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1   Recruitment and facilitation in *Pinus hartwegii*, a Mexican alpine treeline ecotone, with

2   potential responses to climate warming

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Abstract

Key message **Under climate warming the presence of key microsite facilitators modify soil moisture levels associated with successful tree recruitment at the treeline ecotone of *Pinus hartwegii*.**

Abstract Alpine treelines in Mexico are represented by high-elevation forests dominated by *P. hartwegii* Ldl. To address the degree to which the presence of suitable microsite facilitators are factors for successful recruitment within the treeline ecotone of *P. hartwegii* and modulate their responses to climate warming, year of natural tree establishment, number of trees recruited, and the presence of shelter elements at different exposures of Monte Tlaloc (in the Trans-Mexican Volcanic System) were recorded. For tree recruitment and microsite facilitation we recorded each tree and the type of potentially protective elements that may improve microsite conditions within a total of 32 circular plots (r = 18 m) in the alpine treeline ecotone (above 4000 m). Temperatures for Monte Tlaloc at 4000 m were estimated using the thermal gradient for the study area, and standard dendrochronological methods and a regression model were used to date tree recruitment. Vector generalized linear models show that maximum growing season temperatures have significantly influenced the temporal pattern of tree recruitment in this system over the past 50 years, but this influence was mediated by the presence (or absence) of specific shelter elements (shrubs, soil depressions, rocks or bare soil) within a specific treeline ecotone exposure, also shaping the spatial pattern of tree recruitment. The response of the treeline ecotone to climate warming at local scales is qualitatively modified by the presence of microscale features, requiring sufficient soil moisture to be available on the site of recruitment.

Keywords: Treeline; Climate warming; *Pinus hartwegii*; Facilitation; Recruitment.

Introduction

Treelines are temperature sensitive zones ideal for observing and understanding the responses of forest ecosystems to climate warming, which are expected to advance beyond their current position, to occupy higher altitudes and latitudes (Körner and Paulsen 2004; Holtmeier and Broll 2005; Harsch et al. 2009; Wieser et al. 2014).

Interest in alpine zones, also referred to as high-altitude or high-elevation land areas, has increased since the end of 20th century (e.g. Beniston et al. 1997; Messerli and Ives 1997; Körner 1998) and some studies have suggested that mountaintops are likely to be most impacted by climatic changes occurring on a global scale (Diaz et al. 2003; Solomon et al. 2007; Kholer et al. 2014). However, of such areas, the tropical alpine treelines of North America (e.g., Mexico) have received little attention (but see Biondi et al. 2009; Yocom and Fulé 2012).

Alpine treelines in Mexico are represented by high-elevation forests dominated by *P. hartwegii* Ldl. on the Trans-Mexican Volcanic Belt (Perry 1991). These treelines are not abrupt boundaries, but they present a treeline ecotone as defined by Körner and Paulsen (2004); that is, they are zones of transition from the uppermost closed forest, the timberline or forest limit, to the treeless alpine vegetation where the species' limit occurs.

Treeline ecotones with a diffuse form, like that of *P. hartwegii*, have exhibited an earlier, stronger response to climate warming than other ecotone forms, with over 80% of diffuse forms of treeline ecotones world-wide advancing, compared with 20% of abrupt, island or Krummholz forms (Harsch et al. 2009). Thus, a first approach to investigating the impact of climate warming on the recruitment of *P. hartwegii* at the treeline ecotone was demonstrated by Astudillo-Sánchez et al. (2017b), who reported a stronger positive relationship between tree recruitment and maximum temperature than other climate variables such as minimum temperature and precipitation over the last few decades.

74 Treelines are formed when the growing season temperature limits tree growth,

75 determining the potential or climatic treeline elevation or latitude, and this is the most general

76 phenomenon at all treelines world-wide (Körner 1998; Körner and Paulsen 2004). At alpine

77 treelines with a diffuse spatial pattern of trees within the ecotone, the form is maintained

78 primarily by growth limitation, where the primary stressor is low growing season temperature

79 (Harsch and Bader 2011). Thus, it is expected that warming during the growing season should

80 increase growth rates and seedling survival, resulting in more rapid recruitment in the alpine

81 treeline ecotone. However, this positive response would only be considered an early indicator

82 of the effect of climate warming and treeline advance, due to the fact that treeline positions

83 are the result of interactions between growth limitation and additional stresses that influence

84 mortality.

85 Despite climate warming, the upward advance of treelines through tree recruitment is not

86 ubiquitous (Cullen et al. 2001; Camarero and Gutiérrez 2004). Different responses to

87 increased temperature, including slowing or recession of the advance, have been detected at

88 treelines world-wide (Harsch et al. 2009), suggesting that climate is only one of the

89 environmental factors that influence tree recruitment and thus, the treeline dynamics.

90 Therefore, other factors operating at local scales have to be considered.

91 Tree recruitment at treelines in response to climate warming may vary with local

92 conditions (e.g. exposure, latitude or continentality), topography (Holtmeier and Broll 2005;

93 Resler 2006; Butler et al. 2007), disturbance, including human and wild-living animal

94 impacts (Daniels and Veblen 2004; Holtmeier 2009), ecotone composition (Danby and Hik

95 2007) and species–specific traits such as seed production and dispersal (Dullinger et al.

96 2004), shade dependence, frost resistance, among others factors (Harsch and Bader 2011).

97   The fine-scale environment in which a tree species germinates and establishes in harsh

98   environments, such as alpine treeline ecotones, is a reflection of the conditions necessary for

99   successful recruitment and therefore the advance of the treeline, and some authors have

100   described the positive influence (e.g. through seedling abundance) of the presence of safe

101   sites, but also on facilitation or the positive interactions of neighbors buffering one another

102   from stressful conditions (Callaway 1995; Hättenschwiler and Smith 1999; Bekker 2005).

103   Thus, facilitation (intra-or interspecific) and sheltering effects of surface microtopography

104   may be crucial to seedling growth and survival after seed germination in alpine treeline

105   ecotones (Germino et al. 2002; Resler 2006).

106   In this study, we hypothesized that the relationship between maximum growing season

107   temperature and microsite facilitators are two potential factors for successful recruitment

108   within a *P. hartwegii* treeline ecotone in response to climate warming. To address these, our

109   study objectives were: (1) to determine the year of natural tree establishment; and (2) to

110   quantify the trees recruited at different exposures (compass directions) by the presence of

111   shelter elements that have potentially provided safe microsite conditions for survival.

112

113   **Materials and methods**

114

115   *Study area*

116   The study was conducted at Monte Tlaloc, a high volcanic peak located in the central

117   portion of the Trans-Mexican Volcanic Belt within the limits of the state of Mexico and

118   bordering the states of Puebla and Tlaxcala, with an elevation range from 2800 m to 4125 m

119   (Fig. 1a). Lower elevation soils are rich in clay and humus content, but as the elevation

120   increases (> 4000 m) the dominant soils become leptosols, which are of volcanic origin,

121   shallow, morphologically poorly developed and with low-water holding capacity and fertility

122   (IUSS 2015). The topography along the elevational gradient of the treeline ecotone is

123   characterized by a mosaic of convex landforms (bare outcrops of rock), shallow depressions,

124   and erratic rock blocks.
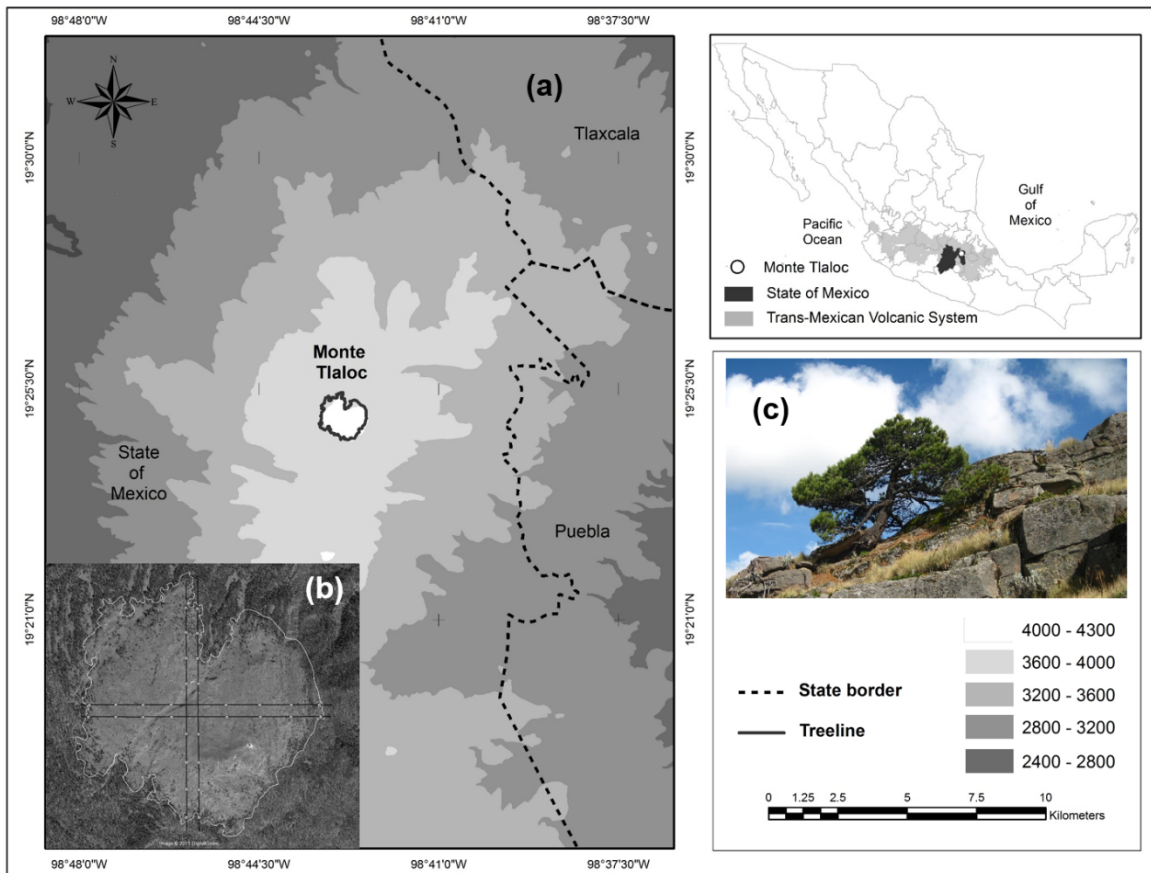
126   **Fig. 1** Geographic location of Monte Tlaloc in the Trans-Mexican Volcanic System (**a**),

127   Treeline ecotone sample sites (**b**) and *P. hartwegii* growing in a microsite (**c**)

129   Above 4000 m altitude, Monte Tlaloc does not show signs of disturbance by human land

130   use, including timber harvesting and livestock grazing, nor browsing by wild-living

6

131   ungulates. However, lightning strike-caused surface fires are frequent in this zone of the

132   mountain, influencing the *P. hartwegii* regeneration dynamics (Lauer and Klaus, 1975;

133   Rodríguez and Fulé, 2003; Robles-Gutiérrez et al. 2016).

134   *Climate*

135   The climate at the alpine treeline in Mexico (around 4000 m) is cold, with summer

136   precipitation (García 2004). However, given the lack of study area-specific climate data, we

137   used records from two local weather stations, both of them located to the west of Monte

138   Tlaloc: Chapingo, 19.5°N, 98.9°W, 2250 m (1955-2009 for air temperature and

139   precipitation), and Nevado de Toluca, 19.1°N, 99.8°W, 4283 m, (1969-2006 for air

140   temperature) located 19 km and 115 km away (Euclidean distance between sites),

141   respectively. Climate data was derived from the *Climate Computing* database (CLICOM,

142   2015; http://clicom-mex.cicese.mx/) from the National Meteorological Service.

143   To estimate the temperatures for Monte Tlaloc at 4000 m we calculated the thermal

144   gradient for the study area (0.6 °C/100 m) applying the principle that the temperature

145   decreases with increasing altitude (García 1986). We calculated the difference in altitude

146   between Chapingo and Nevado de Toluca, as well as the difference in temperature, as

147   follows: $X = 100 \, (H_{Ch} - H_{NT}) \, / \, (T_{Ch} - T_{NT})$, where X = thermal gradient, 100 = increment in

148   altitude in m, H_{Ch} = altitude of Chapingo station in m, H_{NT} = altitude of Nevado de Toluca

149   station in m, T_{Ch} = annual temperature of Chapingo station, and T_{NT} = annual temperature of

150   Nevado de Toluca station. To estimate precipitation in the study area, we assumed that

151   precipitation also exhibits a characteristic height dependence, as has been observed in the

152   highlands of central Mexico, where annual records generally show a precipitation increase

153   with altitude up to 3300 m. Beyond this elevation, a decrease of around 85 mm/100 m occurs

154 (Lauer and Klaus, 1975). Because *P. hartwegii* is dominant around 3500 m in Monte Tlaloc,

155 this value was considered to indicate the altitude at which precipitation begins to decline in

156 the mountain due to a shift of the dominant vegetation from *Abies religiosa* (Kunth) Schltdl.

157 and Cham. forest (< 3500 m) to *P. hartwegii* forest (≥ 3500 m).

158   Based on these considerations, we estimated a mean annual precipitation of 915 mm at

159 the Monte Tlaloc treeline; with the highest rainfall during July and August with 187 and 172

160 mm, respectively, while December and February had the lowest rainfall, each with 7 mm.

161 Mean annual temperature (calculated from the minimum and maximum monthly values) is

162 4.2 °C; the highest monthly mean temperature of 6.8 °C occurs in May, the lowest in

163 December with 1.2 °C and January with 0.9 °C. Mean summer precipitation (June-October)

164 is 736 mm. The mean temperature and precipitation growing season of *P. hartwegii* is 5.4 °C

165 and 108.6 mm, respectively, which corresponds to March to October.

166

167 *Vegetation*

168   *P. hartwegii* dominates the subalpine (3500-4000 m) and alpine treeline ecotones (> 4000

169 m) of Monte Tlaloc at any exposure. Above the treeline (~ 4000 m), trees are found in groups

170 or isolated individuals, with their height diminished due to the strongly limiting

171 environmental conditions, according to the characteristics of a diffuse treeline (Harsch et al.

172 2009; Harsch and Bader 2011; the present study: supplementary material) giving way to the

173 alpine grassland, which principally includes *Calamagrostis tolucensis* (Kunth) Trin. ex

174 Steud. and *Festuca tolucensis* Kunth (Lauer and Klaus 1975). The shrub layer is composed

175   of isolated small patches or scattered specimens of *Juniperus monticola* Mart. (Giménez and

176   Escamilla 1999; Villanueva-Díaz et al. 2016).

177

178   *Sampling*

179   For tree recruitment, and microsite facilitation, we recorded the height and basal

180   diameter (hereafter diameter) of each tree within a total of 32 plots (~ 3.2 ha) in the alpine

181   treeline ecotone of Monte Tlaloc (above 4000 m) between October and November of 2013.

182   At four exposure sites (north, south, east, and west) we placed two sampling transects at a

183   distance of 100 m from each other, within and upwards of the alpine treeline ecotone. Eight

184   circular plots (r = 18 m) with an equidistant separation of 200 m between their central points

185   (sampling points) and with an altitudinal range of 60 m between the lower and upper plots

186   were located along each transect. The sampling points were taken from a previous design

187   based on a satellite image of Monte Tlaloc (Google Inc, 2013); these points were uploaded

188   to a Global Positioning System (GPS) and they were located in the field (Fig. 1b).

189   Additionally, in order to obtain some information on possible seed dispersal sources and

190   recruitment, the prevailing wind direction through flag trees (Körner 2012), the presence of

191   parent trees (trees with cones) and also the slope average at north, south, east and west-facing

192   of the treeline (~ 4000 m) were recorded.

193

194   *Reconstructing tree recruitment dates*

195   We use the term "tree recruitment" to refer to trees that established in the alpine treeline

196   ecotone and have persisted to the sampling time. Therefore, these included only individuals

197   aged ≥ 4 years. Individuals < 4 years were excluded due to the high mortality of conifer

198   seedlings in alpine ecotones at least until the second or third year of growth (Rochefort and

199   Peterson 1996), and hence it cannot be said that such young trees have already been

200   established. To date the trees' establishment, we took a subsample of trees within each plot

201   (Sampling section or subplot). Trees over 10 cm in diameter were cored, and trees with

202   diameter < 10 cm were cut in cross-sections about 2-4 cm thick. Trees were cored and cut as

203   close as possible to their root collar to determine tree ages most accurately. We re-cored trees

204   when the pith of the first core was absent.

205   Standard dendrochronological methods (Stokes and Smiley 1968; Fritts 1976) were used

206   to crossdate all cores and cross-sections against a *P. hartwegii* master chronology of Monte

207   Tlaloc (Astudillo-Sánchez et al. 2017a). The quality of dating was determined with the

208   COFECHA program (Holmes 1983; Grissino-Mayer 2001). Counting rings was necessary

209   with cores from very young trees, which had relatively few rings that also tended to show

210   little variation in width from year to year to be co-dated. Because a better correlation was

211   obtained between age and diameter ($r = 0.80$, $p < 0.01$) than with the height ($r = 0.70$, $p <$

212   0.01), the first correlation was used to generate a regression model and estimate the age of

213   those trees that were not dated with dendrochronological techniques.

214

215   *Microsite facilitation*

216   The exposure of each treeline ecotone (north, south, east and west) was considered as a

217   microsite facilitation, the first approximation to the local site conditions for successful

218   recruitment. The vegetation and microtopographic features (e.g. soil depressions and rocks)

219 with which the trees in their early stages of life are associated, have previously proven to be

220 shelter elements appropriate for microsite facilitation at alpine treeline ecotones (Germino et

221 al. 2002; Akhalkatsi et al. 2006; Resler 2006; Butler et al. 2007; Holtmeier and Broll 2011),

222 with a positive influence under 0.5 m in radius (Batllori et al. 2009). Therefore, for all trees

223 sampled in the plots we considered as shelter elements: (1) shrubs (presence, $\leq$ 0.5 m in

224 radius) such as *J. monticola*, with individuals up to three hundred years old in the study area

225 (Villanueva-Díaz et al. 2016), is the species that would potentially would improve the

226 microhabitat conditions of young trees at alpine treeline ecotone; (2) soil depressions ($\sim$ 50

227 cm) due to runoff and solifluction treads; (3) rocks $\geq$ 60 cm in diameter (lee side); and (4)

228 bare soil (with small stones and pebbles, occasionally bedrock cleft).

229

230 *Evaluating tree recruitment, exposure sites, microsites and climate relationships*

231   We analyzed tree recruitment and microsites along with temperature to assess climatic

232 forcing of recruitment episodes. For this purpose, we used species specific growing season

233 averages of maximum temperature, the best climate variable previously related to *P.*

234 *hartwegii* recruitment from Monte Tlaloc at the treeline (Astudillo-Sánchez et al. 2017b).

235

236 *Statistical analysis*

237   A Pearson product-moment correlation established a first general approach of the

238 influence of temperature on tree recruitment patterns at the treeline ecotone.

239   Tree recruitment (response variable) in relation to exposure sites, microsites, and mean

240 growing season maximum temperature (explanatory variables) was assessed using (vector)

241 generalized linear models (vGLMs) in R version 3.3.3 (R Core Team 2017), with an

242 information theoretic approach to model selection and inference. All vGLMs were fitted by

243 using maximum likelihood methods and tree recruitment was assumed to have a Poisson

244 probability distribution. However, given the absence of zero values in the response variable

245 data (i.e. we did not have information on seed germination rates at the sites), we used zero-

246 truncated Poisson models as a solution for possible bias in the estimated parameters (Zuur et

247 al. 2009), using the 'pospoisson' error family in the 'vglm' function of the 'VGAM' package

248 (Yee 2010, 2017). Exposure sites and microsite explanatory variables each had four levels:

249 north, south, east, and west; and shrub, soil depression, rock and bare soil, respectively.

250 Multiple models were developed using plausible combinations of explanatory variables, and

251 small sample Akaike's information criterion (AIC$_c$) was used to select the "best" models of

252 tree recruitment in relation to explanatory variables, using the 'AICcmodavg' package

253 (Burnham and Anderson 2002; Mazerolle 2017). Akaike weights (w_i) and the natural

254 logarithm of the likelihood function (LL), were also calculated to aid model evaluation.

255 Finally, chi-square tests were conducted to evaluate whether vGLM explanatory variables

256 explained a significant component of the total deviance or not (Guisan et al. 2002).

257

258 **Results**

259

260 *Tree recruitment dates, climate, and age distribution*

261 We measured a total of 259 live trees in the 32 plots, and we were able to estimate ages

262 (date of establishment or recruitment) using cores and cross-sections for 100 of those trees.

263 The number of trees recruited ranged from 37 to 102 in relation to the exposure; the mean

264 tree age at the treeline ecotone was 17 years. Nevertheless, the oldest individuals tended to

265 be established on the southern exposure, while the youngest are located on the western (Table

266 1).

267 **Table 1** Recruitment and age characteristics of *P. hartwegii* for treeline ecotone exposures

268 in Monte Tlaloc (1955-2009)

Exposure	Trees recruited	Density (ha^{-1})	Age[†] (years)				
			Mode	Mean	SD[¶]	Maximum	Minimum
North	102	125.26	15	16.51	9.66	57	4
South	37	45.44	21	25.14	13.40	56	4
East	46	56.49	7	16.98	10.09	51	4
West	74	90.88	11	13.62	5.83	29	4
Total	259	318.07	15	17.00	10.09	57	4

269 [†] Based on dates of recruitment; [¶] Standard Deviation

270

271 We observed parent trees (i.e., those with cones) at the treeline; diameter at breast height

272 ranged from 36 to 47 cm, the one exception was on the east exposure where no parent trees

273 were observed. The absence of adult trees on this exposure is due to an abrupt drop of the

274 slope at about 4000 m altitude. On the other hand, the flag trees indicated that the prevailing

275 wind direction at the treeline ecotone is, in general, from east to west and from north to south,

276 while the inclination of the slopes ranged from 10 to 27 °, with the east exposure slope being

277 the steepest (Table 2).

278 **Table 2** Possible seed dispersing sources of *P. hartwegii* and slope conditions for tree

279 recruitment at each treeline ecotone exposures of Monte Tlaloc

| Exposure	Wind direction	Slope average (°)	Parent trees	
			Trees	DBH* average (cm)

North	E-W	13	8	47
South	NE-SW	12	5	36
East	E-W	27	0	0
West	NW-SE	10	8	37

280   *Diameter at Breast Height (1.3 m)

281   Given these observations, the dispersal of seeds, as well as their possible recruitment, the

282   trees seem to be less successful on the east exposure of the treeline ecotone than in the others,

283   not only because at this point there are no parent trees that disperse their seeds, despite the

284   favorable prevailing wind, but also due to the inclination of the slope, which can affect the

285   establishment of seedlings. Similarly, in the south exposure, where despite trees having cones

286   at the treeline, the wind in general blows in the opposite direction. Conversely, on north and

287   west exposures, trees have greater mean DBH, which, in turn, can result in a greater seed

288   production that are dispersed with a favorable wind direction for seedling recruitment.

289   Recruitment dates are summarized and compared alongside maximum growing season

290   temperature and the number trees recruited over time in north, south, east, and west exposures

291   of Monte Tlaloc (Fig. 2). The overall relationship between the maximum growing season

292   temperature and tree recruitment in *P. hartwegii* was characterized by a strong positive

293   association ($r = 0.74$, $p < 0.001$). Thus, some trees had established before or during the 1960-

294   1970s, representing 6 % of the population, until growing temperature regimes became more

295   favorable between the 1980-2009 period, during which 94 % of the trees established,

296   highlighting, in particular, the year of 1998 with an abundant *P. hartwegii* recruitment (Fig.

297   2a, b). The age distributions for north, south and east exposures were wide, including the

298   trees with the oldest ages, aged 57 (1956), 56 (1957), and 51 (1962) years, respectively.

299   However, the highest frequencies of age were more variable, with 15 (1998, north), 21 (1992,

300   south) and 7 (2006, east) years. The age distribution for the west exposure was narrow with

301   the highest frequency of 11 (2002) years and with maximum age of 29 (1984) years (Fig. 2c).
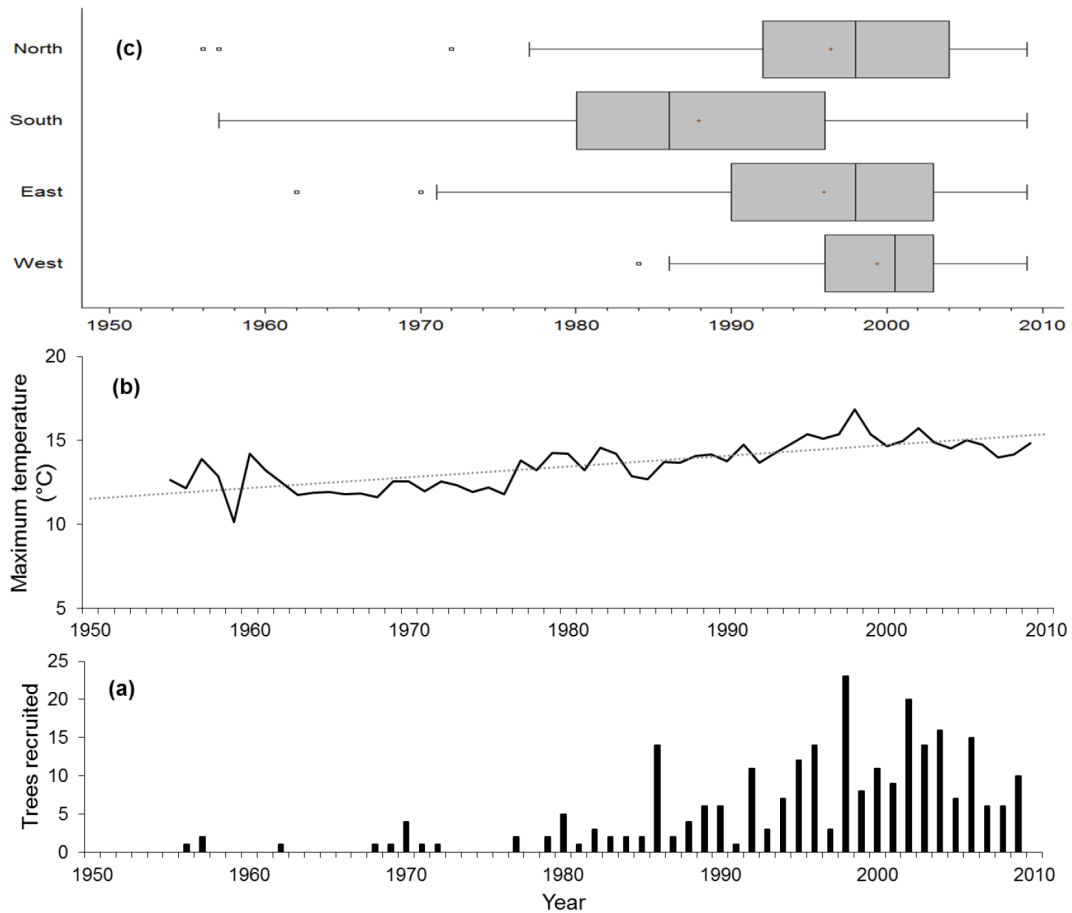
302

303   **Fig. 2** Trees recruited over time at Monte Tlaloc by annual tree recruitment in all treeline

304   ecotone exposures combined (**a**), maximum growing season temperature (**b**) and age

305   distributions at different treeline ecotone exposures (**c**)

306

307   *Tree recruitment, temperature, exposure and microsite facilitation relationships*

308   Evaluation of vGLMs, based on AIC_c values (Table 3) revealed that a model containing

309   an interaction between maximum temperature and microsite, plus the additive effect of

310   exposure, had the strongest empirical support to explain the tree recruitment of *P. hartwegii*

311   at the alpine treeline ecotone. All main and interaction effect terms in this model were found

312   to be significant (Table 4).

313   **Table 3** AIC_c selection of different zero-truncated Poisson General Linear Models (GLMs)

314   of tree recruitment at the alpine treeline ecotone

Models of Recruitment	AIC_c	Δ_i
Tmax	331.88	24.93
Msite	326.72	19.76
Exp	338.12	31.16
Tmax * Msite	311.51	4.56
Tmax * Exp	327.43	20.47
Tmax * Msite + Exp	**306.96**	**0**
Tmax * Exp + Msite	311.58	4.63
Tmax * Msite + Tmax*Exp	308.58	1.62
Tmax * Msite * Exp	347.73	40.35

315   Explanatory variable codes: Tmax, maximum temperature; Msite, microsite; Exp, exposure. The best
316   empirically supported model ($\Delta_i = 0$) in bold.

317

318   **Table 4** Analysis of deviance table from the best zero-truncated Poisson General Linear

319   Models (GLMs) of tree recruitment at alpine treeline ecotone, based on type III sums-of-

320   squares methods. LL = -141.63, D.F. = 157

| Explanatory variable	D.F.*	Chi-sq	p-value
Intercept	1	5.27	0.022
Tmax	1	5.77	0.016
Microsite	3	11.98	0.007
Exposure	3	9.43	0.024
Tmax:Microsite	3	12.53	0.006

321   *Degrees of Freedom

322   Recruitment declined with increasing maximum temperature at shrub microsites (slope

323   estimate = -1.15 ± 0.48 S.E), but this was the only microsite with a significant negative effect

324   of temperature (Table 5, Fig. 3). Soil depressions and bare soil were both associated with a

325   positive effect of increasing maximum temperature on recruitment, but there was no

326   significant effect of maximum temperature in rock microsites (Table 5). Mean effects of

327   maximum temperature on recruitment (intercepts) were highest in North and West exposures

328   (Table 5).

329   **Table 5** Parameter estimates from the zero-truncated Poisson General Linear Model (GLM)

330   of the effect of maximum temperature on tree recruitment at the alpine treeline ecotone,

331   where exposure (levels: north, south, east or west) was included as an additive term and

332   Microsite (shrubs, soil depressions, rocks and bare soil) was included as both an additive and

333   interaction term. Intercept and slope estimates are given for each model parameter (see Table

334   4)

Parameter types/names		Estimate	S.E.*	z-value	p-value
Intercepts	Shrubs, North	14.57	6.34	2.30	0.022
	Soil depressions, North	-7.43	3.55	-2.10	0.036
	Rocks, North	-2.62	3.47	-0.76	0.450
	Bare soil, North	-7.63	2.16	-3.53	<0.001
	South	-0.38	0.39	-0.98	0.328
	East	-0.81	0.33	-2.47	0.014
	West	-0.16	0.22	-0.75	0.454
Slopes	Shrubs	-1.15	0.48	-2.40	0.016
	Soil depressions	0.50	0.23	2.15	0.031
	Rocks	0.18	0.23	0.78	0.436
	Bare soil	0.54	0.14	3.81	<0.001

335   *Standard Error
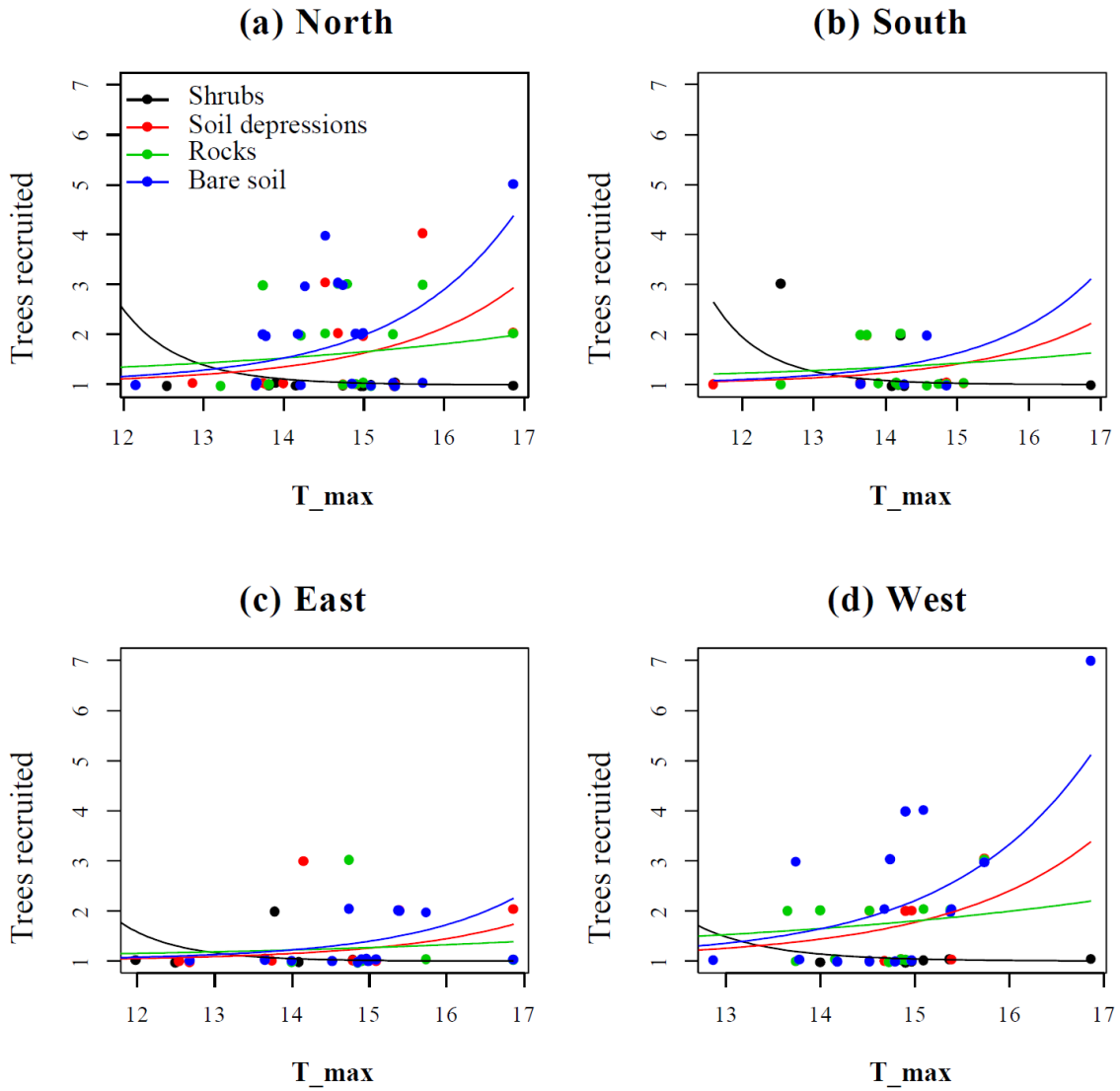
Fig. 3 Tree recruitment in relation to maximum growing season temperature (Tmax), exposure (panels a-d) and microsites (different coloured points/lines) of the different treeline ecotone exposures based on a zero-truncated Poisson generalized linear model (GLM) that includes an interaction between Tmax and Microsite

Discussion

343

344

345   We investigated the fine-scale environment conditions necessary for the successful

346   recruitment of *P. hartwegii* on the treeline ecotone. The results suggest that there have been

347   large increases in the proportion of trees recruited on the treeline ecotone over the past 50

348   years in response to the increase in temperature; yet at the same time, tree recruitment varied

349   as a function of the exposures and the interaction between temperature and the microsite

350   characteristics of the treeline ecotone. Therefore, regional environmental conditions, in the

351   form of maximum growing season temperatures, have significantly influenced the temporal

352   pattern of tree recruitment in this system, but this influence was mediated by the presence of

353   specific shelter elements (shrubs, soil depressions, rocks or bare soil) within a specific

354   treeline ecotone exposure, shaping the small-scale spatial pattern of tree recruitment and

355   resulting in complex recruitment responses to climate warming over time. The most notable

356   outcome was the switch from a negative effect of increasing temperatures on recruitment in

357   shrub microsites, to positive temperature effects on recruitment in soil depressions and bare

358   soils. Due to the role of fire in *P. hartwegii* ecology*,* below, we also consider this factor for

359   the implications of our findings for potential climate warming impacts on tree recruitment

360   and establishment in this system in the future.

361

362   *Microsite facilitation and tree recruitment responses to climate warming*

363   By relating the abundance of *P. hartwegii* recruits to regional climate and microsite

364   characteristics at the treeline ecotone we found evidence that these factors influence both

365 temporal and spatial patterns of tree recruitment in response to climate warming. On a

366 temporal scale, an increase of tree recruitment (across all exposures) with the increase in

367 temperature over time was observed, which is consistent with the response of tree recruitment

368 beyond the treeline of high-elevation forests (Körner and Paulsen 2004; Harsch et al. 2009;

369 Holtmeier and Broll 2010a). However, there were spatial differences in tree recruitment, with

370 *P. hartwegii* recruits clearly more abundant at north and west than at east and south

371 exposures.

372   On bare soil (with small stones and pebbles), tree recruitment was more abundant than in

373 the other microsites, which is likely suitable for tree establishment due to the absence of

374 competition for water or light, since *P. hartwegii* is shade-intolerant (Velázquez-Martínez et

375 al. 1986; Musálem et al. 1991). On the other hand, north and west mountain faces in central

376 Mexico show higher moisture conditions due to lower exposure to solar radiation (Lauer

377 1978). As a result, favorable light and moisture conditions promote tree growth and

378 subsequent establishment. Additionally, the presence of stones and pebbles has been shown

379 to decrease daily temperature variation in the soil, due to the capacity of heat conductivity,

380 especially at night and near sunrise. For example, at the Pico de Orizaba volcano, Mexico,

381 temperature in stony soils remains 5 to 7 °C warmer than in other areas (Lauer and Klaus

382 1975), which increases hours per day without freezing and extends the vegetative period on

383 these shaded mountain sites. Further, tree establishment was observed on bedrock in our

384 study site, particularly on north and west exposures. Holtmeier and Broll (2011; 2012)

385 documented that establishment of Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens*

386 *ssp. czerepanovii*) on bedrock at the upper treeline is due to the presence of clefts in the rock,

387 which are deep enough to accumulate fine inorganic and organic matter that improves

388   moisture conditions and nutrient supply to the young pines, which is similar to the

389   observations of our study.

390   The evidence of isolated tree stands growing on stony outcroppings along all exposures

391   of the treeline ecotone indicates their effective protection against fire. Natural fires in Monte

392   Tlaloc, as across the Trans-Mexican Volcanic System, generally occur at the beginning of

393   the rainy season with the first severe thunderstorms (Lauer and Klaus, 1975). Thus, the initial

394   precipitation soaks the surface vegetation and top soil, conditions that last longer in the north

395   and west exposures than in east and south facings of the mountain, due to lower exposure to

396   solar radiation, limiting the possibilities for the outbreak of natural surface fire and increasing

397   the survival of young trees.

398   Slope inclinations on north and west exposures were gentle (Table 2), characteristic of

399   ground that allows more recruitment than on steep slopes. Soil has stabilized and fine mineral

400   and organic material accumulated on these gentle slopes, which improves moisture and

401   nutrient conditions (Holtmeier and Broll 2010a). Furthermore, the inclination of the terrain

402   is among the topographical factors that could prevent the mortality of seedlings by fire,

403   particularly in *P. hartwegii*, where a survival of 84.3 % versus 8.1 % has been documented

404   on gentle slopes and steep slopes, respectively (Velázquez-Martínez et al. 1986). This is

405   consistent with the greater abundance of trees recruited on these exposures of the treeline

406   ecotone (Figs. 2 and 3).

407   Parent trees are present on north and west treeline exposures, which were more numerous

408   and with a larger diameter than those recorded in other exposures (Table 2). Since the

409   proximity of parent trees influences seed availability and successful reproduction of the

410   species beyond the treeline (Halpern et al. 2010; Holtmeier and Broll 2011; Zald et al. 2012),

411   a possible advance of the forest on north and west facings of the mountain is supported by

412   the evident growing population of *P. hartwegii* within these treeline ecotones (Fig. 2c).

413   On east and south facings, increased sun exposure during the day results in a greater loss

414   of soil moisture, a situation that is even more critical for the east treeline ecotone because it

415   has a steeper slope (Table 2). This combination exacerbates the temperature differences at

416   soil level, with soil temperatures up to three times higher at sites with steep slopes than those

417   with gentle slopes (Wieser 2007). As a result, these conditions cause a physiological drought

418   stress on seedlings (Camarero and Gutiérrez 2004; Elliott and Kipfmueller 2010), and at the

419   same time may limit carbon uptake (Martinelli 2004). Furthermore, such conditions of

420   excessive radiation, photo-oxidative stress and photoinhibition can negatively influence

421   growth and survival of younger trees (Germino and Smith 1999; Johnson et al. 2004; Bader

422   et al. 2007; Tausz 2007). In addition to the steep slope effects described above, tree

423   establishment is likely to be disturbed in an important way by gravitational effects on the east

424   exposure, triggering loss of soil and nutrients, which are necessary for tree growth (Broll et

425   al. 2007; Holtmeier and Broll 2005; 2007). Therefore, it is possible that the interaction of

426   these environmental factors both on the east and south exposures of the treeline ecotone may

427   have adverse effects on tree establishment at these sites despite the existence of apparently

428   suitable thermal conditions during the growing season.

429   Regarding the amount of solar radiation that east and south exposures receive, shelter

430   elements such as soil depressions, rocks and shrubs may take more importance in facilitating

431   *P. hartwegii* establishment under a warmer climate, particularly on the east exposure, as

432   observed in this study. At higher altitudes the effect of the wind restricts the establishment

433   of very young trees within the zones that comprise the treeline ecotone (Holtmeier and Broll

434   2010b). In the mountains of central Mexico, strong and persistent winds usually appear in

435   the spring (Lauer 1978); i.e. winds are stronger at the beginning of the growing season, which

436   also coincides with the months of highest temperature in Monte Tlaloc. The loss of soil

437   moisture is expected to be greater on the eastern and southern slopes, due to increased solar

438   radiation, affecting the development and survival of young trees established in these ecotone

439   exposures. Thus, for a young tree, establishing in a soil depression provides benefits such as

440   reduced solar radiation and wind exposure, which at the same time contribute to a retention

441   of greater soil moisture derived from snow accumulated on the site before the beginning of

442   growing season (Holtmeier 2005; Holtmeier and Broll 2005; Butler et al. 2007; Holtmeier

443   2009). Since nutrient supply from meltwater linked to the local snow is considered to be an

444   important source of nitrogen and phosphorous, this would compensate for the deficiency of

445   these nutrients, which is characteristic in the alpine zones (Bowman 1992). Consequently,

446   soil depressions are key microsites facilitating the successful tree recruitment of *P. hartwegii*

447   particularly at treeline ecotones with an east exposure.

448   In regard to the effect of shrubs near *P. hartwegii,* the model results (Table 5, Fig. 3)

449   suggest that shrubs change the effect of maximum growing season temperature from positive

450   (in the other microsites) to negative; i.e. increasing maximum growing season temperature

451   leads to a reduction in pine recruitment when there are shrubs nearby. This could indicate

452   competition for resources; since *P. hartwegii* is not shade-tolerant, light could be considered

453   the major limiting factor for those young pines that grow under the shadow of *J. monticola.*

454   Ramírez-Contreras and Rodríguez-Trejo (2009) evaluated the photosynthetically active

455   radiation in *P. hartwegii* in the presence of nurse plants, documenting that treatments with

456   shrubs exhibited the lowest radiation levels. The implications of receiving a sufficient level

457   of light, lies in the efficiency in the use of nutrients; for example, in *P. resinosa* Sol. Ex Aiton

458   the greatest efficiency in nutrient use was associated with the greatest amount of available

459   light (Minotta and Pinzauti 1996). This efficiency is not only limited to soil nutrients, but

460   also in the absorption of CO_2, as documented for seedlings growing under the shade of nurse

461   plants in desert environments (Franco and Nobel 1989). In shade-intolerant tree species such

462   as *Quercus robur*, strong interspecific competition for light between young trees and shrubs

463   resulted in a reduced growth and survival after four growing years (Jensen and Löf 2017).

464   Coupled with the competition for light, the presence of shrubs as nurse plants has also

465   resulted in a negative interaction in environments with lower soil water availability as result

466   of water competition (Padilla and Pugnaire 2006; 2007). Therefore, it is possible that strong

467   competition between *P. hartwegii* and *J. monticola* has resulted in a failed recruitment of the

468   pines.

469   Increased exposure to solar radiation on both east and south facings, and the steeper slope

470   in the east exposure, imply a relatively high level of dryness. The impact of fire is therefore

471   of critical importance to the recruitment of *P. hartwegii* in these zones. Lauer (1978) and

472   Yocom and Fulé (2003) suggest a fire regime that usually occurs at 6-to-7-years intervals

473   (maximum 9 years) at high-altitudinal forests in Mexico, but depending on the site, intervals

474   of 3-to-5 years can also occur. Fires are caused primarily by dry thunderstorms occurring

475   quite frequently in May, i.e. thunderstorms without rainfall (Lauer 1978). This regime seems

476   to be related to the recruitment pulses in years 1986, 1992, 1998, 2002 in the treeline ecotone

477   of the zone under study (Fig. 2a). The highest number of forest fires recorded in central

478   Mexico occurred in 1998 as a consequence of the historic droughts under the influence of the

479   strongest 'El Niño' event during the months of March-May (Rodríguez and Pyne, 1999;

480   Duncan et al. 2003) and the evidence of such drought was detected through the narrow tree-

481   rings width of *P. hartwegii* at treeline of Monte Tlaloc (Astudillo et al. 2017a).

482   Conditions of above-mean temperatures and reduced precipitation during March-May of

483   1998 at east and south exposures of the treeline ecotone, already the driest ones, could have

484   increased the availability of fuel, comprised of grasses, needles, woody material, shrubs and

485   young *P. hartwegii* trees. This excess of fuel is likely to develop high intensity fires, which,

486   combined with the presence of fractures and corridors under the stony soil where fuel

487   accumulates, facilitate the presence of underground fires. In these conditions, the impact of

488   fire at east and south exposures could have catastrophic consequences, particularly on the

489   survival of young pines who have not yet developed enough height and bark thickness to

490   resist the fire. Robles-Gutiérrez et al. (2016) determined that the mortality of young *P.*

491   *hartwegii* by fire increases when damage to the canopy is accompanied by damage to the

492   conductive tissue, which results in a decrease in the production and distribution of

493   photosynthates, which implies more than 50 % mortality. Aditionally, the presence of

494   underground fires in these exposures combined with the steep slope and strong winds could

495   also critically affect the adult trees, due to the high rate of fire spread, estimated to reach 60

496   m/min and flame heigths of 6-8 m under this combination of conditions (Rodríguez-Trejo

497   and Fulé 2003). Hence, the south and east exposures of the treeline ecotone showed relatively

498   low recruitment in 1998 (Table 1).

499   Conversely to the south and east exposures, the north facing of treeline ecotone showed a

500   higher tree recruitment in 1998 (Table 1). This facing of the mountain has higher moisture

501   and gentle slopes, thus it is likely that during the spring of 1998, low-intensity fires have

502   developed in this zone. Surface or low-intensity fires, favour the recruitment of *P. hartwegii*

503 seedlings, as they eliminate physical competition (grasses) and the ash provides more

504 nutrients to the soil (Rodríguez-Trejo et al. 2004). Moreover, given the serotine condition of

505 this species, it is likely that the release of seeds in the forest has been encouraged, dispersing

506 through the ecotone to finally germinate and establish under the positive influence of the

507 precipitation during the summer of 1998 (Astudillo et al. 2017b).

508 Most older trees on suth and east exposures that grew above the present treeline are those

509 who could face the episodes of fires over the past decades, and these trees provide inferences

510 about the limiting climatic factors in the past. Thus, notwithstanding the outcome of this

511 study that suggests that shrubs change the effect of maximum growing season temperature

512 from positive to negative, the presence of shrubs may have been crucial in the past acting as

513 a refuge and providing protection in the winter against low temperatures. Moreover, greater

514 soil moisture derived from accumulated, melted snow can be used by recruits during the

515 beginning of the growing season (Dalen and Hofgaard 2005; Hofgaard et al. 2009; Holtmeier

516 and Broll 2010a). All these facts are consistent with the record of older trees at the east and

517 south exposures of the treeline ecotone (Fig. 2b, c), years in which the temperature conditions

518 were not yet favorable for tree establishment and therefore, it is likely that the presence not

519 only of shrubs, but also of soil depressions and rocks, would have been crucial for tree

520 survival on those faces of the mountain during colder periods. While in the north and west

521 facings, being more humid and cold, the same shelter elements have probably had a negative

522 effect on the establishment of young pines due to wet conditions, late-lying snow, and fungal

523 infections (Holtmeier and Broll 2012). Therefore, tree establishment on bare soil at these

524 sites has been more successful.

525   Coupled with the effect of microsite facilitation, the recruitment of new individuals

526   beyond the treeline depends on successful reproduction of the species (Juntunen and

527   Neuvonen 2006). However, the absence of parent trees on the east exposure of the treeline

528   ecotone could severely affect this process. This, added to the fact that most woody species

529   have transient seed banks (Baskin and Baskin 1998), and conifer seeds in particular survive

530   in the soil for a short time (Pratt et al. 1984), the presence of current young pines in this zone

531   would indicate that in fact, the regeneration in this exposure is due to the dispersion of seeds

532   by wind, which come from distant sources of the mountain and less so by a possibly long-

533   term seed bank at the site. Thus, tree recruitment on the east treeline ecotone exposure is

534   uncertain in the future, even though a favorable climate and shelter elements for the

535   development of seedlings can be found. On the other hand, while there are currently young

536   trees on both the east and south exposures, under a warmer climate, the risk of death by fire

537   of these young pines is higher than on the other exposures due to greater soil dryness in these

538   ecotones. Therefore, future forest advance on the east and south facings of the mountain is

539   uncertain under climate warming.

540   Finally, despite a growing literature on the ecological impacts of climate change where it

541   is argued that shifts in the treeline ecotone are not upward in relationship to climate warming,

542   particularly during the growing season (e.g. Davis and Gedalof, 2018), our study evidences

543   different behavior. At the same time, this study highlights the importance of analyzing the

544   local spatial variability and seasonal temperature changes, rather than mean global trends.

545   Thus, according with Harsch and Bader (2011), the form of the treeline is associated with

546   the probability of treeline advance, and in this case, we show that a diffuse form of the *P.*

547   *hartwegii* treeline seems to have a stronger response to climate warming. On the other hand,

548   it has been documented that the influence of temperature as the dominant factor controlling

549   treeline position at some sites may be masked by the presence of human-induced disturbances

550   (Daniels and Veblen 2004; Holtmeier 2009), as well as by the use of general climate data or

551   rescaled data which do not reflect the true dominant environmental conditions of the site

552   (Harsch et al. 2009; Astudillo-Sánchez et al. 2017a). The interaction of these factors were

553   not considered significant at the study site, which implies a clear climate action on the tree

554   recruitment.

555   Notwithstanding the aforementioned, we consider that a positive response of the treeline

556   ecotone to climate warming can be modified by the microsite characteristics where *P.*

557   *hartweegii* trees are established, such that this interaction ultimately will determine the trees

558   survival and therefore their successful recruitment rates and the potential advance of the

559   treeline.

560

561   **Conclusions**

562

563   Successful tree recruitment on the treeline ecotone is related to maximum growing season

564   temperature, which is qualitatively modified by the presence of specific microscale features,

565   requiring sufficient soil moisture to be available on the site of recruitment.

566   The gradient of slope inclination and the absence of parent trees could delay or even

567   prevent tree establishment driven by climate warming in the exposures with the highest solar

568   radiation, particularly on the east face of the mountain. Under excessive heating combined

569   with drought conditions, tree establishment will be restricted to microsites which would

570　result in a highly fragmented treeline and consequently the advance of the forest to higher

571　elevations is unlikely in these sites. On more gentle slopes with shade and moister conditions

572　and the presence of parent trees as in the north and west exposures, closed forest may expand

573　to higher elevations.

574　　The increase of tree recruitment of *P. hartwegii* on the treeline ecotone is likely to play an

575　important role in any landscape change of the current treeline at north and west facings of

576　the mountain. On the other hand, on east and south facings, the treeline landscape is unlikely

577　to change significantly in response to climate warming.

578

579　**Author contribution statement**

580　CA, JV, and AE contributed to the original idea and field sampling. Reconstructing tree

581　recruitment dates and analysis were performed by CA and JV. Statistical analysis were

582　conducted by CA, MF, and LS. CA wrote the draft of the manuscript. MF, JV, AE, and LS

583　provided revisions on the manuscript. The authors approved the final manuscript.

584

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592

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

596

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