05	8.814	**0.003**	7.326	**0.007**
1573					4.503	**0.034**	0.06	0.81	3.033	0.082	0.21	0.65	26.35	**< 0.001**	24.35	**< 0.001**
1680							3.72	0.05	0.202	0.653	6.46	**0.01**	43.17	**< 0.001**	41.58	**< 0.001**
1853									2.345	0.126	0.5	0.48	28.95	**< 0.001**	27.08	**< 0.001**
1995											4.73	**0.03**	40.35	**< 0.001**	38.65	**< 0.001**
2290													23.25	**< 0.001**	21.35	**< 0.001**
2498															0.093	0.76

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