Assisted migration and the rare endemic plant species: The case of two endangered Mexican spruces

Eduardo Mendoza-Maya [1], Erika Gómez-Pineda [2], Cuauhtémoc Sáenz-Romero [3], José Ciro Hernández-Díaz [4], Carlos A. López-Sánchez [5], J. Jesús Vargas-Hernández [6], José Ángel Prieto-Ruíz [7], Christian Wehenkel [Corresp. 4]

[1] Programa Institucional de Doctorado en Ciencias Agropecuarias y Forestales, Universidad Juárez del Estado de Durango, Durango, Durango, Mexico

[2] Centro de Investigaciones en Geografía Ambiental, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

[3] Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, Mexico

[4] Instituto de Silvicultura e Industria de la Madera, Universidad Juárez del Estado de Durango, Durango, Durango, Mexico

[5] SMartForest Group, Department of Biology of Organisms and Systems, Mieres Polytechnic School, Universidad de Oviedo, Mieres, Spain

[6] Postgrado en Ciencias Forestales, Colegio de Postgraduados, Montecillo, Texcoco, Edo. de México, Mexico

[7] Facultad de Ciencias Forestales y Ambientales, Universidad Juárez del Estado de Durango, Durango, Durango, Mexico

Corresponding Author: Christian Wehenkel
Email address: wehenkel@ujed.mx

Background: In the projected climate change scenarios, assisted migration might play an important role in the conservation of the threatened plant species, by translocate them to similar suitable habitats outside their native distributions. However, it is unclear if such habitats will be available for the Rare Endemic Plant Species (REPS), because of their very restricted habitats. The aims of this study were to perform a population size assessment for the REPS *Picea martinezii* Patterson and *Picea mexicana* Martínez, and to evaluate the potential species distributions and their possibilities for assisted migration inside Mexico and worldwide.

Methods: We performed demographic censuses, field surveys in search for new stands, and developed distribution models for Last Glacial Maximum (22,000 years ago), Middle Holocene (6,000 years ago), current (1961-1990) and future (2050 and 2070) periods, for the whole Mexican territory (considering climatic, soil, geologic and topographic variables) and for all global land areas (based only on climate).

Results: Our censuses showed populations of 89,266 and 39,059 individuals for *P. martinezii* and *P. mexicana*, respectively, including known populations and new stands. Projections for Mexico indicated somewhat larger suitable areas in the past, now restricted to the known populations and new stands, where they will disappear by 2050 in a pessimistic climatic scenario, and scarce marginal areas ($p = 0.5$-0.79) remaining only for *P. martinezii* by 2070. Worldwide projections (based only on climate variables) revealed few marginal areas in 2050 only in Mexico for *P. martinezii*, and several large areas ($p \geq 0.5$) for *P. mexicana* around the world (all outside Mexico), especially on The Himalayas in India and the Chungyang mountains in Taiwan with highly suitable ($p \geq 0.8$) climate habitats in current and future (2050) conditions. However, those suitable areas are currently inhabited by other endemic spruces: *Picea smithiana* (Wall.) Boiss and *Picea morrisonicola* Hayata, respectively.

Conclusions: Assisted migration would only be an option for *P. martinezii* on scarce marginal sites in Mexico, and the possibilities for *P. mexicana* would be continental and transcontinental translocations. This rises two possible issues for future *ex situ* conservation programs: the first is related to whether or not consider assisted migration to marginal sites which do not cover the main habitat requirements for the species; the second is related to which species (the local or the foreign) should be prioritized for

conservation when suitable habitat is found elsewhere but is inhabited by other endemic species. This highlights the necessity to discuss new policies, guidelines and mechanisms of international cooperation to deal with the expected high species extinction rates, linked to projected climate change.

Assisted migration and the rare endemic plant species: The case of two endangered Mexican spruces

Eduardo Mendoza-Maya[1], Erika Gómez-Pineda[2], Cuauhtémoc Sáenz-Romero[3], José Ciro Hernández-Díaz[4], Carlos A. López-Sánchez[5], J. Jesús Vargas-Hernández[6], José Ángel Prieto-Ruíz[7], Christian Wehenkel[4]*

[1] Programa Institucional de Doctorado en Ciencias Agropecuarias y Forestales, Universidad Juárez del Estado de Durango, Durango, Durango, Mexico

[2] Centro de Investigaciones en Geografía Ambiental, Universidad Nacional Autónoma de México (UNAM), Morelia, Michoacán, Mexico

[3] Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, Mexico

[4] Instituto de Silvicultura e Industria de la Madera, Universidad Juárez del Estado de Durango, Durango, Durango, México

[5] SMartForest Group, Department of Biology of Organisms and Systems, Mieres Polytechnic School, University of Oviedo, Mieres, Spain

[6] Postgrado en Ciencias Forestales, Colegio de Postgraduados, Montecillo, Texcoco, Edo. de México, Mexico

[7] Facultad de Ciencias Forestales y Ambientales, Universidad Juárez del Estado de Durango, Durango, Durango, Mexico

*Corresponding author:
Christian Wehenkel[4]
Blvd. Del Guadiana 501. Cd. Universitaria, Durango, Durango, 34120, Mexico
Email address: wehenkel@ujed.mx

Abstract

Background: In the projected climate change scenarios, assisted migration might play an important role in the conservation of the threatened plant species, by translocate them to similar suitable habitats outside their native distributions. However, it is unclear if such habitats will be available for the Rare Endemic Plant Species (REPS), because of their very restricted habitats. The aims of this study were to perform a population size assessment for the REPS *Picea martinezii* Patterson and *Picea mexicana* Martínez, and to evaluate the potential species distributions and their possibilities for assisted migration inside Mexico and worldwide.

Methods: We performed demographic censuses, field surveys in search for new stands, and developed distribution models for Last Glacial Maximum (22,000 years ago), Middle Holocene (6,000 years ago), current (1961-1990) and future (2050 and 2070) periods, for the whole Mexican territory (considering climatic, soil, geologic and topographic variables) and for all global land areas (based only on climate).

Results: Our censuses showed populations of 89,266 and 39,059 individuals for *P. martinezii* and *P. mexicana*, respectively, including known populations and new stands. Projections for Mexico indicated somewhat larger suitable areas in the past, now restricted to the known populations and new stands, where they will disappear by 2050 in a pessimistic climatic scenario, and scarce marginal areas ($p = 0.5$-0.79) remaining only for *P. martinezii* by 2070. Worldwide projections (based only on climate variables) revealed few marginal areas in 2050 only in Mexico for *P. martinezii*, and several large areas ($p \geq 0.5$) for *P. mexicana* around the world (all outside Mexico), especially on The Himalayas in India and the Chungyang mountains in Taiwan with highly suitable ($p \geq 0.8$) climate habitats in current and future (2050) conditions. However, those suitable areas are currently inhabited by other endemic spruces: *Picea smithiana* (Wall.) Boiss and *Picea morrisonicola* Hayata, respectively.

Conclusions: Assisted migration would only be an option for *P. martinezii* on scarce marginal sites in Mexico, and the possibilities for *P. mexicana* would be continental and transcontinental translocations. This rises two possible issues for future *ex situ* conservation programs: the first is related to whether or not consider assisted migration to marginal sites which do not cover the main habitat requirements for the species; the second is related to which species (the local or the foreign) should be prioritized for conservation when suitable habitat is found elsewhere but is inhabited by other endemic species. This highlights the necessity to discuss new policies, guidelines and mechanisms of international cooperation to deal with the expected high species extinction rates, linked to projected climate change.

Key words: conservation of threatened species, climate change, narrow endemics, paleodistributions, *Picea martinezii*, *Picea mexicana*, species distribution modelling.

1. Introduction

78   To know the species distributions is fundamental for their conservation. Certainly, understanding
79   the species' niche requirements and habitat specificity is essential to define the possibilities for
80   management in the context of climate change. As linked ecological properties, niche
81   requirements and habitat specificity influence geographical ranges of taxa (Crain et al., 2015)
82   and ultimately, it determines commonness, endemism and rarity. This last ecological property,
83   shared by 36.5 % of the global plant diversity (Enquist et al., 2019), needs special attention
84   because involves taxa with strong influence on ecosystem services (Mouillot et al., 2013) and
85   high vulnerability to extinction (Işik, 2011).
86   Assisted migration is an *ex situ* conservation approach that emerged as a response to the
87   imminent decoupling between climate and species in natural reserves (Peters & Darling, 1985).
88   Pedlar et al. (2012) distinguished two types: forestry assisted migration, the objective of which is
89   to maintain forest health and productivity, and species rescue assisted migration, whose goal is to
90   avoid extinctions of threatened species.
91   Rescue assisted migration, the approach considered in this study (hereafter named only assisted
92   migration), has been recognized as a viable method to conserve vulnerable species, by
93   translocating them to similar suitable habitats outside their native ranges, where they can
94   reproduce and compete successfully (McLane & Aitken, 2012). However, this adaptation
95   strategy continues to be debated, pointing to the potential risk that translocated species could
96   become invasive or could serve as vectors of new pests and diseases (Schwartz et al., 2012;
97   Simler et al., 2019; Butt et al., 2021).
98   Additionally, if assisted migration becomes a regular conservation strategy, some questions
99   remain unanswered regarding the Rare Endemic Plant Species (REPS): (i) is it possible to find
100   potential habitats outside the natural range of REPS, considering their high habitat specificity?;
101   (ii) if new suitable environments are found, is the area large enough to establish populations of a
102   minimum viable size, able to survive in the long-term?; and (iii) furthermore, what can be done if
103   a new suitable habitat is found elsewhere, but is already occupied by other REPS? We do not
104   have the answers to these questions, mainly because field studies of assisted migration with
105   REPS are scarce (Butt et al., 2021).
106   Species Distribution Modelling (SDM), based on empirical associations between species
107   occurrences and environmental variables, has become an important tool to understand current
108   species distributions and for designing management and conservation strategies (López-Tirado &
109   Hidalgo, 2016; Bosso et al., 2017; Ongaro et al., 2018; Sofaer et al., 2019), including assisted
110   migration (McLane & Aitken, 2012). Regarding the rare species, SDM has been improved by a
111   variety of algorithms and methodologies for model construction, in addition to the incorporation
112   of environmental factors with different scales of influence on species distributions (e.g. Pearson
113   et al., 2007; Williams et al., 2009; Patsiou et al., 2014; McCune, 2016; Mi et al., 2017; Feng et
114   al., 2022).
115   Previous studies have proposed systematic decision-making guides for assisted migration (Pérez
116   et al., 2012), have evaluated the need and potential for assisted migration in different taxa
117   through the SDM approach (Hällfors et al., 2016) and have used SDM to delimit current

118 distributions of rare species at local or regional scales (e.g. McCune, 2016), or to evaluate future
119 impacts of climate change, mainly by using climatic variables (Ledig et al., 2010; Pinedo-
120 Alvarez et al., 2019). Nevertheless, studies on the potential value of assisted migration for REPS,
121 considering the most complete sets of environmental variables of recognized influence on
122 species distributions (e.g. Penteriani et al., 2019; Barrio-Anta et al., 2020; López-Sánchez et al.,
123 2021), or global habitat searches using climatic variables, are scarce.
124 In this study we explore the potential of assisted migration as a tool for the conservation of two
125 Mexican REPS (both at the category of endangered; IUCN, 2021): *Picea martinezii* Patterson
126 and *Picea mexicana* Martínez. These species are relicts of the last glacial age, confined to very
127 specific habitats, with scattered, fragmented and few isolated populations (Ledig et al., 2000a).
128 In addition to other threats distinctive of the rare endemic species (Işik, 2011; Cogoni et al.,
129 2019), such as their low genetic diversity (Ledig et al., 2000b; Ledig, Hodgskiss & Jacob-
130 Cervantes, 2002) and decreased reproductive fitness (Flores-López, López-Upton & Vargas-
131 Hernández, 2005; Flores-López et al., 2012), these spruces are threatened by climate change, as
132 indicated by projected alterations in temperature and rain regimes on Mexican temperate forests
133 (Sáenz-Romero et al., 2010), particularly in sites where these species thrive (Ledig et al., 2010),
134 which could increase tree mortality through hotter-drought events (Hammond et al., 2022).
135 Since the discovery of *P. mexicana* (Martínez, 1961) and *P. martinezii* (Müller-Using & Alanis
136 1984; Patterson, 1988), a total of seven populations had been roughly documented, but the
137 population sizes, the exact extent and spatial distribution of these populations remain relatively
138 unknown, and exploration to discover new stands had not been completed. Both spruces
139 represent proper models for testing the viability of assisted migration in the conservation of rare
140 species with restricted habitat.
141 We focused our study on three aspects of these REPS: (i) the exploration of potential new stands
142 and performance of a population size assessment as a starting point for future demographic
143 evaluations; (ii) construction of models describing the potential past and current distributions of
144 these species; and (iii) identification of areas outside their current ranges (inside Mexico and
145 worldwide) with a high probability of harboring suitable habitats for future assisted migration, by
146 modelling future distributions. Our hypothesis is that the suitable climatic habitat of *P. martinezii*
147 and *P. mexicana* can be found elsewhere outside their current ranges and hence, assisted
148 migration is a viable tool for the *ex situ* conservation of both species, considering future
149 projections of climatic change.
150

2. Materials & Methods

151

152 **2.1 Study area, exploration of new stands and species distribution data**
153 The study area is located in the Sierra Madre Oriental (SMOr) and Sierra Madre Occidental
154 (SMOc), two parallel mountain ranges that cross northern Mexico from north to south; SMOr
155 alongside the Gulf of Mexico, SMOc alongside the Pacific Ocean. Both mountain ranges are
156 connected east-west by the Trans-Mexican Neovolcanic Axis (TMNVA) in central Mexico (Fig.

157 1). *Picea martinezii* is only located in the northern SMOr, in four populations: El Butano, Agua
158 de Alardín, Agua Fría and La Encantada, state of Nuevo León (Table 1, Fig. 1). These
159 populations are generally found on north-facing slopes, near creeks, ravines or cliffs in the
160 montane cloud forests at elevations ranging from 1,800 to 2,500 m, (Ledig et al., 2000a). There
161 are only three documented populations of *Picea mexicana* on the north-facing slopes of the
162 highest peaks of the northern SMOc (one single population: El Mohinora, state of Chihuahua)
163 and on SMOr (two populations: La Marta and El Coahuilón, state of Coahuila), in the conifer
164 forests of the subalpine zones in elevations ranging from 3,000 to 3,600 m (Table 1, Fig. 1)
165 (Ledig et al., 2000a). Detailed descriptions of the Mexican montane cloud and subalpine forest
166 vegetation types are provided by Rzedowski (2006).
167
168 >> Table 1 <<
169
170 The distribution models were based on presence/absence data. In order to explore the potential
171 existence of new stands and get more presence records for SDM, high-elevation, moist, cold,
172 north exposure sites were surveyed in the surroundings of the known populations (at distances of
173 up to 39 km). The potential sites were identified from maps of suitable climatic habitat for *P.*
174 *martinezii* and *P. mexicana*, projected under contemporary climate (average 1961-1990)
175 provided by Ledig et al. (2010), as well as from unconfirmed oral testimonies given by local
176 foresters and landowners; this allowed us to get 46 to 50 presence records of *P. martinezii* and *P.*
177 *mexicana*, respectively (Table 1, Supplemental Tables 1, 2 and 3). All these presences were
178 recorded in the center and periphery of the known populations and new stands, during the
179 population size assessments that considered all individuals taller than 30 cm (including
180 recruitment, saplings and trees), which were carried out as part of this study in 2018 and 2019
181 (Table 1). Absences records (22,004 to 32,571) were sampled from the sites listed in the
182 Mexican National Forest and Soil Inventory (MexFI), developed by the Mexican National Forest
183 Commission (CONAFOR, 2009) (Supplemental Table 3). Model projections for mapping the
184 distribution of suitable areas for both tree species were performed for the whole Mexican
185 territory and for all the world land areas (excluding Antarctica).
186
187 >> Figure 1 << 2-column fitting image
188
189 **2.2 Environmental variables and species distribution modelling**
190 Forty two environmental variables of different classes: climate, topography, soil and geology
191 (e.g. succesfully used by Penteriani et al., 2019; Barrio-Anta et al., 2020; López-Sánchez et al.,
192 2021) were considered possible predictors of the distribution of *P. martinezii* and *P. mexicana*.
193 Gridded data of 19 climatic variables (1961-1990 reference period) were retrieved at 30 arc-
194 second resolution from WorldClim dataset (Hijmans et al., 2005, available at URL:
195 https://worldclim.org); data of 14 soil variables were obtained from the SoilGrids250m at
196 250x250 m resolution (available at URL: https://www.soilgrids.org), a repository of the spatial

197   distribution of soil properties across the globe (Hengl et al., 2017); and data on two geological
198   (30 arc-second resolution) and seven topographic variables (250x250 m resolution) were
199   obtained from digital models provided by the Mexican National Institute of Statistics, Geography
200   and Informatics (INEGI) (available at URL: http://www.inegi.mx) (Supplemental Table 4).
201   Presences records were interleaved with each raster layer of the analyzed environmental
202   variables, which were resampled at 30 arc-second cell resolution with the nearest neighbor
203   method; then, mean values of the environmental variables were extracted from pixels holding the
204   presence records.
205   The varying methodologies for SDM may influence the final model metrics and projections, and
206   the need to evaluate such methods in this kind of projects has previously been recommended (e.g.
207   Pearson et al., 2006; Qiao, Soberón and Peterson, 2015). Regarding the rare species with narrow
208   distributions, some methods have shown better results (Mi et al., 2017). Distribution models for
209   *P. martinezii* and *P. mexicana* were constructed with the non-parametric regression Random Forest
210   (RF) algorithm including cross validation, based on its higher performance than other methods
211   (including MaxEnt) to predict the rare species distributions (Mi et al., 2017), and following a
212   similar methodology as Penteriani et al. (2019), Castaño-Santamaría et al. (2019), and Barrio-Anta
213   et al. (2020). In brief, RF constructs a set of regression and classification trees using different
214   independent variables randomly selected from the complete data set (Breiman 2001; Deschamps
215   et al. 2012). To include only the main predictors shaping the species distributions (Hall 1999),
216   collinearity between variables was evaluated before model construction. This was performed with
217   the open source WEKA software (Hall et al. 2009), using the wrapper methodology (Zhiwei and
218   Xinghua 2010) which selects the best ranked variables through the Variable Importance Measure
219   (VIM) function (see Section 3.2 and Table 2 for the list of selected variables included in final
220   models). Variables of different scales were normalized following the methodology of Castaño-
221   Santamaría et al. (2019) to make them comparable, and VIM values were expressed adding up to
222   a unitary value (normalized importance). Spatially continuous maps were generated by applying
223   the final models to environmental spatial variables resampled to a 30 arc-second resolution.
224   We used the k-fold cross validation approach (k-fold = 10) to test the precision (repeated 10
225   times) of the RF classifier on unseen data. This was done by dividing the data set into k subsets
226   and using one subset as the test set and the other k-1 subsets as the training set, each time the
227   model was applied. The accuracy of the model predictions was evaluated with the confusion
228   matrix that shows the four-way classification of a sampled point. From this last evaluation, we
229   calculated the following model metrics, widely used in SDM studies (Freeman and Moisen 2008;
230   Penteriani et al. 2019): (i) the Area Under the Receiver Operating Characteristic Curve (AUC);
231   (ii) the Overall Accuracy (OA); (iii) Matthews Correlation Coefficient (MCC); (iv) the True
232   Skill Statistic (TSS), (v) Cohen's Kappa, (vi) Sensitivity; and (vii) Specificity.
233   To map the species distributions, thresholds for the probability of presence ($PoP_{threshold}$) were
234   selected for each species by combining two approaches: (i) the method that minimizes the
235   difference between the absolute values of sensitivity and specificity (Jiménez-Valverde & Lobo,
236   2007); and (ii) the method that requires an appropriate fixed specificity (Freeman & Moisen,

237 2008), in this case, that based on proper probability values around the thresholds obtained with
238 the first approach (see Section 3.2 and Supplemental Table 5). The last approach mentioned has
239 been recommended particularly for rare species when it is important to include all possible
240 populations in planning. Both approaches for threshold selection were based on the evaluation of
241 models constructed for current conditions for Mexico (section 2.3) and the real species
242 presences/absences (Supplemental Table 5). The final $PoP_{threshold}$ values were used to map the
243 two species distributions in all projections in the hyperspace.
244
245 **2.3 Past, contemporary and future distributions: projections for Mexico**
246 The fitted models were projected onto spatial projections of the most important environmental
247 variables (Table 2) at a 30 arc-second resolution, for the current conditions (1961-1990 reference
248 period) to estimate the contemporary potential distributions of these species. Additionally, the
249 following projections were performed using the Community Atmospheric Model scenario
250 version 4 (CCSM4): 1) to the paleoclimate data of the Last Glacial Maximum (LGM, ~22,000
251 thousand years ago = 22 ka) and the Middle Holocene (MH, ~ 6 ka); and 2) to the future periods
252 centered on years 2050 and 2070 under two different Representative Concentration Pathways
253 (RCPs) (IPCC, 2013): a moderate scenario (RCP 4.5), which assumes a total radiative forcing
254 stabilized at 4.5 Wm^{-2} by 2100; and, a pessimistic scenario (RCP 8.5) which considers a higher
255 radiative forcing of 8.5 Wm^{-2} by 2100. Data sets for current climatic conditions were obtained
256 from WorldClim version 1.4 (Hijmans et al., 2005, available at URL:
257 http://www.worldclim.com) and data of the CCSM4 from the National Center for Atmospheric
258 Research (available at URL: https://www.cesm.ucar.edu/models/ccsm4.0/). The equivalence in
259 surface area considered for each projected pixel of suitable habitat was 0.7 km^2 for latitudes
260 corresponding to the Mexican territory (between 15° to 31° LN).
261
262 **2.4 Contemporary and future distributions: global projections**
263 We also estimated the potential contemporary (1961-1990 reference period) and future (period
264 centered in 2050) distributions of the suitable climate habitats at a global scale, following the
265 previously described methodology for model construction (Section 2.2), but considering only the
266 19 climatic variables available in WorldClim (Supplemental Table 4 and Table 2). The resolution
267 of the climatic data was 30 arc-second, which is the highest uniform resolution available for the
268 entire world. Projections to the future period were performed using the CCSM4. We intended
269 global cautionary projections for the two studied tree species, by considering the most
270 pessimistic climatic scenario (RCP8.5) in an intermediate future period. All distributions maps
271 were created in QGIS v.3.16.1 (QGIS Development Team, 2020).
272

273 **3. Results**

3.1 Demographic census, area extent and exploration of new populations

The population size assessments showed 89,266 *P. martinezii* individuals (including recruitment, saplings and trees) distributed in a total area of 157.4 ha, and 39,059 *P. mexicana* individuals in a total area of 173.1 ha (Table 1). The largest *P. martinezii* population was Agua de Alardín with 84,498 individuals covering an area of 74.3 ha, and the smallest was La Encantada with 712 individuals and 5.2 ha. The largest population of *P. mexicana* was La Marta, with 17,728 individuals covering an area of 41.6 ha; the smallest was El Coahuilón, with 2,253 individuals scattered in an area of 49 ha (Table 1).

On the other hand, seven new (previously unreported) stands were discovered and explored, with numbers of individuals per stand ranging from 12 to 6,300 and areas between 0.1 and 24 ha. All new stands were located close to (0.5 to 5.0 km) and at similar elevations as the previously known populations in both the Sierra Madre Oriental (SMOr) and Sierra Madre Occidental (SMOc) (Table 1).

3.2 Species distribution modelling and model assessment

The RF normalized importance scores selected three variables as the most important predictors for *P. martinezii*, and eight variables for *P. mexicana* in the models for Mexico (Table 2). In the global models, the RF importance analysis selected six and seven climatic variables for *P. martinezii* and *P. mexicana*, respectively (Table 2).

>> Table 2<<

According to the model metrics AUC, OA, MCC, TSS, Kappa, Sensitivity and Specificity with values ≥ 0.9, the *t* goodness-of-fit were highly accurate (Supplemental Table 3). The PoP$_{threshold}$ values for *P. martinezii* and *P. mexicana* were 0.73 and 0.83, respectively, based on the sensitivity-specificity balance approach. With a probability value of 0.8 or more, the correct presence prediction was 100 % for *P. martinezii* and more than 55 % for *P. mexicana* (Supplemental Table 5). Hence, based on the fixed specificity approach, all the performed projections in the hyperspace considered a PoP$_{threshold}$ of 0.8 to denote the presence (above this value) or absence (under the value) of the highly suitable habitat. However, to show the area holding less suitable habitat, a minimum probability of presence of 0.5 was considered too. Finally, two categories of presence were used for displaying the results: 0.5 - 0.79 = intermediate and 0.8 - 1.0 = high.

3.3 Mapping suitable habitat: projections for Mexico and the World

Projections of suitable habitat during the Last Glacial Maximum (LGM) and the Middle Holocene (MH) indicate overall a very small and fragmented distribution for both species. In particular for *P. martinezii*, it was projected only 15.4 km^2 (probability ≥ 0.5) during the LGM, and 12.6 km^2 (none of them with $p ≥ 0.8$) for the MH (Fig. 2); all those pixels were found highly scattered, mainly at the Trans-Mexican Neovolcanic Axis (Central Mexico) and at the Sierra

314 Madre Oriental, close to the contemporary distribution (near the border of Nuevo León and
315 Tamaulipas states) (Fig. 3A and B). *Picea mexicana* had a maximum of 423.5 km² of suitable
316 habitat ($p \geq 0.5$) during the LGM (Fig. 2), mostly at the Trans-Mexican Neovolcanic Axis, with
317 an important area at northwest of Veracruz state, Sierra Madre Oriental (Fig. 3C, panels a, b, c),
318 an area where the species is completely absent today. It is interesting to notice that suitable
319 habitat of *P. mexicana* was absent at the Sierra Madre Occidental during the LGM (Fig. 3C), and
320 then was present during the MH (Fig. 3D, panels a-d), around the place where the contemporary
321 population of El Mohinora is located (Fig. 3D, panel c).
322 Contemporary projections (reference period 1961-1990) of highly suitable habitat distribution
323 predicted perfectly all the actual populations for both species (Fig. 4A and 4B, panels a, b),
324 which represent an area of 4.9 km² for *P. martinezii* and 13.3 km² for *P. mexicana* (Fig. 2).
325 Besides, the predicted highly suitable areas outside the current distribution were totally absent
326 for both species. For *P. martinezii*, there were very few scattered isolated pixels (all with
327 probability 0.5 to 0.79) at northwest of Chihuahua state (Fig. 4A, panel c), along the TMNVA
328 (Fig. 4A, panels d, e, f), and at the Sierra Madre del Sur (states of Guerrero, Oaxaca and Chiapas;
329 Fig. 4A, panels g, h, i). For *P. mexicana*, there were even less regions with predicted pixels
330 outside its natural distribution in the SMOc and SMOr (all of them with probabilities 0.5 to 0.79;
331 Fig. 4B, panels c, d).
332
333 >> Figure 2<< single-column fitting image
334
335 >> Figure 3 << 2-column fitting image
336
337 >> Figure 4 << 2-column fitting image
338
339 Projections of suitable habitat to the future within Mexico, under climatic change scenarios,
340 indicate a severe reduction for both species' habitats (Figs. 2 and 5). Suitable habitat ($p \geq 0.5$)
341 predicted for *P. martinezii* drops from a total of 15.4 km² at present, to only 7.0 and 2.8 km² for
342 2050, scenarios RCP 4.5 and 8.5, respectively. For year 2070, the drop is even further, to have
343 just 3.5 and 2.1 km² for scenarios RCP 4.5 and 8.5, respectively (Fig. 2). And still worse: by
344 2050, the highly suitable habitat ($p \geq 0.8$) disappears completely at and nearby all the current
345 contemporary *P. martinezii* populations (Fig. 5A). For *P. mexicana*, projections show an even
346 worse situation, with 0.7 km² (a single pixel) for year 2050 RCP 8.5 and 1.4 km² for year 2070
347 RCP 4.5; there is not a single pixel predicted for 2070 RCP 8.5 inside Mexico (Figs. 2 and 5C,
348 D).
349
350 >> Figure 5 << 2-column fitting image
351

352 Worldwide projections for *P. martinezii*, show similar and extremely grim scenarios, either for
353 contemporary climate and for 2050 RCP 8.5: there is not a single pixel available outside Mexico,
354 but some areas in the Mexican territory, few of which will remain in the future (Figs. 2 and 6).
355
356 >> Figure 6 << 2-column fitting image
357
358 Worldwide projections for *P. mexicana* show a quite different and complex picture outside
359 Mexico: a total of about 141,000 pixels appears suitable for contemporary climate, and nearly
360 119,000 pixels for year 2050 RCP 8.5 (Figs. 2 and 7). Thus, despite the drastic contraction or
361 even vanishing of suitable area for *P. mexicana* in Mexico (when modeling considered climate,
362 soil, geology and topography; Fig 5C, D), worldwide projections (considering only climate)
363 indicate that there is and there will be suitable climatic habitat ($p \geq 0.5$) in: Laurentian mountains
364 in Canada, Appalachian Mountains in USA, the Andes in south Chile, the Pyrenees in the Spain-
365 France border, the Alps in the France-Switzerland border, the Caucasus mountains at Georgia-
366 Russia border, Khingan mountains in China, Sayan mountains in the Mongolia-Russia border,
367 The Himalayans in India, Sobaek and Taebaek mountains in South Korea, Taebaek mountains in
368 North Korea, the Japanese Alps in Japan, Chungyang mountains in Taiwan, and the Southern
369 Alps in New Zealand (Fig. 7). For the projected year 2050 RCP 8.5, a large proportion of those
370 suitable areas under contemporary climate will remain for *P. mexicana* in all regions, except in
371 Mexico, the Appalachian Mountains in USA and the Pyrenees in the Spain-France border (Figs.
372 2 and 7B). Outside Mexico, the highly suitable habitat ($p \geq 0.8$) for *P. mexicana* is currently
373 available only in The Himalayans in India (Fig. 7A, panel j) and the Chungyang mountains in
374 Taiwan (Fig. 7A, panel l), where 10 pixels (about 6.4 km^2; Fig. 7B, panel g) and 25 pixels (about
375 18.0 km^2; Fig. 7B, panel i), respectively, will remain by 2050.
376
377 >> Figure 7 << 2-column fitting image
378

4. Discussion

4.1 Demographic census, area extent and exploration of new populations
380 The results of the first complete population size assessments, as well as better knowledge of
381 population areas and delimitations, provide the basis for the monitoring and management of the
382 two studied species, and therefore, are important for conservationists, local communities,
383 stakeholders and governmental institutions. The seven new natural stands located by field
384 surveys, showed that these species thrive only on very specific habitats at similar elevations than
385 the previously known populations, both in the Sierra Madre Oriental and Sierra Madre
386 Occidental. These new stands may be portions of the nearest known populations, as suggested by
387 their proximity of 0.5 to 5.0 km to each other. Therefore, the total number of populations can be
388 considered as previously reported for these spruce species: four populations of *P. martinezii* and
389 three populations of *P. mexicana* (Ledig et al., 2000a). However, the new stand located at 5.0 km

391   from La Marta, and holding ~6,300 individuals (La Marta 2; Table 1), could be considered a
392   fourth sub-population of *P. mexicana*, although this hypothesis remains to be confirmed by
393   genetic analysis.
394   The population size assessment of *P. martinezii* (e. g., populations of La Encantada and Agua de
395   Alardín) and *P. mexicana* (e.g., populations of La Marta 3 and La Marta) (Table 1) support the
396   findings of Murray & Lepschi (2004), who reported that rare species could be sparse or abundant
397   in different locations. These dissimilar population sizes and their area extents, allowed us to
398   identify the stands which are more prone to local extinction, given their reduced number of
399   individuals (Table 1). Overall, the total number of individuals of *P. martinezii* and *P. mexicana*,
400   the new reported stands and the total area occupied by both species confirm their status as rare
401   species (Table 1). According to McCune (2016), both species could be classified as extremely
402   rare (i.e. with less than five known populations); according to Rabinowitz (1981) both
403   correspond to rare species that are locally abundant in specific habitats but restricted
404   geographically, or sparse and geographically restricted in specific habitats.
405
406   **4.2 Species niche requirements, distribution modelling and model assessment**
407   The results of predictors selection by RF highlight the importance of not only taking into account
408   climatic variables to construct the distribution models for *P. martinezii* and *P. mexicana* (Table
409   2), thus adding to the previous knowledge of the main factors underlying the distribution of the
410   same species (Ledig et al., 2010). According to Sexton et al. (2009), species distributions depend
411   on many environmental factors, and it is known that while some environmental variables
412   represent large scale processes (macro-environment), others define the micro-environmental
413   conditions (Franklin, 2009). In the present study, the models constructed for Mexico showed that
414   both micro- and macro-environmental variables may be the factors with the greatest influence on
415   species distributions. For *P. martinezii* the most important predictor was the profile curvature
416   (Table 2), which is a proxy of the microenvironment related to groundwater availability. For *P.*
417   *mexicana* the main factor was minimum temperature of coldest month (Table 2), a macro-
418   environmental variable indicating winter severity, and probably related to its adaptation to cold
419   subalpine zones. Similar results to those observed for *P. martinezii* were reported for the rare
420   species *Hesperocyparis forbesii* (Jeps.) Bartel (Tecate cypress), where two proxies of the micro-
421   environment (a topographic and a soil variable) were the most important predictors of the species
422   distribution (Regan et al., 2012). On the other hand, the results obtained for *P. mexicana* were
423   similar to those reported for other widespread forest species, for which similar sets of
424   environmental variables were used and the main drivers of species distributions were found to be
425   climatic variables (Penteriani et al., 2019). However, there were soil and topographic variables
426   among the most important predictors for *P. mexicana*.
427   Regarding the model metrics, some authors have prevented that the AUC tends to increase when
428   the calibration areas are larger and further from presence records (Lobo, Jiménez-Valverde &
429   Real, 2008; Hijmans, 2012), making preferable to consider additional model evaluators like
430   sensitivity, specificity (Lobo, Jiménez-Valverde & Real, 2008), or TSS which accounts for both

431   omission and commission errors and is not influenced by the sample size of each class
432   (Allouche, Tsoar & Kadmon, 2006; Wehenkel et al., 2020). The high values of the seven metrics
433   used to evaluate our regional and global models (including AUC, sensitivity, specificity and
434   TSS; Supplemental Table 3), suggested acceptable model performances. Lower model
435   performances have been reported for different widespread species and similar sets of
436   environmental variables and model metrics (Penteriani et al., 2019; López-Sánchez et al., 2021),
437   or only climate variables and AUC (Dyderski et al., 2018). Nevertheless, similar results (only for
438   AUC) have been obtained for *P. chihuahuana* Martínez (Pinedo-Alvarez et al., 2019), another
439   rare Mexican spruce. The overall better model performance for rare than for widespread species,
440   observed in the comparable metrics, can be explained in part by the reliance on the spatially
441   restricted environmental conditions of the former (McCune, 2016).
442   Regarding the worldwide projections, to our knowledge, this is the first time that a global study
443   of the suitable climate habitat for a plant species has been carried out; but, similar AUC values
444   have been reported by Taucare-Ríos, Bizama & Bustamante (2016) for an animal species.
445   Additionally to their high metrics, the regional models (developed with climate, soil and
446   topographic variables) matched with observations in the field (Fig. 4), while global models
447   (developed with climate variables) almost matched with observations on terrain (Figs. 6 and 7A)
448   and identified highly suitable patches where other endemic spruces and similar tree communities
449   thrive in different biogeographic regions (Lin et al., 2012; Bodare et al., 2013; Panthi et al.,
450   2017) (Fig. 7).
451   Ledig et al. (2010) made habitat projections for the same two spruce species by using only
452   climatic variables and a threshold of presence ≥ 0.5, and marked several sites near the natural
453   populations with high potential to hold *P. martinezii* (e.g. a large area at the northwest of El
454   Butano population, at the Coahuila-Nuevo León states border, Mexico) and *P. mexicana* (e.g.
455   mountains Cerro San Rafael, Cerro Potrero de Ábrego and Cerro El Potosí, all above 3000 m of
456   elevation, in Coahuila and Nuevo León states, Mexico), but where this species does not occur at
457   present. Our models showed that no habitat was available in any site near the current populations
458   of *P. martinezii* using a $PoP_{threshold} \geq 0.5$ (Fig. 4A), as confirmed by field observations. For *P.*
459   *mexicana*, our models coincide with the projections of Ledig et al. (2010), for the sites
460   mentioned before, at a $PoP_{threshold} \geq 0.5$; however, the absences of *P. mexicana* on those
461   mountains confirmed by field surveys were correctly predicted by our models at a $PoP_{threshold} \geq$
462   0.8, which indicate that the more accurate probability of presence of *P. mexicana* is above this
463   threshold.
464
465   **4.3 Mapping suitable habitat: past and contemporary distributions**
466   The reduced and scattered distributions of the highly suitable habitat for both species during the
467   Last Glacial Maximum, the Middle Holocene and at present (Figs. 3 and 4), indicate that these
468   species have had restricted habitat for a long period of time, and have survived in climatic
469   refugia. These refugia appear to have been more widespread in the past for *P. mexicana* than for
470   *P. martinezii*. Apparently, the main refugia in the past for *P. mexicana* was at south and central

471   Mexico (Fig. 3C). From that high elevations and rugged regions, likely *P. mexicana* migrated to
472   its current locations. That is consistent with pollen records which suggest that members of the
473   *Picea* genus reached the north of Chiapas and the south of Veracruz in the Miocene in southern
474   Mexico (Graham, 1976; Rzedowsky, 2006) and the Texcoco lake in central Mexico (bordering
475   with what is today Mexico city) in the Last Glacial Maximum (Lozano-García et al., 1993);
476   although it would be discarded that such *Picea* pollen might belong to *P. martinezii* because of
477   the very scattered marginal areas in the LGM and MH (Fig. 3A and 3B), it cannot be discarded
478   for *P. chihuahuana* (Pinedo-Álvarez et al., 2019).
479
480   **4.4 Potential for future assisted migration: projections for Mexico and worldwide**
481   Future projections of suitable habitat show an extremely grim situation for both species inside
482   Mexico; which could imply the loss of all natural populations (including recruitment, saplings
483   and trees). For *P. martinezii*, there will be available only a few square kilometers of marginal
484   habitat, and none of them near the current populations when considering climate, soil, geologic
485   and topographic variables for modeling (Fig. 5B); however, more areas holding the suitable
486   climatic habitat (considering only climate) will be available near the populations of Agua de
487   Alardín, Agua Fría and La Encantada (Fig. 6, panel c). The reason why more areas appear
488   available inside Mexico, all close to the contemporary populations, is because the global
489   modeling is more inclusive, by considering only climatic variables and excluding the proxies of
490   micro-environment.
491   As for *P. mexicana*, since it is anticipated a complete loss of the highly suitable habitat in
492   Mexico by 2050 (both considering climate, soil, geology and topography, or only climate), it is
493   needed to take into account the possibility of assisted migration outside the Mexican borders,
494   either to the zones holding the marginal (p = 0.5 - 0.79) or the highly suitable habitat ($p \geq 0.8$)
495   (Fig. 7). However, the two zones holding the highly suitable habitat, i.e., Chungyang mountains
496   in Taiwan and the Indian Himalayan region, are inhabited by other two endemic spruce species:
497   *P. morrisonicola* (Bodare et al., 2013) and *Picea smithiana* (Panthi et al., 2017), respectively
498   (Fig. 7B, panels g, i).
499   Based on this, assisted migration would be an option for *P. martinezii* only on marginal sites in
500   Mexico (p = 0.5 - 0.79; Fig. 5B, panels a, b, c; and Fig. 6, panel c). For *P. mexicana*, a possibility
501   would be continental and transcontinental translocations to sites holding the marginal or the
502   highly suitable habitat (Fig. 7B). This rises two conservation issues: the first is related to whether
503   or not perform assisted migration to marginal sites which do not cover the main habitat
504   requirements for the species; the second is related to which species (the local or the foreign)
505   should be prioritized for conservation when suitable habitat is found elsewhere but is inhabited
506   by similar endemic species.
507   We argue that priority for assisted migration should be given to areas with the least potential
508   negative impact on other local spruce species or their close relatives. Such negative implications
509   could be: (i) the unintended introduction of pests and diseases (Simler et al., 2019) or, (ii)
510   introgression through unintended pollen dispersal (Gómez et al., 2015). Therefore, two essential

511   issues should be considered in potential assisted migration projects: (i) a detailed examination of
512   the targeted suitable areas, as well as analyzing the potential impact of physiography and local-
513   scale edaphic variables, as suggested by Wang et al. (2019) for *Spiranthes parksii* Correl and by
514   Wilson, Roberts & Reid (2011) for *Margaritifera margaritifera* (L.); and (ii) the costs and
515   benefits balance of this kind of projects, such as the potential negative effects that introduced
516   species could have over local species.
517   This results give insights of a future biodiversity scenario, where REPS will rely on
518   translocations beyond their native ranges (including across country borders) to subsist in nature,
519   considering the global amount of rare species and their vulnerabilities (Işik, 2011; Enquist et al.
520   2019). Therefore, new mechanisms of international cooperation need to be discussed to deal with
521   this expected crisis triggered by climatic change (Román-Palacios & Wiens, 2020; Brodie et al.,
522   2021; McDonald & McCormack, 2021).
523   In this sense, international bodies such as the International Union for Conservation of Nature, the
524   Convention on Biological Diversity, the Ramsar Convention on Wetlands, the Man and
525   Biosphere Programme, or the United Nations Convention to Combat Desertification, would be
526   valuable institutions in providing recommendations, guidelines, and mechanisms to reduce the
527   loss of biodiversity, weighting the risks involved in potential assisted migration projects across
528   country borders (Schwartz et al., 2012; Brodie et al., 2021). In general, such instruments of
529   conservation should be based on the ecological, ethical and social implications and the cost-
530   benefit balance that species translocations beyond nations' borders would imply (IUCN/SSC,
531   2013), considering the scientific, government and stakeholders support as well as local people
532   acceptance (Pérez et al., 2012).
533   Finally, a parallel strategy of *in situ* conservation should not be discarded as recommended by
534   the Global Strategy for Plant Conservation (available at URL: https://www.cbd.int/gspc/),
535   considering the possibilities for permanence in local microrefugia (Dawson et al., 2011), as
536   reported for other rare plant species (Patsiou et al., 2014). Such *in situ* conservation activities
537   could include the following: (i) protection of natural recruitment against livestock, plagues,
538   illegal logging, and wildfire, (ii) establishment of artificial recruitment with autochthonous
539   genotypes in well-selected sites near (but not within) the respective population, (iii) removal of
540   competing vegetation (including other tree species) in the vicinity of the natural stands, (iv)
541   assisting biotic dispersal vectors, and (v) monitoring the existing *in situ* populations (Wehenkel
542   & Saenz-Romero, 2012).
543
544   **4.5 Potential limitations of the study**
545   Our distribution models included only a set of climate, soil, geologic and topographic
546   environmental factors, with more factors in models for Mexico (42 variables) than for worldwide
547   models (19 climate variables) (Supplemental Table 4). By sampling only abiotic factors, we were
548   not able to search for future suitable areas based on biotic factors like the amount of genetic
549   differentiation among populations, that result in differential degrees of local adaptation (Benito-

550 Garzón, Robson & Hampe, 2019; Zhao et al., 2020) or biotic interactions (Godsoe et al., 2017;
551 Flores-Tolentino et al., 2020), due to the lack of such data for these species.
552 On the other hand, some new stands of the studied spruces occupy areas as small as 0.1 ha (Table
553 1), similar to microrefugia. As detection of such very small suitable areas depends on grid
554 resolution (Franklin et al., 2013; Patsiou et al., 2014), our models could not identify these
555 microhabitats outside the species ranges, with a resolution of 30 arc-seconds ($\approx$ 0.7 km^2 or 70
556 ha). Moreover, SDMs are highly susceptible to produce different results in their geographic
557 projections, and future suitable areas for the species will depend on the used method (Pearson et
558 al., 2006; Qiao, Soberón and Peterson, 2015). Hence, we cannot exclude that there are or will be
559 even better models. However, the findings of potential areas for *P. mexicana* in zones with very
560 similar spruce forest communities in Asia is a good indicator of the quality of these models.
561

562 5. Conclusions

563 Our findings confirm that *Picea martinezii* and *Picea mexicana* are narrow endemics with
564 varying populations sizes, but viable total populations (Table 1), and suggest that the habitats of
565 both tree species were limited since the last glacial age (Figs. 2 and 3). Considering the surface
566 areas holding the highly suitable habitats ($p \geq 0.8$), contemporary conditions appear to be more
567 suitable than conditions during the Last Glacial Maximum and Middle Holocene for *P.*
568 *martinezii*; and vice versa for *P. mexicana* (Fig. 2). Current highly suitable areas will mostly
569 disappear in the near future (Figs. 2 and 5). For *Picea martinezii*, the possibility for future
570 assisted migration in northern and central Mexico is only on marginal sites ($p = 0.5 - 0.79$), all
571 far from its current distribution. Regarding *Picea mexicana*, a complete disappearance of the
572 suitable habitat within Mexico is anticipated; hence, it is needed to discuss the possibility of
573 species translocations beyond the national borders of Mexico, to sites holding the intermediated
574 ($p = 0.5 - 0.79$) or the highly ($p \geq 0.8$) suitable climatic habitat, even considering sites so far
575 away as The Himalayans or Taiwan. In the expected stage where species translocations will
576 become necessary to avoid the high extinction rates because of climate change, new mechanisms
577 of international cooperation need to be discussed. In this sense, institutions similar to the
578 International Union for Conservation of Nature, the Convention on Biological Diversity, the
579 Ramsar Convention on Wetlands, the Man and Biosphere Programme, or the United Nations
580 Convention to Combat Desertification would promote this international collaboration and set
581 guidelines and recommendations in assisted migration projects. Meanwhile, *in situ* conservation
582 should not be discarded, considering marginal microhabitat sites. Future decisions for *ex situ*
583 conservation would be reinforced with data from common garden assays displaying the species'
584 resilience to environmental gradients.
585

586 6. References

587 **Barrio-Anta M, Castedo-Dorado F, Cámara-Obregón A, López-Sánchez CA. 2020.**
588   Predicting current and future suitable habitat and productivity for Atlantic populations of
589   maritime pine (*Pinus pinaster* Aiton) in Spain. *Annals of Forest Science* 77. DOI:
590   10.1007/s13595-020-00941-5.

591 **Allouche O, Tsoar A, Kadmon R. 2006.** Assessing the accuracy of species distribution models:
592   Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43:1223–
593   1232. DOI: 10.1111/j.1365-2664.2006.01214.x.

594 **Benito-Garzón M, Robson TM, Hampe A. 2019.** ΔTraitSDMs: Species distribution models
595   that account for local adaptation and phenotypic plasticity. *New Phytologist* 222:1757–
596   1765. DOI: 10.1111/nph.15716.

597 **Bodare S, Stocks M, Yang JC, Lascoux M. 2013.** Origin and demographic history of the
598   endemic Taiwan spruce (*Picea morrisonicola*). *Ecology and Evolution* 3:3320–3333. DOI:
599   10.1002/ece3.698.

600 **Bosso L, Luchi N, Maresi G, Cristinzio G, Smeraldo S, Russo D. 2017.** Predicting current and
601   future disease outbreaks of *Diplodia sapinea* shoot blight in Italy: species distribution
602   models as a tool for forest management planning. *Forest Ecology and Management*
603   400:655–664. DOI: 10.1016/j.foreco.2017.06.044.

604 **Breiman LEO. 2001.** Random Forests. *Machine Learning* 45:5–32. DOI:
605   10.1023/A:1010933404324.

606 **Brodie JF, Lieberman S, Moehrenschlager A, Redford KH, Rodríguez JP, Schwartz M,**
607   **Seddon PJ, Watson JEM. 2021.** Global policy for assisted colonization of species. *Science*
608   372:456–458. DOI: 10.1126/science.abg0532.

609 **Butt N, Chauvenet ALM, Adams VM, Beger M, Gallagher R V, Shanahan DF, Ward M,**
610   **Watson JEM, Possingham HP. 2021.** Importance of species translocations under rapid
611   climate change. *Conservation Biology* 35:775–783. DOI: 10.1111/cobi.13643.

612 **Castaño-Santamaría J, López-Sánchez CA, Ramón-Obeso J, Barrio-Anta M. 2019.**
613   Modelling and mapping beech forest distribution and site productivity under different
614   climate change scenarios in the Cantabrian Range (North-western Spain). *Forest Ecology*
615   *and Management* 450:117488. DOI: 10.1016/j.foreco.2019.117488.

616 **Cogoni D, Sulis E, Bacchetta G, Fenu G. 2019.** The unpredictable fate of the single population
617   of a threatened narrow endemic Mediterranean plant. *Biodiversity and Conservation*
618   28:1799–1813. DOI: 10.1007/s10531-019-01757-0.

619 **CONAFOR (Comisión Nacional Forestal). 2009.** Inventario Nacional Forestal y de Suelos.
620   *Available at https://www.cnf.gob.mx:8443/snif/portal/infys/temas/resultados-2004-2009*
621   (Accessed 14 November 2019)

622 **Crain BJ, Sánchez-Cuervo AM, White JW, Steinberg SJ. 2015.** Conservation ecology of rare
623   plants within complex local habitat networks. *Oryx* 49:696–703. DOI:
624   10.1017/S0030605313001245.

625 **Deschamps B, McNairn H, Shang J, Jiao X. 2012.** Towards operational radar-only crop type
626   classification: Comparison of a traditional decision tree with a random forest classifier.

627   *Canadian Journal of Remote Sensing* 38:60–68. DOI: 10.5589/m12-012.

628   **Dyderski MK, Paź S, Frelich LE, Jagodziński AM. 2018.** How much does climate change

629   threaten European forest tree species distributions? *Global Change Biology* 24:1150–1163.

630   DOI: 10.1111/gcb.13925.

631   **Enquist BJ, Feng X, Boyle B, Maitner B, Newman EA, Jørgensen PM, Roehrdanz PR,**

632   **Thiers BM, Burger JR, Corlett RT, Couvreur TLP, Dauby G, Donoghue JC, Foden**

633   **W, Lovett JC, Marquet PA, Merow C, Midgley G, Morueta-Holme N, Neves DM,**

634   **Oliveira-Filho AT, Kraft NJB, Park DS, Peet RK, Pillet M, Serra-Diaz JM, Sandel B,**

635   **Schildhauer M, Šímová I, Violle C, Wieringa JJ, Wiser SK, Hannah L, Svenning JC,**

636   **McGill BJ. 2019.** The commonness of rarity: Global and future distribution of rarity across

637   land plants. *Science Advances* 5:1–13. DOI: 10.1126/sciadv.aaz0414.

638   **ESRI. 2018.** Topographic basemap. Scale Not Given. World Topographic Map. Available at

639   http://www.arcgis.com/home/item.html?id=30e5fe3149c34df1ba922e6f5bbf808f (accessed

640   October 21, 2021).

641   **Feng L, Sun J, El-Kassaby YA, Yang X, Tian X, Wang T. 2022.** Predicting potential habitat

642   of a plant species with small populations under climate change: Ostrya rehderiana. *Forests*

643   13:129. DOI: 10.3390/f13010129.

644   **Flores-López C, Geada-López CG, López-Upton CJ, López-Ramírez E. 2012.** Reproductive

645   indicators in natural populations of *Picea martinezii* T. F. Patterson. *Revista Forestal*

646   *Baracoa* 31:49–58.

647   **Flores-López C, López-Upton J, Vargas-Hernández JJ. 2005.** Reproductive indicators in

648   natural populations of *Picea mexicana* Martínez. *Agrociencia* 39:117–126.

649   **Flores-Tolentino M, García-Valdés R, Saénz-Romero C, Ávila-Díaz I, Paz H, Lopez-Toledo**

650   **L. 2020.** Distribution and conservation of species is misestimated if biotic interactions are

651   ignored: the case of the orchid *Laelia speciosa*. *Scientific Reports* 10:1–14. DOI:

652   10.1038/s41598-020-63638-9.

653   **Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L. 2013.**

654   Modeling plant species distributions under future climates: How fine scale do climate

655   projections need to be? *Global Change Biology* 19:473–483. DOI: 10.1111/gcb.12051.

656   **Franklin J. 2009.** *Mapping species distributions: spatial inference and prediction*. Cambridge:

657   Cambridge University Press.

658   **Freeman EA, Moisen GG. 2008.** A comparison of the performance of threshold criteria for

659   binary classification in terms of predicted prevalence and kappa. *Ecological Modelling*

660   217:48–58. DOI: 10.1016/j.ecolmodel.2008.05.015.

661   **GBIF: The Global Biodiversity Information Facility. 2021.** What is GBIF? Available at

662   https://api.gbif.org/v1/ (accessed August 10, 2021).

663   **Godsoe W, Holland NJ, Cosner C, Kendall BE, Brett A, Jankowski J, Holt RD. 2017.**

664   Interspecific interactions and range limits: contrasts among interaction types. *Theoretical*

665   *Ecology* 10:167–179. DOI: 10.1007/s12080-016-0319-7.

666   **Gómez JM, González-Megías A, Lorite J, Abdelaziz M, Perfectti F. 2015.** The silent

667 extinction: climate change and the potential hybridization-mediated extinction of endemic
668 high-mountain plants. *Biodiversity and Conservation* 24:1843–1857. DOI: 10.1007/s10531-
669 015-0909-5.
670 **Graham A. 1976.** Studies in neotropical paleobotany. II. The Miocene communities of
671 Veracruz, Mexico. *Annals of the Missouri Botanical Garden* 63:787–842. DOI:
672 10.2307/2395250.
673 **Hall M, Frank E, Holmes G, Pfahringer B, Reutemann P, Witten IH. 2009.** The WEKA data
674 mining software: An update. *SIGKDD Explorations Newsletter* 11:10–18. DOI:
675 10.1145/1656274.1656278.
676 **Hall M. 1999.** Correlation-based feature selection for Machine Learning. Thesis, University of
677 Waikato.
678 **Hällfors MH, Aikio S, Fronzek S, Hellmann JJ, Ryttäri T, Heikkinen RK. 2016.** Assessing
679 the need and potential of assisted migration using species distribution models. *Biological
680 Conservation* 196:60–68. DOI: 10.1016/j.biocon.2016.01.031.
681 **Hammond WM, Williams AP, Abatzoglou JT, Adams HD, Klein T, López R, Sáenz-
682 Romero C, Hartmann H, Breshears DD, Allen CD. 2022.** Global field observations of
683 tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature communications*
684 13:1–11. DOI: 10.1038/s41467-022-29289-2.
685 **Hengl T, Mendes de Jesus J, Heuvelink GBM, Ruiperez Gonzalez M, Kilibarda M, Blagotić
686 A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B, Guevara MA,
687 Vargas R, MacMillan RA, Batjes NH, Leenaars JGB, Ribeiro E, Wheeler I, Mantel S,
688 Kempen B. 2017.** SoilGrids250m: Global gridded soil information based on machine
689 learning. *PLoS ONE* 12:1–40. DOI: 10.1371/journal.pone.0169748.
690 **Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005.** Very high resolution
691 interpolated climate surfaces for global land areas. *International Journal of Climatology*
692 25:1965–1978. DOI: 10.1002/joc.1276.
693 **Hijmans RJ. 2012.** Cross-validation of species distribution models: removing spatial sorting
694 bias and calibration with a null model. *Ecology* 93:679–688. DOI: 10.1890/11-0826.1.
695 **IPCC (Intergovernmental Panel of Climate Change). 2013.** Climate Change 2013: The
696 physical science basis. *Available at http://www.climatechange2013.org/* (Accessed 17
697 November 2019)
698 **Işık K. 2011.** Rare and endemic species: Why are they prone to extinction? *Turkish Journal of
699 Botany* 35:411–417. DOI: 10.3906/bot-1012-90.
700 **IUCN (International Union for Conservation of Nature). 2021.** The IUCN Red List of
701 Threatened Species. Version 2020-3. *Available at https://www.iucnredlist.org* (Accessed 21
702 January 2021)
703 **IUCN/SSC. 2013.** Guidelines for reintroductions and other conservation translocations. Version
704 1.0. Gland, Switzerland: IUCN Species Survival Commission, pp viiii + 57. *Available at
705 https://www.iucnsscrsg.org* (Accessed 17 January 2022)
706 **Jiménez-Valverde A, Lobo JM. 2007.** Threshold criteria for conversion of probability of

707   species presence to either-or presence-absence. *Acta Oecologica* 31:361–369. DOI:
708   10.1016/j.actao.2007.02.001.
709 **Ledig FT, Bermejo-Velázquez B, Hodgskiss PD, Johnson DR, Flores-López C, Jacob-**
710   **Cervantes V. 2000b.** The mating system and genic diversity in Martínez spruce, an
711   extremely rare endemic of México's Sierra Madre Oriental: an example of facultative
712   selfing and survival in interglacial refugia. *Canadian Journal of Forest Research* 30:1156–
713   1164. DOI: 10.1139/x00-052.
714 **Ledig FT, Hodgskiss PD, Jacob-Cervantes V. 2002.** Genetic diversity, mating system, and
715   conservation of a Mexican subalpine relict, *Picea mexicana* Martínez. *Conservation*
716   *Genetics* 3:113–122. DOI: 10.1023/A:1015297621884.
717 **Ledig FT, Mapula-Larreta M, Bermejo-Velázquez B, Reyes-Hernández V, Flores-López C,**
718   **Capó-Arteaga MA. 2000a.** Locations of endangered spruce populations in Mexico and the
719   demography of *Picea chihuahuana*. *Madroño* 47:71–88. DOI:
720   http://www.jstor.org/stable/41425349.
721 **Ledig FT, Rehfeldt GE, Sáenz-Romero C, Flores-López C. 2010.** Projections of suitable
722   habitat for rare species under global warming scenarios. *American Journal of Botany*
723   97:970–987. DOI: 10.3732/ajb.0900329.
724 **Lin CT, Li CF, Zelený D, Chytrý M, Nakamura Y, Chen MY, Chen TY, Hsia YJ, Hsieh**
725   **CF, Liu HY, Wang JC, Yang SZ, Yeh CL, Chiou CR. 2012.** Classification of the high-
726   mountain coniferous forests in Taiwan. *Folia Geobotanica* 47:373–401. DOI:
727   10.1007/s12224-012-9128-y.
728 **Lobo JM, Jiménez-Valverde A, Real R. 2008.** AUC: a misleading measure of the performance
729   of predictive distribution models. *Global Ecology and Biogeography* 17:145–151. DOI:
730   10.1111/j.1466-8238.2007.00358.x.
731 **López-Sánchez CA, Castedo-Dorado F, Cámara-Obregón A, Barrio-Anta M. 2021.**
732   Distribution of *Eucalyptus globulus* Labill. in northern Spain: Contemporary cover, suitable
733   habitat and potential expansion under climate change. *Forest Ecology and Management*
734   481:118723. DOI: 10.1016/j.foreco.2020.118723.
735 **López-Tirado J, Hidalgo PJ. 2016.** Predictive modelling of climax oak trees in southern Spain:
736   insights in a scenario of global change. *Plant Ecology* 217:451–463. DOI: 10.1007/s11258-
737   016-0589-6.
738 **Lozano-García MS, Ortega-Guerrero B, Caballero-Miranda M, Urrutia-Fucugauchi J.**
739   **1993.** Late Pleistocene and Holocene paleoenvironments of Chalco lake, central Mexico.
740   *Quaternary Research* 40:332–342. DOI: 10.1006/qres.1993.1086.
741 **Martínez M. 1961.** Una nueva especie de *Picea* en México. *Anales del Instituto de Biología*
742   *UNAM* 32:137–142.
743 **McCune JL. 2016.** Species distribution models predict rare species occurrences despite
744   significant effects of landscape context. *Journal of Applied Ecology* 53:1871–1879. DOI:
745   10.1111/1365-2664.12702.
746 **McDonald J, McCormack PC. 2021.** Rethinking the role of law in adapting to climate change.

747   *Wiley Interdisciplinary Reviews: Climate Change* 12:e726. DOI: 10.1002/wcc.726.

748 **McLane SC, Aitken SN. 2012.** Whitebark pine (*Pinus albicaulis*) assisted migration potential:
749   Testing establishment north of the species range. *Ecological Applications* 22:142–153. DOI:
750   10.1890/11-0329.1.

751 **Mi C, Huettmann F, Guo Y, Han X, Wen L. 2017.** Why choose Random Forest to predict rare
752   species distribution with few samples in large undersampled areas? Three Asian crane
753   species models provide supporting evidence. *PeerJ* 5:e2849. DOI:
754   doi.org/10.7717/peerj.2849.

755 **Morrone JJ, Escalante T, Rodríguez-Tapia G. 2017.** Mexican biogeographic provinces: Map
756   and shapefiles. *Zootaxa* 4277:277–279. DOI: 10.11646/zootaxa.4277.2.8.

757 **Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M,**
758   **Lavergne S, Lavorel S, Mouquet N, Paine CET, Renaud J, Thuiller W. 2013.** Rare
759   species support vulnerable functions in high-diversity ecosystems. *PLoS Biology* 11. DOI:
760   10.1371/journal.pbio.1001569.

761 **Müller-Using B, Alanis G. 1984.** New records of Chihuahua spruce (*Picea chihuahuana*
762   Martínez) in Nuevo León proposed for the legal protection of two areas of special
763   ecological interest. In: Secretaría de Desarrollo Urbano y Ecología ed. *Reunión Regional de*
764   *Ecología Norte, 25, 26 y 27 de abril 1984, Monterrey, N.L. SEDUE - Secretaría de*
765   *Desarrollo Urbano y Ecología, Subsecretaría de Ecología*. Monterrey, N.L.: SEDUE, 130–
766   132.

767 **Murray BR, Lepschi BJ. 2004.** Are locally rare species abundant elsewhere in their
768   geographical range? *Austral Ecology* 29:287–293. DOI: 10.1111/j.1442-
769   9993.2004.01365.x.

770 **Ongaro S, Martellos S, Bacaro G, De Agostini A, Cogoni A, Cortis P. 2018.** Distributional
771   pattern of Sardinian orchids under a climate change scenario. *Community Ecology* 19:223–
772   232. DOI: 10.1556/168.2018.19.3.3.

773 **Panthi S, Bräuning A, Zhou ZK, Fan ZX. 2017.** Tree rings reveal recent intensified spring
774   drought in the central Himalaya, Nepal. *Global and Planetary Change* 157:26–34. DOI:
775   10.1016/j.gloplacha.2017.08.012.

776 **Patsiou TS, Conti E, Zimmermann NE, Theodoridis S, Randin CF. 2014.** Topo-climatic
777   microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21
778   millennia. *Global Change Biology* 20:2286–2300. DOI: 10.1111/gcb.12515.

779 **Patterson TF. 1988.** A new species of *Picea* (Pinaceae) from Nuevo León, México. *SIDA,*
780   *Contributions to Botany* 13:131–135. DOI: https://www.jstor.org/stable/41966770.

781 **Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A. 2007.** Predicting species
782   distributions from small numbers of occurrence records: a test case using cryptic geckos in
783   Madagascar. *Journal of biogeography* 34:102–117. DOI: 10.1111/j.1365-
784   2699.2006.01594.x.

785 **Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L,**
786   **Segurado P, Dawson TP, Lees DC. 2006.** Model-based uncertainty in species range

787   prediction. *Journal of Biogeography* 33:1704–1711. DOI: 10.1111/j.1365-
788   2699.2006.01460.x.

789   **Pedlar JH, McKenney DW, Aubin I, Beardmore T, Beaulieu J, Iverson L, O'Neill GA,**
790   **Winder RS, Ste-Marie C. 2012.** Placing forestry in the assisted migration debate.
791   *BioScience* 62:835–842. DOI: 10.1525/bio.2012.62.9.10.

792   **Penteriani V, Zarzo-Arias A, Novo-Fernández A, Bombieri G, López-Sánchez CA. 2019.**
793   Responses of an endangered brown bear population to climate change based on predictable
794   food resource and shelter alterations. *Global Change Biology* 25:1133–1151. DOI:
795   10.1111/gcb.14564.

796   **Pérez I, Anadón JD, Díaz M, Nicola GG, Tella JL, Giménez A. 2012.** What is wrong with
797   current translocations? A review and a decision-making proposal. *Frontiers in Ecology and*
798   *the Evironment* 10:494–501. DOI: 10.1890/110175.

799   **Peters RL, Darling JDS. 1985.** The greenhouse effect and nature reserves. *BioScience* 35:707–
800   717. DOI: 10.2307/1310052.

801   **Pinedo-Alvarez C, Renteria-Villalobos M, Aguilar-Soto V, Vega-Mares JH, Melgoza-**
802   **Castillo A. 2019.** Distribution dynamics of *Picea chihuahuana* Martínez populations under
803   different climate change scenarios in Mexico. *Global Ecology and Conservation* 17:e00559.
804   DOI: 10.1016/j.gecco.2019.e00559.

805   **QGIS Development Team. 2020.** QGIS Geographic Information System. Open Source
806   Geospatial Foundation Project. http://qgis.osgeo.org

807   **Qiao H, Soberón J, Peterson AT. 2015.** No silver bullets in correlative ecological niche
808   modelling: Insights from testing among many potential algorithms for niche estimation.
809   *Methods in Ecology and Evolution* 6:1126–1136. DOI: 10.1111/2041-210X.12397.

810   **Rabinowitz D. 1981.** Seven forms of rarity. In: Singe H, ed. *The biological aspects of rare plant*
811   *conservation*. Chichester: John Wiley, 205–217.

812   **Regan HM, Syphard AD, Franklin J, Swab RM, Markovchick L, Flint AL, Flint LE,**
813   **Zedler PH. 2012.** Evaluation of assisted colonization strategies under global change for a
814   rare, fire-dependent plant. *Global Change Biology* 18:936–947. DOI: 10.1111/j.1365-
815   2486.2011.02586.x.

816   **Román-Palacios C, Wiens JJ. 2020.** Recent responses to climate change reveal the drivers of
817   species extinction and survival. *Proceedings of the National Academy of Sciences*
818   117:4211–4217. DOI: 10.1073/pnas.1913007117.

819   **Rzedowski J. 2006.** *Vegetación de México*. Mexico: Comisión Nacional para el Conocimiento y
820   Uso de la Biodiversidad.

821   **Sáenz-Romero C, Rehfeldt GE, Crookston NL, Duval P, St-Amant R, Beaulieu J,**
822   **Richardson BA. 2010.** Spline models of contemporary, 2030, 2060 and 2090 climates for
823   Mexico and their use in understanding climate-change impacts on the vegetation. Climatic
824   Change 102:595–623. DOI: 10.1007/s10584-009-9753-5.

825   **Schwartz MW, Hellmann JJ, McLachlan JM, Sax DF, Borevitz JO, Brennan J, Camacho**
826   **AE, Ceballos G, Clark JR, Doremus H. 2012.** Managed relocation: integrating the

827   scientific, regulatory, and ethical challenges. *BioScience* 62:732–743. DOI:
828   10.1525/bio.2012.62.8.6.

829 **Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009.** Evolution and ecology of species range
830   limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436. DOI:
831   10.1146/annurev.ecolsys.110308.120317.

832 **Simler AB, Williamson MA, Schwartz MW, Rizzo DM. 2019.** Amplifying plant disease risk
833   through assisted migration. *Conservation Letters* 12:1–9. DOI: 10.1111/conl.12605.

834 **Sofaer HR, Jarnevich CS, Pearse IS, Smyth RL, Auer S, Cook GL, Edwards TC, Guala**
835   **GF, Howard TG, Morisette JT, Hamilton H. 2019.** Development and delivery of species
836   distribution models to inform decision-making. *BioScience* 69:544–557. DOI:
837   10.1093/biosci/biz045.

838 **Taucare-Ríos A, Bizama G, Bustamante RO. 2016.** Using global and regional Species
839   Distribution Models (SDM) to infer the invasive stage of *Latrodectus geometricus*
840   (Araneae: Theridiidae) in the Americas. *Environmental Entomology* 45:1379–1385. DOI:
841   10.1093/ee/nvw118.

842 **Wang H-H, Wonkka CL, Treglia ML, Grant WE, Smeins FE, Rogers WE. 2019.**
843   Incorporating local-scale variables into distribution models enhances predictability for rare
844   plant species with biological dependencies. *Biodiversity and Conservation* 28:171–182.
845   DOI: 10.1007/s10531-018-1645-4.

846 **Wehenkel C, Sáenz-Romero C. 2012.** Estimating genetic erosion using the example of *Picea*
847   *chihuahuana* Martínez. *Tree Genetics and Genomes* 8:1085–1094. DOI: 10.1007/s11295-
848   012-0488-5.

849 **Wehenkel C, del Rocío Mariscal-Lucero S, González-Elizondo MS, Aguirre-Galindo VA,**
850   **Fladung M, López-Sánchez CA. 2020.** Tall *Pinus luzmariae* trees with genes from *P.*
851   *herrerae*. *PeerJ* 8:e8648. DOI: 10.7717/peerj.8648.

852 **Williams JN, Seo C, Thorne J, Nelson JK, Erwin S, O'Brien JM, Schwartz MW. 2009.**
853   Using species distribution models to predict new occurrences for rare plants. *Diversity and*
854   *Distributions* 15:565–576. DOI: 10.1111/j.1472-4642.2009.00567.x.

855 **Wilson CD, Roberts D, Reid N. 2011.** Applying species distribution modelling to identify areas
856   of high conservation value for endangered species: A case study using *Margaritifera*
857   *margaritifera* (L.). *Biological Conservation* 144:821–829. DOI:
858   https://doi.org/10.1016/j.biocon.2010.11.014.

859 **Zhao W, Sun Y, Pan J, Sullivan AR, Arnold ML, Mao J, Wang X. 2020.** Effects of
860   landscapes and range expansion on population structure and local adaptation. *New*
861   *Phytologist* 228:330–343. DOI: 10.1111/nph.16619.

Figure 1

Locations of the four known contemporary populations of *Picea martinezii* (circle symbols) and the three known populations of *Picea mexicana* (star symbols).

Prominent geographic regions of the Sierra Madre Occidental (SMOc, dark blue), Sierra Madre Oriental (SMOr, bluish green) and Trans-Mexican Neovolcanic Axis (TMNVA, vermilion) are shown. Note: The population of Agua de Alardín is also known as Agua Lardín. The SMOc, SMOr and TMNVA provinces file shapes were taken from Morrone, Escalante & Rodríguez-Tapia (2017), and the topographic base map for all figures was taken from ESRI (2018).

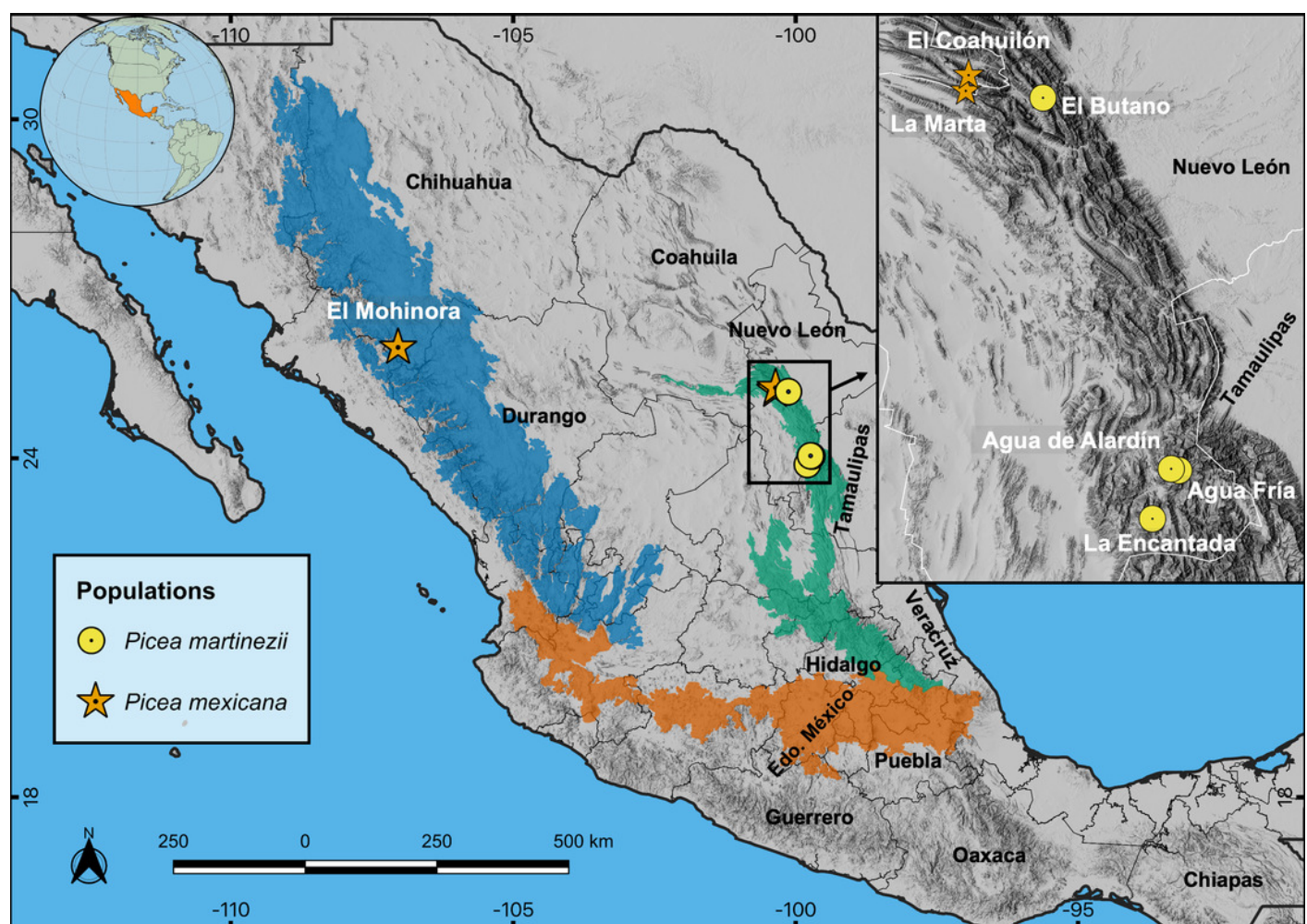



Figure 2

Projected area of suitable habitat for *P. martinezii* and *P. mexicana* in Mexico and the world at different times.

Projections for Mexico, made after modeling considering climate, topographic, soil and geological variables, included the Last Glacial Maximum (LGM, ~ 22 thousand years ago = ka), Middle Holocene (MH, ~ 6 ka), current (1961-1990 period), and future time (decades 2050 and 2070, both with RCP 4.5 and RCP 8.5). Worldwide projections, made after modeling using only climate variables, included the 1961-1990 period (Wcurrent) and the decade 2050-2060 with RCP 8.5 (W2050 RCP 8.5). Pixel counts for global projections excluded predicted areas for Mexico in this Figure. All periods show projections made at 30-arc second resolution and pixels with probabilities of occurrence of 0.5 - 0.79 (yellow) and 0.8-1.0 (vermilion). Numbers above the bars indicate the projected number of pixels.

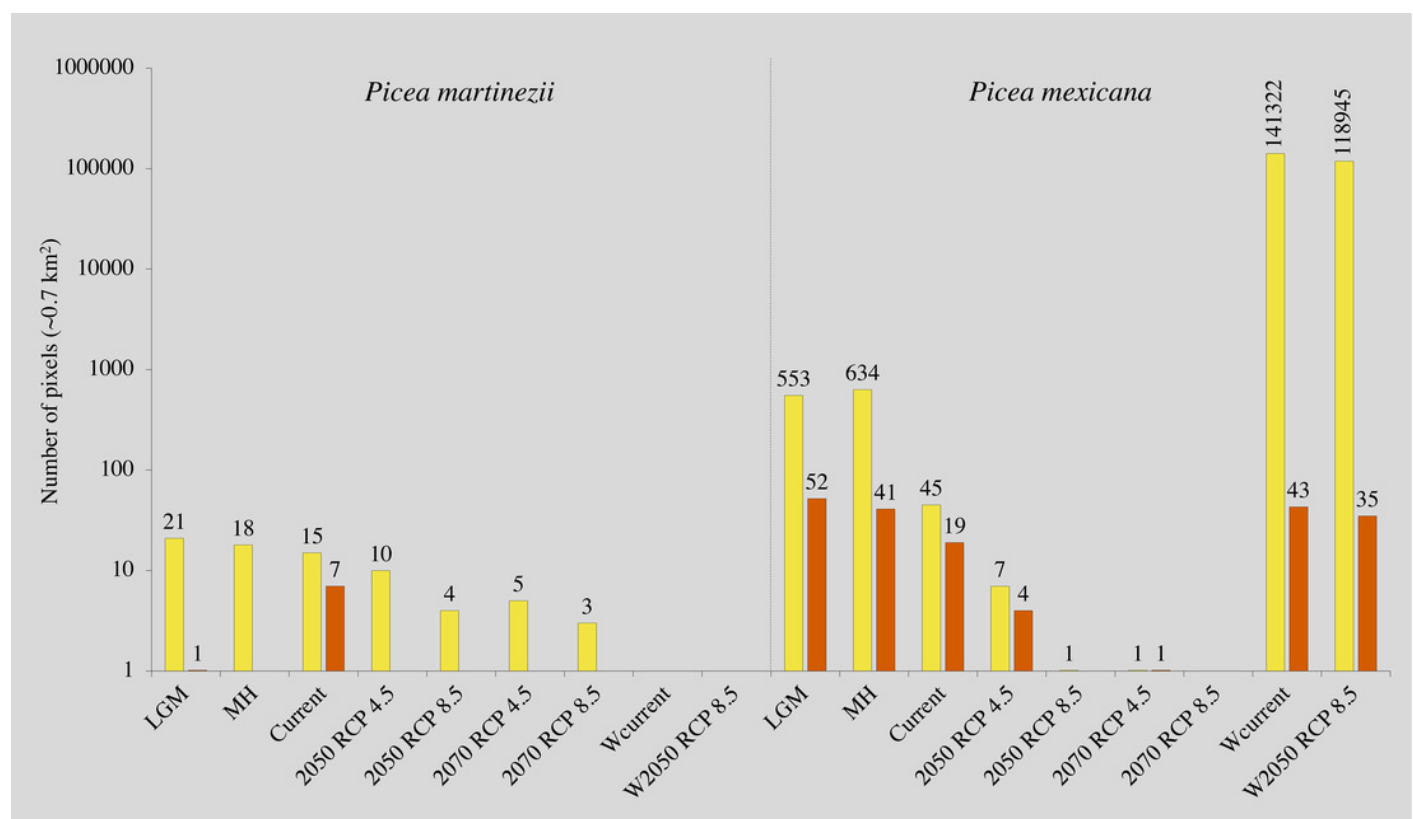



Figure 3

Potential distribution of the habitat for *Picea martinezii* and *P. mexicana* in the Last Glacial Maximum (~22 thousand years ago = ka) (A and C) and the Middle Holocene (~6 ka) (B and D).

The Last Glacial Maximum projection for *P. martinezii* shows the less suitable habitat on the Mexican territory (A, panels a to l), with only one pixel holding the highly suitable habitat in the northwest of Veracruz state (A, panel h); the Middle Holocene projection shows the distribution of the less suitable areas (B panels a to i). For *P. mexicana*, the Last Glacial Maximum projection shows suitable areas in the center of Mexico at northeast of Hidalgo state (C, panel a), borders of Puebla and Hidalgo states (C, panel b), and west of Veracruz state (C, panel c), with some less suitable areas in Estado de México (C panels d and e) and Chiapas states (C, panel f); the Middle Holocene projection shows suitable areas in northern Mexico, at north (D, panel a) and center (D panel b) of Chihuahua, borders of Chihuahua and Durango states (D panel c), south of Durango (D panel d), borders of Coahuila and Nuevo León states (D panel e), and south of Nuevo León state (D panel f).

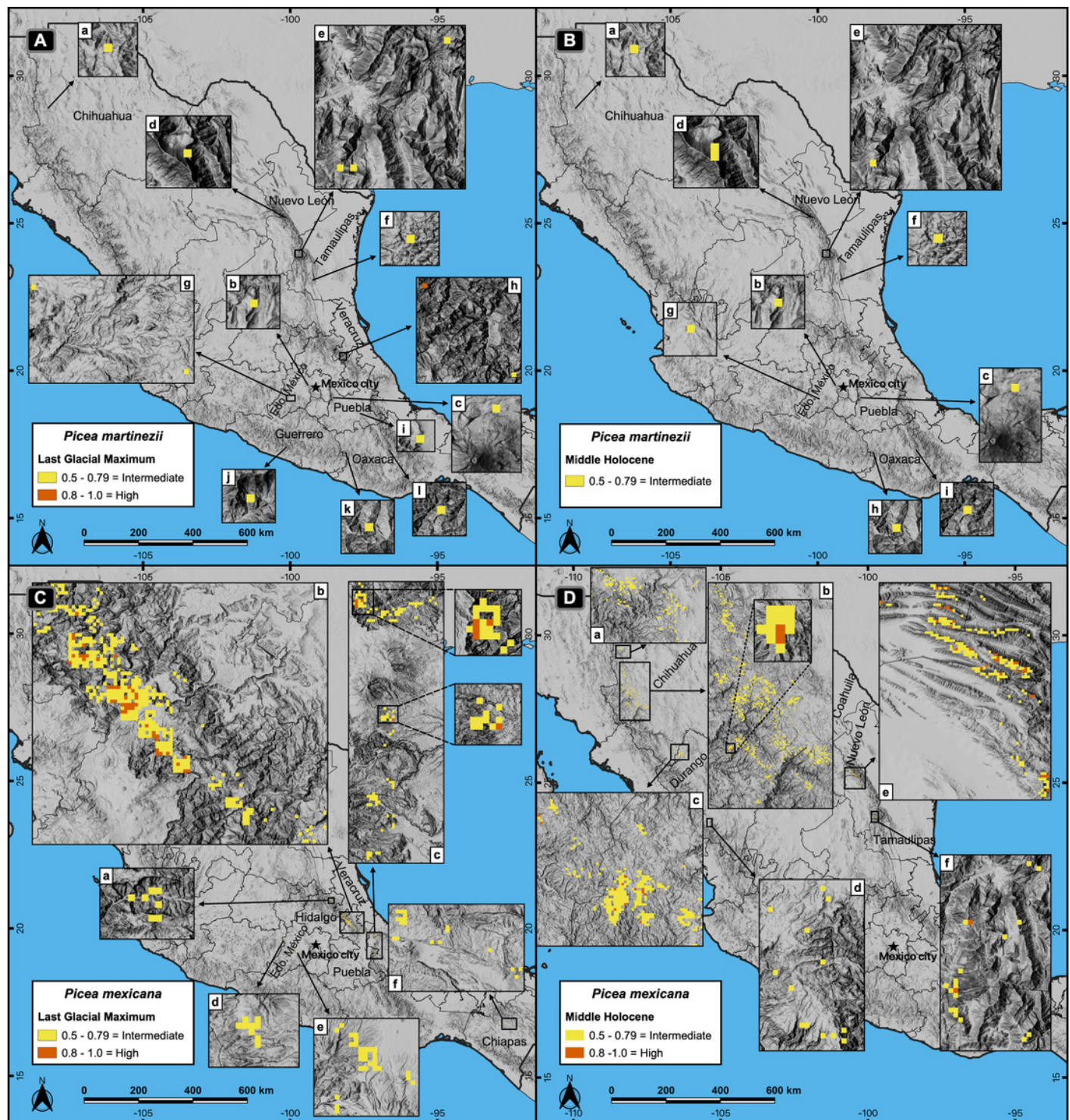



Figure 4

Actual and potential distribution of the suitable habitat in current conditions (1961-1990 reference period) for *P. martinezii* (A) and *P. mexicana* (B).

Projection for *P. martinezii* shows the highly suitable habitat (probability ≥ 0.8) restricted to the natural populations (EB = El Butano, AL = Agua de Alardín, AF = Agua Fría, and LE = La Encantada) in the center west (A-a) and southeast (A-b) of Nuevo León state, and less suitable areas (probability 0.5 to 0.79) spread in northern (A-c) and central (A-d to A-i) Mexico. Projection for *P. mexicana* shows the presence of the highly suitable habitat restricted to the natural populations (EM = El Mohinora, EC = El Coahuilón, and LM = La Marta) (B-a and B-b), and less suitable areas near the populations at center (B-c) and south (B-d) of Nuevo León state.

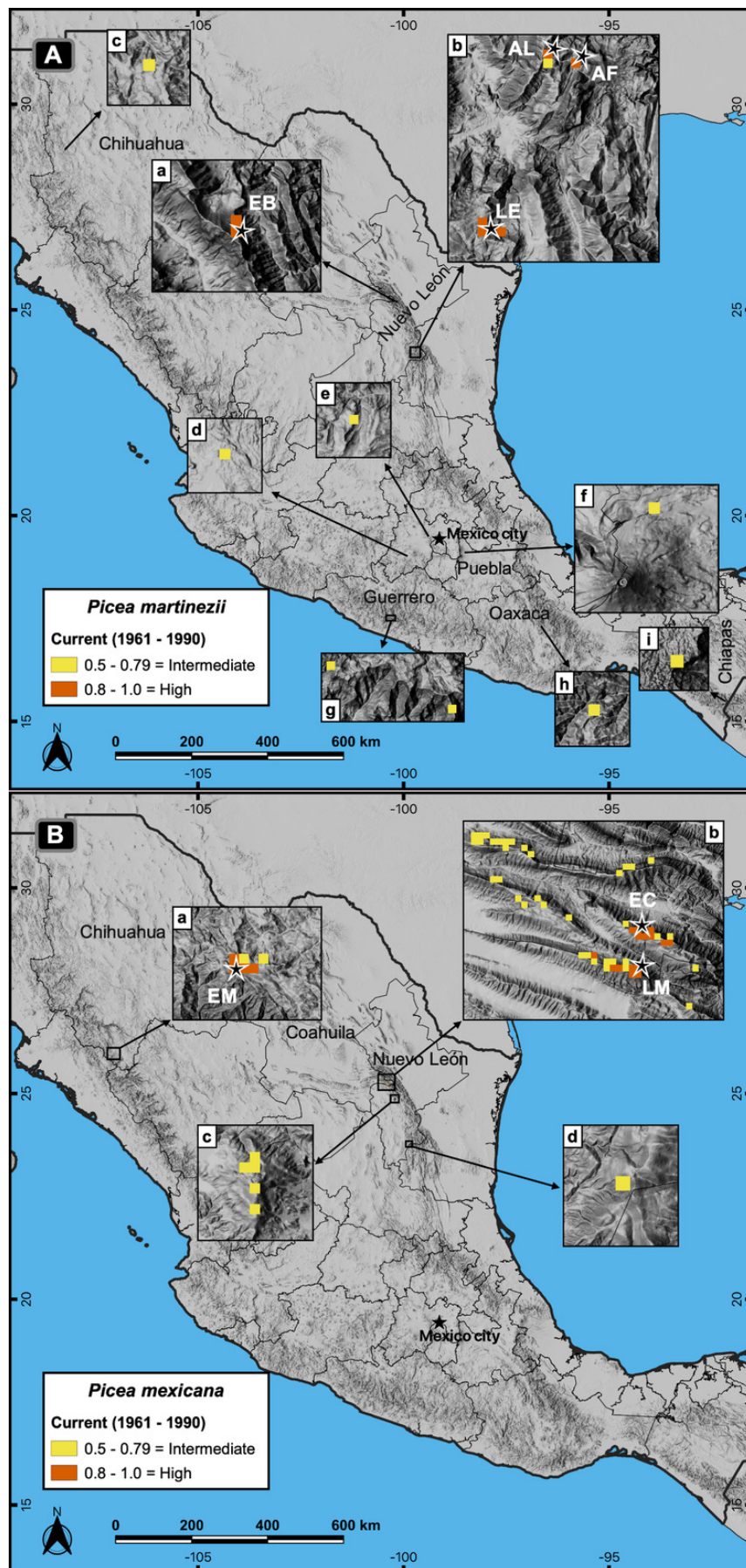



Figure 5

Potential distribution of the habitat (modeling based on climate, topography, soil and geological variables) for *Picea martinezii* (A-B) and *P. mexicana* (C-D) for 2050 and 2070, in both the moderate (RCP 4.5) and pessimistic (RCP 8.5) scenarios

Blue pixels shared by RCP 4.5 and 8.5, mean that the same pixel is projected as suitable in both scenarios. The 2050 (A) and 2070 (B) projections for *P. martinezii* show the spread distribution of the less suitable habitat in the Mexican territory, with more area in the moderate (A-a to A-f in 2050; B-a to B-d in 2070) than in the pessimistic (A-a to A-d in 2050; B-a to B-c in 2070) scenarios, and only three pixels of the less suitable habitat remaining by 2070 in the pessimistic scenario at the west of Chihuahua (B-a), center of Estado de México (B-b) and Estado de México-Puebla border (B-c); these three sites are present in all projections for *P. martinezii* from current to future conditions. The 2050 (C) and 2070 (D) projections for *P. mexicana* show the highly suitable habitat only in the moderate scenario, on and near the current populations of La Marta and El Coahuilón in the Coahuila-Nuevo León border (C-a and D) and center of Nuevo León (C-b); in the pessimistic scenario, only a pixel with the less suitable habitat in 2050 (C-b) and no area at all (highly nor less suitable habitat) in 2070 (D).

A

Chihuahua

Nuevo León

Picea martinezii

Future: 2050 RCP 4.5
☐ ☐ 0.5 - 0.79 = Intermediate

Future: 2050 RCP 8.5
☐ 0.5 - 0.79 = Intermediate

Edo. México
★ Mexico city
Puebla
Guerrero

0   200   400   600 km

B

Chihuahua

Edo. México
★ Mexico city
Puebla

Picea martinezii

Future: 2070 RCP 4.5
☐ ☐ 0.5 - 0.79 = Intermediate

Future: 2070 RCP 8.5
☐ 0.5 - 0.79 = Intermediate

0   200   400   600 km

C

Coahuila

Nuevo León

Picea mexicana

Future: 2050 RCP 4.5
☐ ☐ 0.5 - 0.79 = Intermediate
☐ 0.8 - 1.0 = High

Future: 2050 RCP 8.5
☐ 0.5 - 0.79 = Intermediate

★ Mexico city

0   200   400   600 km

D

Coahuila

Nuevo León

Picea mexicana

Future: 2070 RCP 4.5
☐ 0.5 - 0.79 = Intermediate
☐ 0.8 - 1.0 = High

Future: 2070 RCP 8.5
NO AREA

★ Mexico city

0   200   400   600 km

Figure 6

Global projections of the potential distribution of the climatically suitable habitat (based only on climatic variables) for *Picea martinezii* in current conditions (1961-1990 reference period) and for 2050 (pessimistic scenario).

All sites for the contemporary and future projections are located in Mexico, on and around the current natural populations of El Butano (EB) at the Coahuila-Nuevo León border (a), the center of Nuevo León state (b), and at Agua de Alardín (AL), Agua Fría (AF) and La Encantada (LE) which are at southern Nuevo León state, where a reduced area holding the less suitable habitat will remain by 2050 (c, blue pixels).

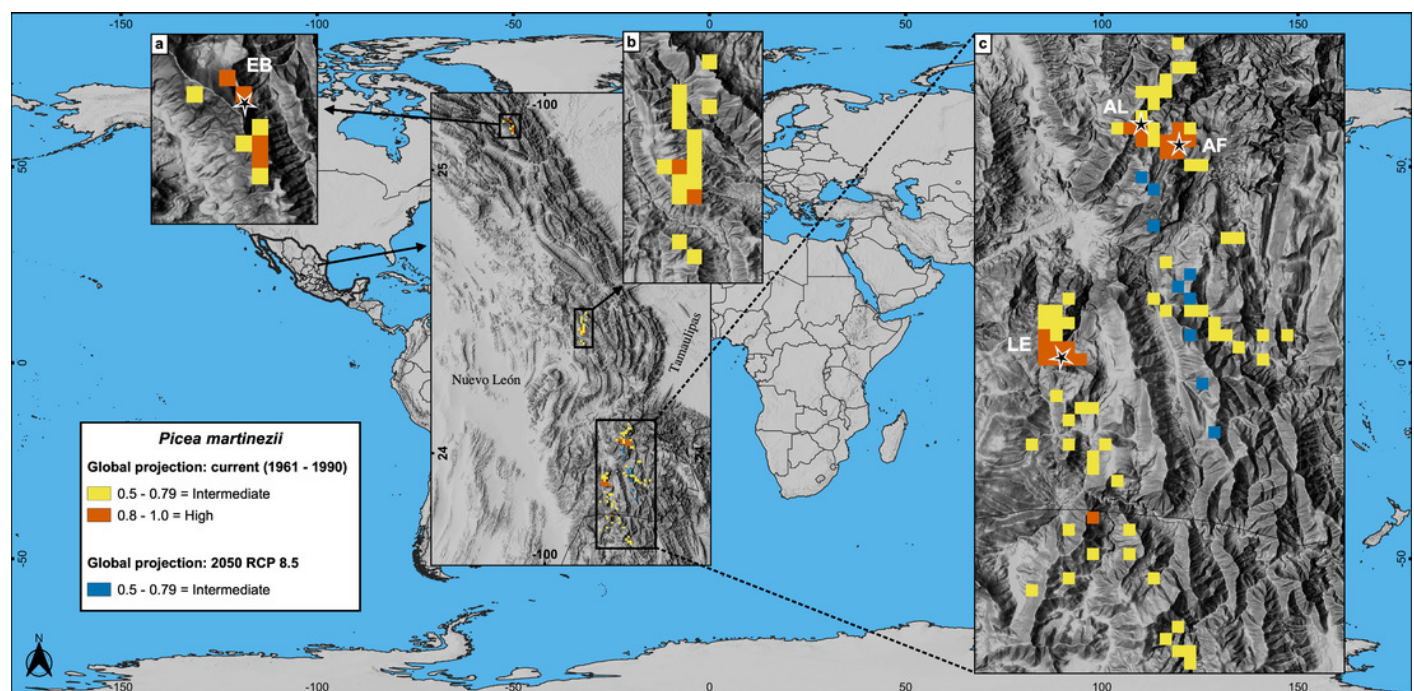
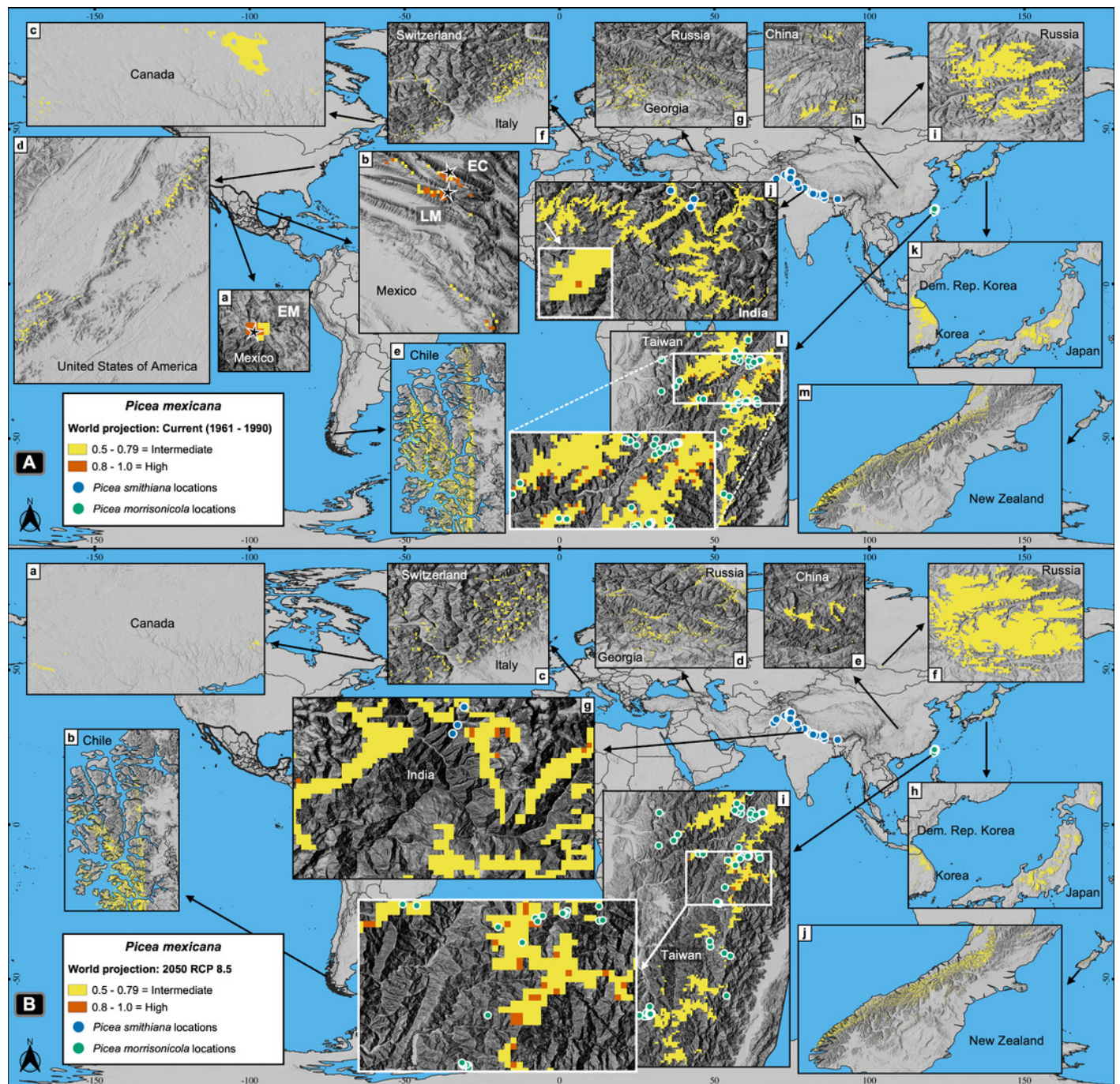



Figure 7

Global projections of the potential distribution of the climatically suitable habitat for *Picea mexicana* in contemporary conditions (A) and 2050 (B).

All sites for the contemporary projection are located in many mountainous regions of the world, such as: Sierra Madre Occidental (A-a), Sierra Madre Oriental (A-b), Laurentian mountains (A-c), Appalachian Mountains (A-d), southern Andes (A-e), The Pyrenees (not shown), The Alps (A-f), the Caucasus mountains (A-g), Khingan mountains (A-h), Sayan mountains (A-i), The Himalayans (A-j), Sobaek-Taebaek mountains (A-k), the Japanese Alps (A-k), Chungyang mountains (A-l) and the Southern Alps (A-m), where the habitat will remain by 2050, except for Mexico, the Appalachian Mountains and the Pyrenees. The highly suitable habitat by 2050 outside Mexico coincide with the geographical distribution of other endemic spruce species: *Picea smithiana* (blue circles) on The Himalayans in India (A-j and B-g) and *P. morrisonicola* (yellow circles) on Chungyan mountains in Taiwan (A-l and B-i). Contemporary projection (A) shows the natural populations of El Mohinora (EM), La Marta (LM) and El Coahuilón (EC). Occurrences of *P. smithiana* and *P. morrisonicola* were obtained from the Global Biodiversity Information Facility (GBIF, 2021).

Populations of *Picea martinezii* and *Picea mexicana* used to characterize the habitats and for modelling distributions of both species.

Population or stand	Code	Municipality and State[a]	Elevation (m)	Coordinates (decimals)	Status (number of individuals[b])	Area (ha)
		Picea martinezii				
El Butano	EB	Montemorelos, NL	2,180	25.178N -100.126W	Known (1,253)	23.0
Agua de Alardín [c]	AL	Aramberri, NL	2,120	24.042N -99.734W	Known (84,498)	74.3
Agua Fría	AF	Aramberri, NL	1,820	24.038N -99.710W	Known (2,769)	53.8
La Encantada[d]	LE	Zaragoza, NL	2,515	23.890N -99.791W	Known (712)	5.2
La Encantada 2	LE-2	Zaragoza, NL	2,378	23.890N -99.778W	New (12)	0.1
Zaragoza	ZA	Zaragoza, NL	2,483	23.890N -99.773W	New (22)	1.0
Total					(89,266)	157.4
		Picea mexicana				
El Mohinora	EM	Guadalupe y Calvo, Chi.	3,113	25.961N -107.042W	Known (11,383)	33.0
El Coahuilón	EC	Arteaga, Coah.	3,528	25.247N -100.354W	Known (2,253)	49.0
La Marta	LM	Arteaga, Coah.	3,494	25.198N -100.364W	Known (17,728)	41.6
La Marta 2	LM-4	Arteaga, Coah.	3,393	25.213N -100.413W	New (6,300)	24.0
La Marta 3	LM-3	Arteaga, Coah.	3,475	25.205N -100.386W	New (35)	6.5
La Marta 4	LM-2	Arteaga, Coah.	3,364	25.203N -100.369W	New (50)	1.7
La Marta 5	LM-5	Arteaga, Coah.	3,096	25.207N -100.369W	New (60)	1.0
El Mohinora 2	EM-2	Guadalupe y Calvo, Chi.	3,139	25.957N -107.029W	New (1,250)	16.3
Total					(39,059)	173.1

2 Note: [a]NL = Nuevo León; Coah. = Coahuila (both in the Sierra Madre Oriental); Chi. = Chihuahua (in the Sierra
3 Madre Occidental).
4 [b] Including trees, saplings and natural regeneration (heights > 30 cm).
5 [c] Agua de Alardín (also known as Agua Alardín) = Cañada El Puerto (I, II, III) in Ledig et al. (2000).
6 [d] La Encantada = La Tinaja in Ledig et al. (2000).

Environmental variables of greatest importance in the *Picea martinezii* and *Picea mexicana* distribution models for Mexico and the world at 30 arc-second, as indicated by Random Forest analysis.

Class	Variable	Description	Normalized importance
		Picea martinezii model for Mexico	
Topography	PRC	Profile curvature	41.89
Soil	SC	Soil organic carbon content (g kg-1)	32.46
Climate	Bio_01	Annual mean temperature (ºC)	25.65
		Picea martinezii global model	
Climate	Bio_02	Mean diurnal range (mean of monthly (max temp - min temp)) (ºC)	22.90
Climate	Bio_13	Precipitation of wettest month (mm)	17.85
Climate	Bio_04	Temperature seasonality (standard deviation *100) (ºC)	17.57
Climate	Bio_07	Temperature annual range (BIO5-BIO6) (ºC)	17.48
Climate	Bio_08	Mean temperature of wettest quarter (ºC)	15.28
Climate	Bio_19	Precipitation of coldest quarter (mm)	8.93
		Picea mexicana model for Mexico	
Climate	Bio_06	Min temperature of coldest month (ºC)	18.27
Topography	WI	Wetness index	13.89
Soil	SC	Soil organic carbon content (g kg-1)	13.75
Soil	BD	Bulk density of the fine earth fraction (< 2mm) (kg m⁻³)	12.71
Topography	ASP	Aspect (°)	11.89
Climate	Bio_09	Mean temperature of driest quarter (ºC)	11.77
Climate	Bio_17	Precipitation of driest quarter (mm)	9.83
Geology	Geo	Geological units	7.90
		Picea mexicana global model	
Climate	Bio_04	Temperature seasonality (standard deviation *100) (ºC)	17.72
Climate	Bio_16	Precipitation of wettest quarter (mm)	15.73
Climate	Bio_08	Mean temperature of wettest quarter (ºC)	14.49
Climate	Bio_11	Mean temperature of coldest quarter (ºC)	14.09
Climate	Bio_18	Precipitation of warmest quarter (mm)	13.59
Climate	Bio_01	Annual mean temperature (ºC)	13.57
Climate	Bio_14	Precipitation of driest month (mm)	10.82

3