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1 Recruitment and facilitation in *Pinus hartwegii*, a Mexican alpine treeline ecotone, with
2 potential responses to climate warming

3

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26 **Abstract**

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

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

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

49 **Introduction**

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

54 Interest in alpine zones, also referred to as high-altitude or high-elevation land areas, has
55 increased since the end of 20th century (e.g. Beniston et al. 1997; Messerli and Ives 1997;
56 Körner 1998) and some studies have suggested that mountaintops are likely to be most
57 impacted by climatic changes occurring on a global scale (Diaz et al. 2003; Solomon et al.
58 2007; Kholer et al. 2014). However, of such areas, the tropical alpine treelines of North
59 America (e.g., Mexico) have received little attention (but see Biondi et al. 2009; Yocom and
60 Fulé 2012).

61 Alpine treelines in Mexico are represented by high-elevation forests dominated by *P.*
62 *hartwegii* Ldl. on the Trans-Mexican Volcanic Belt (Perry 1991). These treelines are not
63 abrupt boundaries, but they present a treeline ecotone as defined by Körner and Paulsen
64 (2004); that is, they are zones of transition from the uppermost closed forest, the timberline
65 or forest limit, to the treeless alpine vegetation where the species' limit occurs.

66 Treeline ecotones with a diffuse form, like that of *P. hartwegii*, have exhibited an earlier,
67 stronger response to climate warming than other ecotone forms, with over 80% of diffuse
68 forms of treeline ecotones world-wide advancing, compared with 20% of abrupt, island or
69 Krummholz forms (Harsch et al. 2009). Thus, a first approach to investigating the impact of
70 climate warming on the recruitment of *P. hartwegii* at the treeline ecotone was demonstrated
71 by Astudillo-Sánchez et al. (2017b), who reported a stronger positive relationship between
72 tree recruitment and maximum temperature than other climate variables such as minimum
73 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

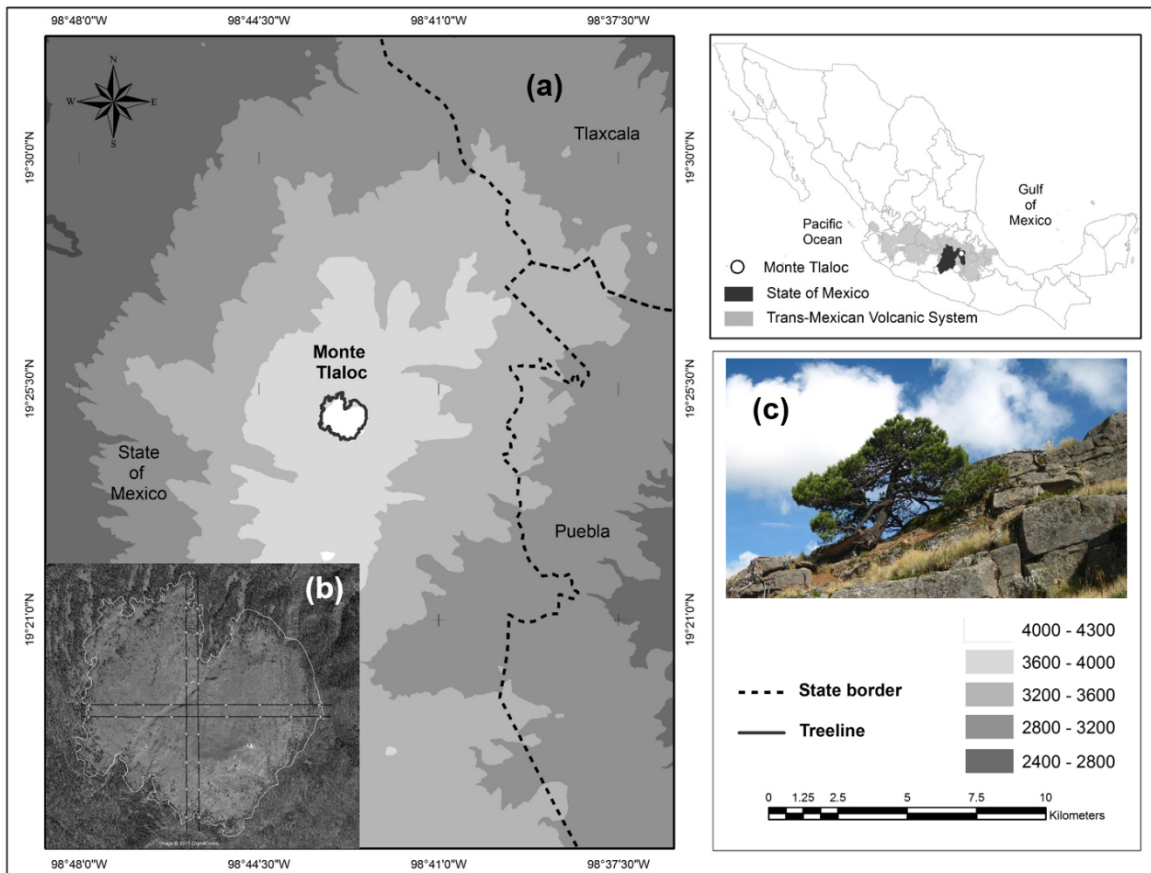
113 **Materials and methods**

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.



125
 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)

128

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

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 (\geq 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 toluensis* (Kunth) Trin. ex
174 Steud. and *Festuca toluensis* 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, ≤ 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 (~ 50
227 cm) due to runoff and solifluction treads; (3) rocks ≥ 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, microsities and climate relationships*

231 We analyzed tree recruitment and microsities 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, microsities, 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)

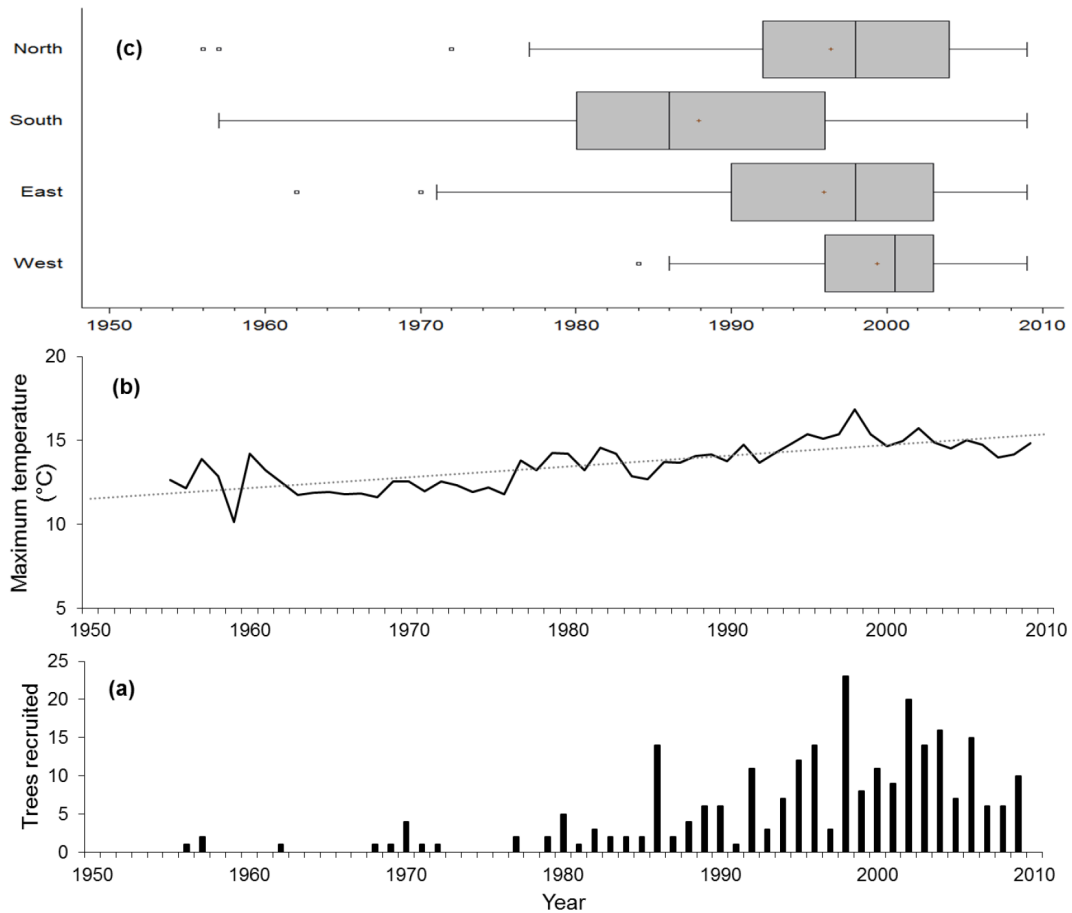
North	E-W	13	8	47
South	NE-SW	12	5	36
East	E-W	27	0	0
West	NW-SE	10	8	37

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 (Δ_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

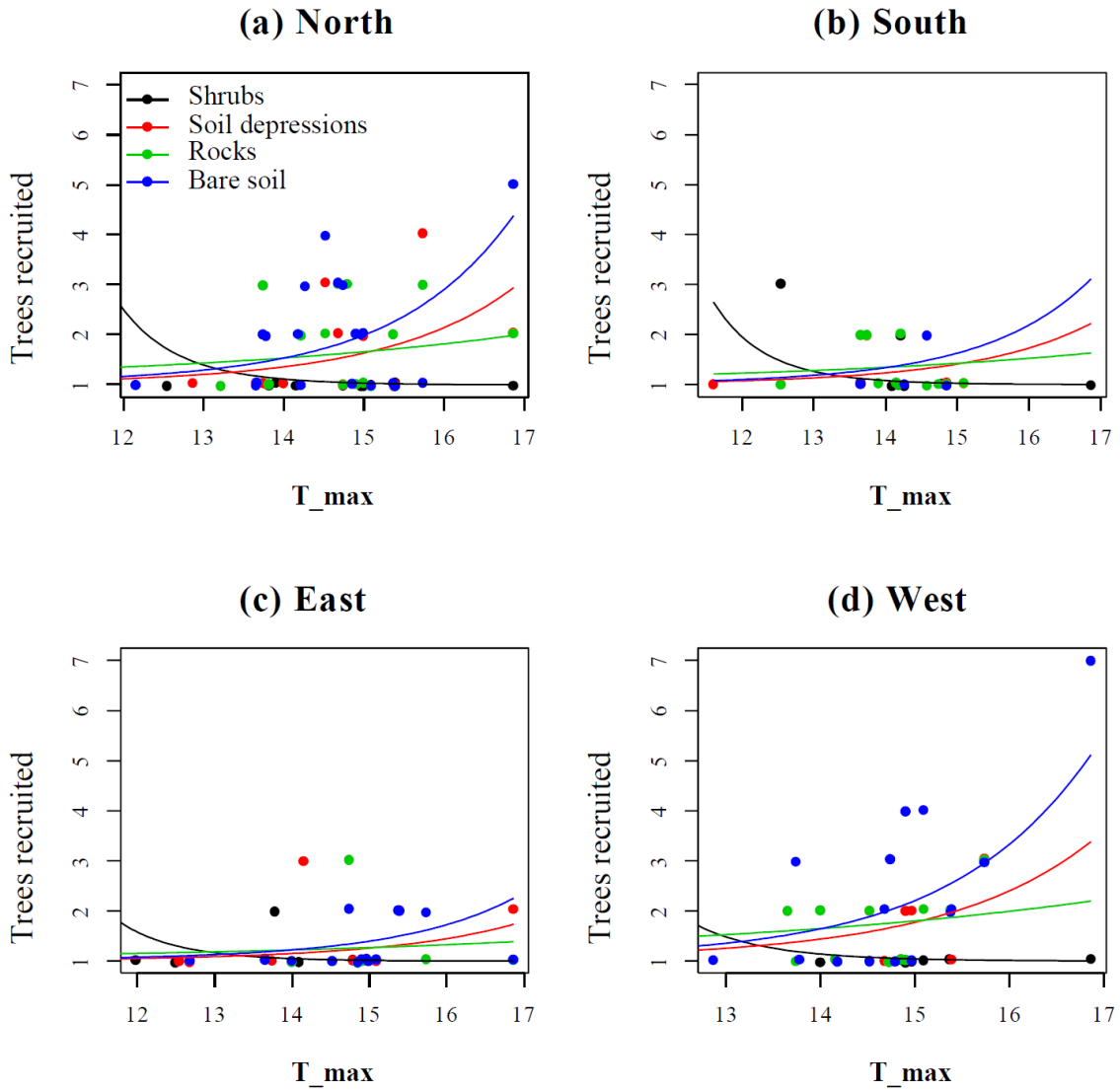
321 *Degrees of Freedom

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
	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



336

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

341

342

343 **Discussion**

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 Kipfmüller 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 CO₂, 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. Additionally, 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 heights 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 south 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 *hartwegii* 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

593 **Compliance with ethical standards**

594 **Conflict of interest**

595 The authors declare that they have no conflict of interest.

596

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