Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines
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   **How to use it**
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   - Click at the point in the proof where the comment should be inserted.
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Similar but not equivalent: ecological niche comparison across closely related Mexican white pines

Jesús Aguirre-Gutiérrez1,2,*, Héctor M. Serna-Chavez2, Alma R. Villalobos-Arambula3, Jorge A. Pérez de la Rosa3 and Niels Raes1

ABSTRACT

Aim In the face of global environmental change, identifying the factors that shape the ecological niches of species and understanding the mechanisms behind them can help to draft effective conservation plans. The differences in the ecological factors that shape species distributions may then help to highlight differences between closely related taxa. We investigate the applicability of ecological niche modelling and the comparison of species distributions in ecological niche space to detect areas with priority for biodiversity conservation and to analyse differences in the ecological niche spaces used by closely related taxa.

Location United States of America, Mexico and Central America.

Methods We apply ordination and ecological niche modelling techniques to assess the main environmental drivers of the distribution of Mexican white pines (Pinus: Pinaceae). Furthermore, we assess the similarities and differences of the ecological niches occupied by closely related taxa. We analyse whether Mexican white pines occupy similar or equivalent ecological niches.

Results All the studied taxa presented different responses to the environmental factors, resulting in a unique combination of niche conditions. Our stacked habitat suitability maps highlighted regions in southern Mexico and northern Central America as highly suitable for most species and thus with high conservation value. By quantitatively assessing the niche overlap, similarity and equivalency of Mexican white pines, our results prove that the distribution of one species cannot be implied by the distribution of another, even if these taxa are considered closely related.

Main conclusions The fact that each Mexican white pine is constrained by a unique set of environmental conditions, and thus, their non-equivalence of ecological niches has direct implications for conservation as this highlights the inadequacy of one-fits all type of conservation measure.

Keywords Conifers, conservation, forest, niche comparison, pinus, species distribution models.

INTRODUCTION

The conservatism of ecological niches (sensu Grinnell, 1917) has become an issue of concern given the expected impacts of climate change on biodiversity (Thomas et al., 2004; Chen et al., 2011; Araújo et al., 2013). This has prompted the development of new tools to assess how the ecological niche of species can shrink/contract, expand or persist, in environmental and geographic space, anticipating the effects of global climate change (Warren et al., 2010; Peterson, 2011; Broennimann et al., 2012). Understanding how the ecological niche of species will change can be used to implement or guide conservation actions, especially in biodiversity-rich areas (Guisan et al., 2013).
Species groups that are highly diverse and present a varied set of ecological adaptations along an environmental gradient may be of importance for understanding ecological niche differences and to prepare mitigation actions against global change impacts. The plant family Pinaceae (Farjon, 2008) includes 11 genera and 228 species around the world and has a centre of diversity in North and Central America. The genus Pinus has its centre of diversity in Mexico with 49 of the 120 recognized species inhabiting habitats from alpine tree line elevations to lowland sea level (Gernandt & Pérez de la Rosa, 2014). Particularly, the taxa in the subgenus Strobus, commonly known as the Mexican white pines, are highly important on a global scale because the ecological processes in which they are involved (e.g. carbon sequestration, soil nutrient retention and cycling, ecosystem structure) and because of their provision of ecosystem services in the form of wood, resin and pulp (Richardson, 1998). Moreover, this subgenus contains taxa that have been classified as ‘closely related’ (Brueederle et al., 2001). There is no general agreement on the taxonomic status of some Mexican white pines, even after recent morphological and phylogenetic studies (Price et al., 1998; Castro-Félix et al., 2008; Tomba & Achuff, 2010). For instance, Pinus strobiiformis and Pinus ayacahuite were formerly classified as the same species (Perry, 1991; Farjon & Styles, 1997; Brueederle et al., 2001). This highlights the ongoing problems with cryptic species, problems that are not unique to taxonomy but also to biogeography and conservation studies (Bickford et al., 2007; Pfenninger & Schwenk, 2007).

The development of ecological niche models (ENMs; Soberón & Nakamura, 2009), also referred to as species distribution models (Guisan & Thuiller, 2005; Araújo & Peterson, 2012), has facilitated the extraction of ecological niche characteristics that can assist taxonomic delineations and biodiversity conservation (Raxworthy et al., 2007; Blair et al., 2013).

In this study, we analyse how the species-specific responses to environmental factors and the differences between distributions in ecological niche space can aid future species conservation plans and in the ongoing debate on differentiation between closely related taxa of the subgenus Strobus. To this end, we use ENM and ordination techniques to characterize the ecological niches of Mexican white pine taxa and to quantify similarities between them. First, we identify the main environmental variables that constraint their distributions. We then use the information on their environmental constraints to generate a ‘global’ habitat suitability map for Mexican white pines to highlight hotspots of habitat suitability to inform conservation planning. We also assess whether different Mexican white pine taxa share the same ecological niche space. Finally, we discuss how differences in the distribution of ecological niche spaces and the species-specific responses to environmental factors may inform conservation plans. Following the niche conservatism assumption (e.g. Kozak & Wiens, 2006; Rödder & Lötters, 2009), we would expect more genetically closely related species to share more of their environmental niche space, resulting in high ecological niche space overlap, high similarity and high spatial overlap. Meanwhile with niche divergence as a speciation mechanism, we would expect the ecological niches of closely related species to differ significantly (Rice et al., 2003; Jakob et al., 2010). Due to the similarities in morphological and physiological characteristics between the Mexican white pines, we expect their ecological niches to be similar. However, due to the different adaptations to different environments, we expect ecological niches to be non-equivalent.

**METHODS**

**Study area and species data**

The study area includes the native distribution of Mexican white pines, extending from the southern United States of America (USA) into Central America (Perry, 1991), and covers approximately 15 million km², comprising a wide variety of biomes, with an elevation gradient ranging from sea level to more than 5450 masl.

We selected five Mexican white pine taxa (genus Pinus, subgenus Strobus, section Strobus, subsection Strobi. Little and Critchfield, 1969): *P. strobiiformis* Engelm, *P. ayacahuite* Ehrenb. ex Schltdl., *P. ayacahuite* var. *veitchii* (Roezl) Shaw, *P. lambertiana* Doug., *P. strobus* var. *chiapensis* (Martínez). We were not able to include *P. flexilis* var. *reflexa* Engelm because of the low number of available sample locations (< 5). Except for *P. lambertiana*, all white pine taxa in our study have their main geographic distribution in Mexico. The current distributions of *P. strobiiformis* and *P. lambertiana* extend further north into the USA, while *P. strobus* var. *chiapensis* and *P. ayacahuite* extend further south into Central America. We obtained species presence data from the University of Guadalajara Herbarium (IRUG, 2013), the National Commission for the Knowledge and Use of Biodiversity (CONABIO, 2013), the Global Biodiversity Information Facility (GBIF, 2013) and the Conifers database (Farjon, 2013a) collected during the last 30 years. After removing duplicates and screening for incomplete meta-information, we obtained a total of 593 presence records for the five pine taxa (Table 1).

**Environmental data**

We selected environmental data related to different eco-physiological constraints of the pine taxa. We obtained annual trends in extreme limiting conditions related to precipitation and temperature from WorldClim (Hijmans et al., 2005). The selected variables presented Pearson’s correlation ≤ 0.70 (Dormann et al., 2013) and had a resolution of 1 km² (Table 2). We included the mean temperature of coldest quarter (°C) and isothermality (the quotient of mean diurnal and annual temperature ranges), given the reported different preferences in temperature of the taxa in the genus *Pinus* (Perry, 1991; Farjon & Styles, 1997). These climatic variables relate to temperature extremes, which are one of the main constraints to the distribution of vegetation (van Zonneveld...
Table 1 Ecological niche models evaluation by their AUC and null model results

<table>
<thead>
<tr>
<th>Pinus species</th>
<th>n</th>
<th>AUC*</th>
<th>Null model AUC</th>
<th>Niche breadth</th>
<th>Area predicted suitable (1000 km²)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. ayacahuite</td>
<td>239</td>
<td>0.85</td>
<td>0.72</td>
<td>0.0382</td>
<td>193</td>
</tr>
<tr>
<td>P. ayacahuite var. veitchii</td>
<td>18</td>
<td>0.95</td>
<td>0.87</td>
<td>0.0194</td>
<td>61</td>
</tr>
<tr>
<td>P. strobiformis</td>
<td>144</td>
<td>0.93</td>
<td>0.77</td>
<td>0.0671</td>
<td>362</td>
</tr>
<tr>
<td>P. strobos var. chiapensis</td>
<td>88</td>
<td>0.88</td>
<td>0.79</td>
<td>0.0673</td>
<td>543</td>
</tr>
<tr>
<td>P. lambertiana</td>
<td>103</td>
<td>0.98</td>
<td>0.79</td>
<td>0.0590</td>
<td>439</td>
</tr>
</tbody>
</table>

n, number of sample locations used for modelling the species distributions.

*All models have a significantly higher AUC value when compared to their null distribution (P < 0.01) based on 99 repetitions (only the highest null model score presented).

†The area predicted as suitable corresponds to the ENMs projections of habitat suitability in geographic extent for each of the species after converting to presence/absence binary maps.

Table 2 Percentage of variable contribution to the model construction, derived from the permutation importance analysis from MaxEnt. Top three ranking variables printed in bold. The results represented the drop in AUC after the values from the focus variable are permuted and the model is re-evaluated and compared with the original model. This drop is standardized and converted to percentage contribution. For each Pinus taxon, the three variables with the highest contributions are presented in bold

<table>
<thead>
<tr>
<th>Variable</th>
<th>P. ayacahuite</th>
<th>P. ayacahuite var. veitchii</th>
<th>P. strobiformis</th>
<th>P. strobos var. chiapensis</th>
<th>P. lambertiana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isothermality</td>
<td>39.3</td>
<td>1.3</td>
<td>4.8</td>
<td>28.2</td>
<td>16.9</td>
</tr>
<tr>
<td>Mean temperature of coldest quarter</td>
<td>2.2</td>
<td>0.4</td>
<td>2.4</td>
<td>16.3</td>
<td>7.0</td>
</tr>
<tr>
<td>Annual precipitation</td>
<td>7.2</td>
<td>0.1</td>
<td>2.5</td>
<td>21.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Precipitation seasonality</td>
<td>8.1</td>
<td>66.2</td>
<td>3.9</td>
<td>13.6</td>
<td>28.5</td>
</tr>
<tr>
<td>Elevation</td>
<td>35.8</td>
<td>28.1</td>
<td>49.0</td>
<td>13.3</td>
<td>2.2</td>
</tr>
<tr>
<td>NDVI</td>
<td>2.9</td>
<td>2.8</td>
<td>6.7</td>
<td>2.5</td>
<td>0.8</td>
</tr>
<tr>
<td>Slope</td>
<td>0.6</td>
<td>0.2</td>
<td>2.8</td>
<td>2.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>0.3</td>
<td>0.0</td>
<td>24.8</td>
<td>1.1</td>
<td>40.0</td>
</tr>
<tr>
<td>Soil total organic carbon</td>
<td>1.5</td>
<td>0.2</td>
<td>0.3</td>
<td>1.4</td>
<td>1.7</td>
</tr>
<tr>
<td>Soil pH</td>
<td>1.9</td>
<td>0.8</td>
<td>2.9</td>
<td>0.3</td>
<td>1.3</td>
</tr>
</tbody>
</table>

species distributions, we used ENMs. Based on a previous study (Aguirre-Gutiérrez et al., 2013), we selected maximum entropy modelling as implemented in MaxEnt (Phillips et al., 2006). We used the autofeatures settings and the logistic output format in MaxEnt because these options have proven to be appropriate for extensive multispecies studies (Phillips & Dudik, 2008). We used the target group approach, as suggested by Mateo et al. (2010) and Elith et al. (2011), when extracting background points for MaxEnt as it has performed with higher accuracy than other methods (i.e. random selection). In this approach, the collection localities where other Mexican white pine species have been found but where the species being modelled was not present where used as background locations. As suggested by Elith et al. (2011), this approach provides also the advantage of accounting for possible records selection biases. We used the null model approach of Raes & ter Steege (2007) to test the significance of our model predictions. The null model approach tests the area under the curve (AUC) value of the receiver-operating characteristic of the species niche model against a null distribution of 99 repetitions. The null distribution was generated from the sample localities of the target group. Added advantage of testing against a null model is that all collection localities can be used for model calibration.

Ecological niche modelling

To analyse the spatial distribution of Mexican white pines and identify key environmental variables that constrain the...
The models of Mexican white pines were projected on the study area to identify suitable habitats for their distribution and conservation. To assess the importance of the different environmental variables in our models, we used the permutation importance values rendered by MaxEnt and their ecological response curves (Phillips & Dudik, 2008).

**Calculating niche characteristics: breadth, overlap, equivalency and similarity**

We calculated ecological niche characteristics to assess the degree of shared environmental niche space between Mexican white pines. We obtained the niche breadth of each species (i.e. the amount of ecological niche space available to the different pine species) by applying the Levins' inverse concentration metric (Levins, 1968). The niche breadth ranges from 0, when all but one grid cell has non-zero suitability, to 1 when all the grid cells in the study area are equally suitable (Mandle et al., 2010). Therefore, species with a wider environmental distribution render higher niche breadth values.

The assessment of niche overlap allows quantifying the niche shared by the Mexican white pines. In this study, niche overlap between pairs of Mexican white pines was computed by means of the Schoener’s D statistic directly from ecological niche space (Schoener, 1968; Warren et al., 2008). The value of D ranges between 0, when two species have no overlap in the environmental space, and 1 when two species share the same environmental space.

We used the niche equivalence test to assess whether the ecological niches of pairs of Mexican white pines are significantly different from each other and if the two niche spaces are interchangeable. We performed the niche equivalence test by comparing the niche overlap values (D) of pairs of Mexican white pines to a null distribution of 100 overlap values. We determined non-equivalence of ecological niches if the niche overlap value of the species being compared was significantly lower than the overlap values from the null distribution (P ≤ 0.05).

The test for niche equivalence is conservative as it only assesses if the two species are identical in their niche space by using their exact locations and does not consider the surrounding space. Therefore, we also performed a niche similarity test, which assesses if the ecological niches of any pair of species are more different than expected by chance, accounting for the differences in the surrounding environmental conditions in the geographic areas where both species are distributed (Warren et al., 2010). A significant difference from the niche similarity test would not only indicate differences in the environmental niche space the two species occupy, but also that these differences are not due to the environmental conditions that are geographically available.

To extract the ecological niche space occupied by each Mexican white pine species and to quantify niche overlap, equivalence and similarity, we used an ordination technique that applies kernel smoothers to the species presence in environmental space for the selection, combination and weighting of environmental variables (Broennimann et al., 2012). We specified a division of the environmental space into a grid of 100 × 100 cells, in which each cell corresponds to a unique vector of the available environmental conditions in the study area. The number of occurrences per species can be bias and not represent the total distribution of the species in environmental space; this might result in an underestimation of their density in some of the cells and overestimation in others. Because of this possibility of over- and underestimations, a kernel density function is applied for the smoothing density of occurrences for each of the cells in environmental space, thus obtaining a better indication of the environmental conditions suitable for each species. Further details about the kernel density estimator and its parameters can be found in Broennimann et al. (2012). We implemented this approach by means of a principal component analysis that is calibrated on the entire environmental space present in the study area (hereafter referred to as 'PCA-ent'). All analyses were performed in the R platform (R Development Core Team, 2014).

**RESULTS**

**Responses to environmental gradients**

The distributions of Mexican white pines are underpinned by their different responses to the environment (Fig. 1; Table 2). The distributions of all Mexican white pines were mainly constrained by a combination of isothermality, precipitation seasonality, elevation and solar radiation. Highly suitable areas for P. ayacahuite were found at high elevations (∼2000 m) and high isothermality (∼0.95), both of these variables being the most important predictors of its distribution. For P. ayacahuite var. Veitchii, the suitability increased along with both, precipitation seasonality and elevation. The distribution of P. strobiformis was mainly constrained by elevation and, to a lesser extent by solar radiation (Table 3). Pinus strobiformis showed an optimum suitability at altitudes between 2500 and 3000 m and at radiation of around 15 kW m⁻². Isothermality was an important environmental factor constraining the distribution of P. strobiformis var. chiapensis, with highest suitability at values of 0.90. Annual precipitation was also a main constraint for the distribution of P. strobiformis var. chiapensis, with suitability sharply increasing at initial increments of precipitation. Finally, P. lambertiana was mainly constrained by the solar radiation and precipitation seasonality, areas with radiation around 13–14 kW m⁻² and with a variation in precipitation of ∼60 mm showing highest suitability. Unlike expected, none of the Mexican white pines were strongly constrained by soil factors. Most of the pine taxa had responses to soil variables that rarely overpassed suitability estimates of 0.5.

**White pines distribution and hotspots**

We developed ecological niche models for each of the five Mexican white pine taxa (Fig. 2). Although, P. ayacahuite var.
Figure 1 The ecological response curves for each of Mexican white pine. The response curves are based on the ENMs. Response curves show the ranges in environmental conditions that are more favourable for the distribution of the species. The x-axis of the variables represents their ranges for the complete study area, while the y-axis represents the predicted suitability of the focus variable when all of the other variables are set to their average. In Table 2, we highlight the three most relevant variables for each species.
Table 3 Ecological niche comparisons for the Mexican white pines. Niche overlap values are presented for the comparisons of niche similarity and equivalency of species \( a \) with species \( b \). All of the comparisons between the Mexican white pines highlight the non-equivalency of their ecological niches.

<table>
<thead>
<tr>
<th>Pinus species</th>
<th>Niche overlap (D)</th>
<th>Niche similarity</th>
<th>Niche equivalency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( a )</td>
<td>( b )</td>
<td>( a \rightarrow b )</td>
</tr>
<tr>
<td>( P. ayacahuite )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( P. ayacahuite )</td>
<td>0.124</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>( P. strobiformis )</td>
<td>0.353</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>( P. strobus ) var. chiapensis</td>
<td>0.554</td>
<td></td>
<td>Similar*</td>
</tr>
<tr>
<td>( P. lambertiana )</td>
<td>0.022</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>( P. ayacahuite ) var. veitchii</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( P. strobiformis )</td>
<td>0.429</td>
<td></td>
<td>Similar*</td>
</tr>
<tr>
<td>( P. strobus ) var. chiapensis</td>
<td>0.058</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>( P. lambertiana )</td>
<td>0.045</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>( P. strobus ) var. chiapensis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( P. lambertiana )</td>
<td>0.248</td>
<td></td>
<td>ns</td>
</tr>
<tr>
<td>( P. strobiformis )</td>
<td>0.167</td>
<td></td>
<td>ns</td>
</tr>
</tbody>
</table>

ns, not significantly different.

For the niche similarity test, none of the pairwise comparison rendered species that differed significantly.

*The ecological niches are significantly \( (P < 0.05) \) more similar or different than expected by random.

Figure 2 Distribution models for the five Mexican white pines representing the areas in geographic space with high environmental suitability. Panel (a) presents the results from an ensemble of the five niche models, highlighting regions of shared habitat suitability. Value of 0 indicates an area that is not suitable and 5 area with high habitat suitability for the five Mexican white pine taxa. For panels (b) to (f) the blue colour represents the areas that have high habitat suitability after applying the 10% presence threshold criteria to the models’ suitability scores, for example, 10% of the most extreme presence observations in environmental niche space are forced outside the predicted presence area because they may represent errors in the ‘presence’ recordings or outliers in the environmental space (Tinoco et al., 2009). Black dots represent the sample/presence locations.
veitchii was modelled using only 18 presence records, the null model protocol we applied suggests that our results are significantly better than expected by a random model. In fact, all our ENMs performed significantly better than expected by chance alone ($P < 0.01$; Table 1). 'Stacking' of the five distribution models resulted in a map model with centres of high environmental suitability for Mexican white pines (Fig. 2a). Centres of high suitability were located on the Mexican transvolcanic belt and on the mountain chain connecting southern Mexico and Guatemala. Additional hotspots were found on the Mexican occidental and south-eastern mountain chains, and on the central-southern areas of Mexico, with only a narrow area in northern Mexico highlighted as highly suitable for most taxa (Fig. 2a).

**Ecological niche properties**

The analysis of ecological niche properties rendered a PCA-ent with the first axis mainly loaded by isothermality, solar radiation and average temperature of coldest quarter, explaining 32.3% of the total variation in environmental conditions for the taxa in the study area (Fig. 3). The second axis explained about 28% of the variation and was loaded by soil pH, annual precipitation, elevation and NDVI variables.

**Niche breadth and overlap**

The results from the niche breadth assessment showed a high variation in environmental suitability for Mexican white pines (Table 1). The highest niche breadth that we found was 0.0673 for *P. strobus var. chiapensis*, which also presented the broadest distribution of suitable habitat (see 'Area predicted suitable' in Table 1). The niche breadth for *P. strobiformis* was also similarly high (0.0671); however, this species had a narrower distribution of suitable habitat than *P. strobus var. chiapensis*. *Pinus lambertiana* presented a niche breadth smaller than that of *P. strobus var. chiapensis*, while, the niche breadth of *P. ayacahuite var. veitchii*, exhibited both the narrowest distribution of suitable habitat and the lowest niche breadth—three times smaller than that of the *P. strobus var. chiapensis* (Table 1).

Niche overlap results suggest a great variability in the environmental space inhabited by the different Mexican

![Figure 3](image_url) Ecological niche of the five analysed Mexican white pines in environmental space produced by the principal component analysis method (PCA-ent). The PCA-ent results represent the niche of the species in the two main axes with the environmental conditions of the complete study area. For each species, the grey-to-black shading represents the grid cell density of the species' occurrences (black being the highest density). The first dashed line represents the 50% of the available environment and the solid line represents the 100%. The last panel presents the contribution of variables for loading the main PCA-ent axes and the percentage of inertia explained by axes one and two.
white pines (Table 3; Fig. 3). Some species, such as P. ayacahuite and P. lambertiana, occupy considerably different environmental niches. Even closely related taxa such as P. ayacahuite and its variety P. ayacahuite var. veitchii, also differed in their occupied niche space (Fig. 3; Table 3). All niche overlap values are presented in Table 3.

Niche equivalency and similarity

For all possible pairwise comparisons between Mexican white pines, the null hypothesis of the niche equivalency test was rejected (Table 3). On the other hand, in our analysis of niche similarity, the null hypothesis held for all pairs of Mexican white pines (‘Niche similarity’ in Table 3). For some pairs of Mexican white pines, the niche similarities were higher than expected by chance, for example, P. ayacahuite with P. strobos var. chiapensis, and P. ayacahuite var. veitchii with P. strobiiformis. The environmental niches of P. ayacahuite and P. strobos var. chiapensis were not statistically different ($P > 0.05$), exhibiting 55% of geographic overlap (Table 3). Other pairs of pine taxa shared niche spaces that were more similar than expected by chance, but only in one direction, e.g., P. strobiiformis with P. ayacahuite, and P. strobiiformis with P. strobos var. chiapensis. This suggests that the ecological niche of P. strobiiformis was more similar than expected by chance to the one of P. ayacahuite but not vice versa. The same is true for P. strobiiformis, whose ecological niche was more similar to the one of P. strobos var. chiapensis but not vice versa. Combined with our results from niche equivalency, our findings highlight how the ecological niches of the Mexican white pine species although similar, are not identical.

DISCUSSION

We have identified the environmental constraints for the distribution of Mexican white pines by applying state-of-the-art ecological niche modelling and ordination techniques. The identification of the main environmental constrains of the present distribution of species is key for current conservation actions and when investigating the impacts of future climate change on biodiversity. The wide distribution of Mexican white pines in the American continent underlines the variety of environmental conditions to which they are adapted and also may reflect on the physiological differences between them. This is particularly important as the physiology of pine trees may limit their distribution across environmental gradients, however, more physiologically oriented models (see Prentice et al., 1992; Pearson & Dawson, 2003) should be applied to test this for the Mexican white pines. Moreover, we observed that the variables reflecting climate-extreme characteristics play an important role when investigating current species distributions, as found in our variable importance analysis, and may also render insights when investigating future species distributions responses to climate change and future conservation actions (Zimmermann et al., 2009).

The environment shaping the distribution of Mexican white pines

The environmental factors shaping the distribution of the Mexican white pines varied considerably. The two more northerly distributed pine species, P. strobiiformis and P. lambertiana, were highly constrained by solar radiation and temperature (Table 3). This is as expected, for these species as they inhabit the northernmost regions of the distribution of Mexican white pines, where low-temperatures winters last long and where access to light and heat are some of the main constrains for the survival and distribution of plant species (Maravilla et al., 2004; Weiss et al., 2004).

Isothermality is the quotient of the differences between the daily and annual temperature ranges. Presence at high values of isothermality may indicate that the species prefers areas where the differences in daily temperature across the day and night are than those across the year. The importance of isothermality for the distribution of different Mexican white pines shown in our models is supported by the great variation in daily and seasonal temperatures found across their distributional range (e.g., the mountain range in the state of Chihuahua Mexico in comparison with central and southern Mexico). In the northern areas, where P. strobiiformis and part of P. lambertiana have their main distribution, the daily temperatures fluctuations appear to be smaller than the great variation in temperature observed across the year, meanwhile southern Mexico and Central America regions (where P. ayacahuite and P. strobos var. chiapensis are mainly distributed) present higher daily temperature variation in comparison with that found across the year (Maravilla et al., 2004; Weiss et al., 2004).

The potential distribution of Mexican white pines obtained from our ENMs is in accordance with previously outlined ranges (Perry et al., 1998), rendering the added value of been spatial explicit models and of delineating the differences in ecological niche space conditions that shape the species distribution. Our results build upon previous knowledge, improving the differentiation of the ecological niche ranges and highlighting the different habitats for each Mexican white pine. Specifically, areas where P. ayacahuite (Fig. 2b) and P. strobos var. chiapensis (Fig. 2d) are both found are of particular importance as the latter is considered endangered under the IUCN (International Union for Conservation of Nature) Red List categories and the populations of the former are declining (Thomas & Farjon, 2013). We have shown a wider environmental niche space for P. strobos var. chiapensis than for other species (Fig. 3). The populations of P. strobos var. chiapensis have decreased in the past years (Thomas & Farjon, 2013). Some of the main threats identified for P. strobos var. chiapensis are high deforestation rates, land conversion to agriculture, the introduction of exotic species (e.g. Casuarinaequisetifolia L. and Cupressuslusitanaica Miller), and the fragmentation of populations (del Castillo et al., 2009; Thomas & Farjon, 2013). Our results highlight opportunities for the re-introduction and imple-
The only white pine species whose range did not overlap with other white pines was *P. lambertiana*, (Fig. 2f). For *P. lambertiana*, suitable habitat was also projected in small locations where it has not been previously recorded in southern USA (Fig. 2f). For *P. lambertiana*, these areas might not yet have been populated because of the long distance to the main distributional range in California (Kinloch & Dulitz, 1990), or given any restricting biological interactions and environmental or anthropogenic barriers (Pearson & Dawson, 2003; Keith et al., 2011).

The highlighted suitability hotspots areas (Fig. 2a) are of singular importance as it has been shown that most species of the genus *Pinus* in Mexico are not adequately protected by the currently proposed network of natural protected areas (Aguirre-Gutiérrez & Duivenvoorden, 2010). This is corroborated by our results that show that from a total area of 9,85,568 km² predicted as suitable at least for one white pine species only 12% is inside declared/official protected areas (Fig. 4). Furthermore, from the 49,717 km² predicted as highly suitable for most Mexican white pine species only 10,966 km² are currently under protection (Fig. 4). The highlighted hotspots regions are crucial to delimitate networks of protected areas and safeguard the centre of diversity of the Mexican white pines.

**The niche overlap, equivalency and similarity**

Given the wide variation in environmental conditions where white pine species occur, it is perhaps not surprising that niche overlap between Mexican white pines was low. The low niche overlap values between *P. ayacahuite* and *P. lambertiana*, and between the latter and *P. Strobus var. chiapensis*, are also reflected on their different environmental constraints (Farjon et al., 1997; Richardson, 1998).

In our analysis, we show how the ecological niches of Mexican white pines are not interchangeable: our assessment of niche equivalency rejected the null hypothesis that the ecological niches of all species pairs are equivalent. This shows why it is not accurate to imply niche characteristics for one species based on the niche of another—even for these considered ‘closely related’ pine species. The niche similarity results suggest that Mexican white pines share more
characteristics of their environmental niche spaces than randomly expected. Together, the findings above are not contradictory but suggest a tight link between these pine species, which share environmental niche spaces, thus corroborating they are closely related but still different taxa. The observed similarities in ecological niche space between Mexican white pines suggest that they have similar environmental constraints but that a different set of variables within this environmental niche space restrict their distribution. Further taxonomic analyses that take information on ecological niche similarity and equivalency into account, as well as morphological and molecular information, are needed to generate a comprehensive classification scheme for the Mexican white pines.

Implications for a broader context

The differences in environmental constraints shown in our study offers insights on the ecological niches of Mexican white pines as well as on individual impacts that on-going changes in climatic conditions may likely have on them. This is an important issue as an increase in temperature from 1.8 to 4.0 °C, and a reduction in precipitation up to 20% are expected in the ‘worst case’ climate change scenario for the regions of Central America to northern Mexico (Solomon et al., 2007). Changes in climatic conditions will have a direct effect on the distribution of the Mexican white pines whose ranges are strongly constrained by temperature and precipitation (Gomez-Mendoza & Arriaga, 2007; Chen et al., 2011). Nonetheless, to comprehensively assess the impacts of climate change, ENMs need to consider not only climatic information of the future conditions but also integrate the species dispersal mechanisms, crucial biological interactions and barriers for dispersion.

Information on niche breadth has direct implications in planning conservation actions, as widely distributed species might be less vulnerable to localized anthropogenic exploitation (Bellard et al., 2012; Mantyka-pringle et al., 2012). Conservation actions for the Mexican white pines can include protection of current forest stands, re-introduction of species in deforested/disturbed areas and increasing the connectivity between forested patches of pine populations. Furthermore, considering the effects of habitat fragmentation and land use change on forest biodiversity is pivotal as these pressures can have delayed and long-term negative impacts (extinction debt, Tilman et al., 1994) that need to be accounted for if conservation plans are to be successful (Gonzalez, 2013). Particularly, the narrow distribution of P. ayacahuite var. veitchii is likely at risk given logging actions and the intense urban activities that are expanding into the trans-volcanic belt area (Farjon, 2013b). There are few protected areas along or close to the Mexican transvolcanic belt, though most of them are small and scattered (Fig. 4). Some of the main protected areas are the ‘Zempoala - La Bufa’ national park, the ‘Sierra de Manantlan’ and the ‘Monarch butterfly’ reserve. These reserves represent important areas that can act as reservoirs of pines diversity, however, even in the Monarch butterfly reserve that has high protection status, current logging actions and land conversion continue their negative impact on biodiversity (Navarrete et al., 2011). Still, protected areas and social awareness seem to be a main asset for the conservation of biodiversity and particularly of the Mexican white pines.

CONCLUSIONS

The significant differences in ecological niche spaces that we have shown also reflect the reported taxonomic divisions among Mexican white pines (Syring et al., 2007; del Castillo et al., 2009). Differences in environmental constrains of the different Mexican white pine species are also reflected on the niche similarity, overlap and equivalency results. Based on these differences, our results support the taxonomic division between the P. ayacahuite–P. strobiformis complex.

Several drivers of declines of pine species around the world have been discussed in recent work (Richardson et al., 2007), and Mexican white pines are among the most threatened of pine taxa. Deforestation for agriculture and wood extraction are key drivers of the alarming decline of taxa in this group (i.e. Richardson et al., 2007; Navarrete et al., 2011; Vidal et al., 2014) and thus of their unique genetic diversity (Farjon et al., 1997). Reduced genetic diversity will reduce the ability of these pines to respond to changing environmental conditions, making it imperative to protect remaining populations. Current and future conservation actions, not only for the Mexican white pines but also for other taxa, could benefit from insights derived from knowledge of the role of environmental variables in shaping the ecological niche of focus species. In this context, effective conservation actions must take into account intrinsic requirements of different species and the main environmental drivers that shape their distributions. Different conservation interventions may be required even for closely related taxa (e.g. Pinus ayacahuite and the veitchii variety). Insights from this study should be useful for improving the on-going conservation actions to mitigate the declining trends in the populations of Mexican white pines by directing re-introductions and guiding the establishment of effective networks of protected areas.

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Author contributions: J.A.G. and H.S.C. conceived the idea. J.A.G designed and carried out the analyses and together with H.S.C. and N.R. interpreted the results. A.V.A. and J.P.R. gathered the data, prepared it for the analyses and/or provided information to help with data interpretation. J.A.G. drafted the text and all other authors provided corrections to manuscript drafts and discussed ideas within it.

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