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Invasive fountain grass (*Pennisetum setaceum* (Forssk.) Chiov.) increases its potential area of distribution in Tenerife island under future climatic scenarios

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Invasive fountain grass (*Pennisetum setaceum*
(Forssk.) Chiov.) increases its potential area of
distribution in Tenerife island under future climatic
scenarios

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Abstract

1 Mapping the distribution of invasive species under current and future climate
2 conditions is crucial to implement sustainable and effective conservation strategies.
3 Several studies showed how invasive species may benefit from climate change foster-
4 ing their invasion rate and, consequently, affecting the native species community. In
5 the Canary Islands and on Tenerife in particular, previous research mostly focused
6 on climate change impacts on the native communities, whereas less attention has
7 been paid on alien species distribution under climate change scenarios.

8 In this study, we modelled the habitat distribution of *Pennisetum setaceum*, one
9 of the most invasive alien species on Tenerife. In addition, we described the species'
10 potential distribution shift in the light of two climate change scenarios (RCP2.6,
11 RCP8.5), highlighting the areas that should be prioritized during management and
12 eradication programs.

13 *P. setaceum*'s suitable areas are located in the coastal area, with higher habitat
14 suitability near cities and below 800 m asl. In both future climate change scenarios,
15 the geographic distribution of *P. setaceum* suitable areas is characterized by an
16 elevational shift, which is more pronounced in the RCP8.5 scenario.

17 Despite being drought resistant, water supply is crucial for the species' seed
18 germination, thus supporting future species' shift to higher elevation and in the
19 north-north-west part of the island, where it could benefit from the combined effect
20 of orographic precipitations and humidity carried by trade winds.

21 **Keywords:** Habitat suitability models, invasive alien species, Canary Archipelago,
22 global warming
23

1 Introduction

Climate change is having strong ecological impacts on biodiversity from the polar regions to the tropics, and predicting the response of biodiversity to future climate change scenarios has become a primary field of research (Pereira et al., 2010; Bellard et al., 2012; Matías and Jump, 2013; Dyderski et al., 2018). Global warming, along with the reduction in precipitation during the growing season, may strongly alter species distribution (Kleinbauer et al., 2010; Stocker, 2014). Furthermore, the increase in CO₂ atmospheric concentration and Nitrogen deposition promote the presence of invasive species and enhance the risk of biological invasions (Dukes and Mooney, 1999). In this context, special attention should be paid to island systems: islands are, in fact, at the forefront against global changes such as sea-level rise and biological invasions (Bellard et al., 2014; Pyšek et al., 2017). Islands are well-known to host habitats rich in rare and endemic species, hence more than one third of biodiversity hotspots in the world are entirely, or largely, within islands (Bellard et al., 2014).

Biological invasions are dramatically threatening island biodiversity and ecosystem integrity (Hulme, 2009; Scalera et al., 2012) since invasive alien species (hereafter IAS, see Pyšek et al., 2004 for comprehensive definitions) may directly reduce local plant species diversity (Tordoni et al., 2019). However, the deleterious effect of plant invasion is not limited to competition with native species, but it could affect the whole ecosystem, especially enclosed and fragile ones such as islands. Firstly, changes in carbon and nitrogen soil dynamics, resulting from alien plants invasions (Vilà and López-Darias, 2006; Vilà et al., 2011; Qian and Ricklefs, 2006) impact soil biotic community and potentially alter important processes, such as mutualism. In nutrient enriched soils for example, mycorrhizal populations can become antagonistic to hosts (Toby Kiers et al., 2010). The balance in macroinvertebrate communities can be disrupted (Gremmen et al., 1998), with potential effects on the whole ecosystems. Secondly, invasive alien plant species could promote alien insect presence (Morales and Aizen, 2002), which has the potential to affect entire habitats and ultimately alter ecosystem functioning and services (Kenis et al., 2009). Finally, recent studies suggest that IAS may benefit from climate change (e.g. Kleinbauer et al., 2010; Brundu and Richardson, 2016; Dyderski et al., 2018), which foster their invasion rate and, consequently, invasion-related risks.

Due to the high rate of endemism (Whittaker and Fernández-Palacios, 2007; Fernández-Palacios et al., 2016), the Canary archipelago represents an extremely vulnerable area for alien species invasions (Courchamp et al., 2003; Assessment, 2005; Kueffer et al., 2010; Bacaro et al., 2015). Particularly, the island of Tenerife hosts a total of 9325 species, 1468 of them being vascular plants with 279 local endemic plant species (Arechavaleta et al., 2010). This island has been affected by an intense human activity that altered the natural ecosystems, causing fragmentation and the introduction of invasive species in protected areas (Delgado et al., 2004), such as fountain grass (*Pennisetum setaceum* (Forssk.) Chiov.).

Pennisetum setaceum is a perennial, wind-dispersed, apomictic, C4 bunch grass native to North Africa and the Middle East (Williams et al., 1995; Poulin et al., 2007). It was introduced in the Canary Islands as an ornamental plant and its presence has been reported since 1940s (Hansen et al., 1970; de Paz et al., 1999). Currently, it is considered one of the most invasive species on Tenerife (Arechavaleta et al., 2010; Francisco-Ortega et al., 2009) as well as in other areas (e.g. California, Hawaii, South Africa; Williams et al., 1995; Poulin et al., 2007; Rahlao et al., 2010), constantly expanding its range along roads, from

71 urbanized areas toward natural ones (Martín Esquivel et al., 1995; González-Rodríguez
72 et al., 2010). Elevated phenotypic plasticity, characterised by variation in functional trait
73 value according to the environment, and its resilience, makes *P. setaceum* well adapted
74 to different ecological conditions (Poulin et al., 2007; González-Rodríguez et al., 2010).
75 Moreover, it can establish symbiosis with different local mycorrhizal fungi (AMF) com-
76 munities, further promoting a successful establishment and spread (Rodríguez-Caballero
77 et al., 2018). It is an aggressive invader of arid and semiarid coastal habitats such as
78 thermo-xerophilous grasslands and shrublands. Here it establishes almost monospecific
79 stands and causes long-lasting ecological consequences (Cordell and Sandquist, 2008;
80 González-Rodríguez et al., 2010). The species is known to have negative impacts on re-
81 sources acquisitions in the dry forest plant communities and it can interact with the soil
82 bacterial community, shifting its structure and composition, which can result in severe
83 alterations of the N cycle (Rodríguez-Caballero et al., 2017). Moreover, it is a fire pro-
84 moting species that can cause dramatic environmental changes, since fire is one of the
85 most important drivers of land use and atmospheric changes globally (D’Antonio and
86 Vitousek, 1992). Finally, it can promote the presence of the alien invasive leafhopper
87 *Balclutha brevis* (Bella et al., 2012). It has been estimated that approximately 30% of all
88 protected areas of the Canary Islands have been invaded by fountain grass (Martín Es-
89 quivel et al., 1995; González-Rodríguez et al., 2010). Considering the dramatic effects
90 that an uncontrolled increase in its distribution could create on Tenerife, understanding
91 *P. setaceum* future habitat distribution is particularly important both from a conserva-
92 tional and ecological perspective, and it is a time-sensitive task.

93 Correlative models such as Habitat Suitability Models (HSMs) have extensively been
94 used so far to estimate the geographic distribution of a species based on an index of envi-
95 ronmental similarity (Kearney, 2006; Peterson et al., 2011; Guisan et al., 2017) which, in
96 turn, is estimated starting from its occurrences in relation to its environmental determi-
97 nants (Thuiller, 2007; Steiner et al., 2008; Jiménez-Valverde et al., 2011). HSMs became
98 a central tool in invasion biology, providing both interesting insight on species’ ecology
99 and practical suggestions for eradication management. For invasive species, the correct
100 projection in space and time of HSMs estimates depends on different assumptions, which
101 are defined by the research questions. It is fundamental to consider niche conservatism
102 among native and invasive range when the research objective is to project the suitability
103 index estimated in the native range into the invasive one. When using the species invaded
104 range to train a HSM, the invasive species must be at quasi-equilibrium with the environ-
105 ment in which it occurs (Guisan and Thuiller, 2005; Gallien et al., 2012). However, these
106 assumptions are not always met, since the naturalized climatic niche of invasive species
107 may differ from the natives climatic niches (e.g. Medley 2010; Early and Sax 2014) and
108 since an invasive species is not at equilibrium with its environment until the latest stage
109 of invasion (Barbet-Massin et al., 2018). Both cases result in a likely underestimate on
110 the species predicted habitat suitability distribution. However, in situations where as-
111 sumptions cannot be met for practical reasons (e.g. impossibility to compare native and
112 invasive niche), HSMs may still provide predictions which are useful for invasive species
113 management, such as highlighting the areas of likely expansion in the near future, which
114 should be targeted and prioritized by conservation efforts (West et al., 2016).

115 Considering the importance of predictive tools to halt the loss of biodiversity, espe-
116 cially in relation to the spread of IAS fostered by climate change, here we aimed at i)
117 estimating *P. setaceum*’s current habitat distribution through HSM, across its’ invaded
118 range in Tenerife and, ii) assessing the effect of climate change in shaping *P. setaceum*’s

119 habitat distribution under two climate change scenarios (RCP2.6, RCP8.5). We hypoth-
120 esize that *P. setaceum* may benefit from climate warming, increasing its current habitat
121 distribution by spreading toward more humid zone of the island (e.g. at higher elevation),
122 hence potentially increasing its impact on native habitats. Final goal of this study is to
123 disclose a clearer image of those portions of Tenerife which will be more prone to the
124 invasion process and therefore in urgent need of eradication and control activities.

125 2 Materials and Methods

126 2.1 Study area

127 The study was carried out in Tenerife (27–29 °N, 13–18 °W; Fig. 1), the largest island of
128 the Canary archipelago and the one with the highest elevation within Macaronesia (Mount
129 Teide, 3718 m asl). Strong variations in elevation and aspect define local mesoclimatic
130 zones and land uses, that are primary factors in structuring both native and alien plant
131 communities on the Canary Islands (Whittaker and Fernández-Palacios, 2007). Meso-
132 climate is affected by the trade winds that create a contrast between the northern or
133 windward aspect (more humid and cloudier) and the southern or leeward aspect (more
134 arid and cloudless).

135 2.2 Response variable

136 Data of *P. setaceum* occurrences were obtained from ATLANTIS (Gobierno de Canarias,
137 2015), a regional database containing IAS occurrences within a grid of 500 x 500 m
138 square cells covering the entire archipelago. Species records spanned in time from 1970
139 to 2017 but only those from 2005 to 2014 were considered for the analysis in order to
140 maintain data consistency with the climatic data available. Only the grid cells covering
141 Tenerife landmass were selected from the grid covering the whole Canary archipelago,
142 (5515 selected out of 8519 total cells). This dataset was complemented with records
143 obtained by the Teno Rural park internal database (Suppl. Mat.).

144 2.3 Predictors

145 Three abiotic variables were selected to predict species' habitat distribution based on
146 previous knowledge on the ecology and biology of *P. setaceum*.

147 Mean winter precipitation and mean spring precipitation were chosen since the period
148 October-March concentrate the 87.3 % of Canary Islands' annual precipitation (Sánchez-
149 Benítez et al., 2017). Moreover, it has been reported that in Mediterranean-type climate
150 areas, *P. setaceum* germination occurs primarily in the Winter-Spring period (especially
151 in December-January), followed by a constant decline towards the Summer due to mois-
152 ture reduction (Hernandez and Sandquist, 2011). Mean spring temperature was also
153 selected, since it is know to be a limiting factor for alien species colonization along an el-
154 evational gradient, being usually correlated to elevation (Barni et al., 2012; Bacaró et al.,
155 2015; Steinbauer et al., 2017) and because the species has a maximum growth in warmer
156 conditions (Sweet and Holt, 2015).

157 Finally, road kernel density was selected as a proxy of propagule pressure and species
158 dispersion, especially for *P. setaceum* (Foxcroft et al., 2019). Indeed anthropogenic activ-
159 ities enhance alien species' spread (Pyšek et al., 2010; Tordoni et al., 2017), and roads are

160 known to be primary introduction pathways. Particularly, roadside may serve as invasion
161 epicenters for annual species with high reproductive rates (Pauchard and Alaback, 2004;
162 Bacaro et al., 2015; Da Re et al., 2019).

163 Monthly precipitation of October-March periods and monthly temperature of March-
164 May periods, spanning from 2005 to 2014, were obtained from Agencia Estatal de Mete-
165 orología (AEMET, accessed on April 2016). The methodology presented in Da Re et al.
166 (2019) was used for filtering and the processing of the meteorological data in order to
167 obtain continuous climatic interpolated surfaces through a co-Kriging procedure, using
168 elevation as covariate (Myers, 1984; Garzón-Machado et al., 2014; Wilson and Silander,
169 2014) and the R-package “geoR” (Ribeiro Jr et al., 2001). Road kernel density, calculated
170 on the road network using 10 km regularly distributed sample points, was used here as a
171 proxy of human disturbance and as a source of propagule pressure (Bacaro et al., 2015;
172 Da Re et al., 2019). The Digital Elevation Model (DEM, 10 m of spatial resolution)
173 and road network of Tenerife Island were downloaded from Cartográfica de Canarias S.A.
174 (GRAFCAN, <https://www.grafcan.es/>, accessed on March 2016), all the derived vari-
175 ables were calculated using the grid spatial resolution as for the IAS occurrences (500 m)
176 (Tab. 1).

177 2.4 Climate change predictions

178 Temperature time series analysis of the Canary Islands reported a temperature increase
179 tendency, showing the greatest increases on island summit (above 2000 m asl) and above
180 the cloud layer of windward mid-altitude areas (Martín et al., 2012; Luque et al., 2014).
181 In regard to precipitation, there is no clear and significant change (García-Herrera et al.,
182 2003; Cropper and Hanna, 2014).

183 Cropper (2013) estimates an increase in surface air temperature of 1 °C and a decrease
184 in water availability of 15–20% due to more than 30% reduction in precipitation (Giorgi,
185 2006; Somot et al., 2008). In order to get a reliable estimate of climate change effects
186 on the climatic variables considered (though deemed approximate), we apply a constant
187 correction on interpolated climatic surfaces. Specifically, we considered the two Repre-
188 sentative Concentration Pathways (RCPs), namely RCP2.6 and RCP8.5, as described
189 by the 5th Intergovernmental Panel on Climate Change (IPCC) report representing pos-
190 sible ranges of radiative forcing values in the year 2100 relative to pre-industrial values
191 (+2.6 and +8.5 W/m², respectively). Winter and Spring precipitation were corrected
192 by -10.6% and -36.7% (RCP2.6 and RCP8.5) according to Winter (December – January
193 – February, DJF) precipitation reduction prevision made by Cropper (2013), while for
194 Spring temperature 0.96 °C (RCP2.6) and 2.68 °C (RCP8.5) were added.

195 2.5 Habitat Suitability Modelling

196 HSMs were performed using Maxent v3.4.1 (Phillips et al., 2017) through the R pack-
197 age "dismo" (Hijmans et al., 2017). Maxent estimates the relationship between species
198 occurrences and various environmental predictors, identifying areas with suitable envi-
199 ronmental conditions for the species, given a background uniform probability of 0.5 (Elith
200 et al., 2011). To reduce the effects of sampling bias and thus avoiding a possible source
201 of model inaccuracy (Phillips et al., 2006, 2009; Syfert et al., 2013), spatial filtering with
202 a thinning distance of 2 km was applied to the *P. setaceum* occurrence dataset using the
203 R package "spThin" (Aiello-Lammens et al., 2015). The thinned-occurrence data were

204 then randomly divided into a training set and testing dataset applying a spatial block ap-
205 proach (Guevara et al., 2018; Roberts et al., 2017). Models with different combinations of
206 feature classes (FC: Linear; Quadratic; Linear and Quadratic; Hinge; Linear, Quadratic,
207 and Hinge) and beta regularization multipliers (RM: 0.5 – 5.0 with 0.5 intervals) were
208 computed in order to avoid overfitting and to approximate optimal levels of complexity.
209 The best model was then chosen based on Akaike Information Criterion corrected for
210 small sample sizes (AICc, Warren and Seifert 2011; Muscarella et al. 2014). Following
211 Guevara et al. (2018), we used all 8134-island pixel as background point to ensure a full
212 representation of environments available for the species. The optimal settings obtained
213 from above were used to train the final models using maxent.jar software. Model outputs
214 were set as logistic response of the predicted distribution. The logistic output was then
215 interpreted conservatively as a suitability index rather than as a probability (Merow et al.,
216 2013) and it was evaluated using both the area under the curve (AUC) provided for the
217 test data (Phillips et al., 2006), and the Boyce's Index (Hirzel et al., 2006). The Boyce's
218 Index, computed through the "ecospat" R-package (Di Cola et al., 2017), ranges between
219 -1 (the model predict areas where presences are more frequent as being highly suitable
220 for the species) and +1 (the model predictions are consistent with the distribution of
221 presences in the evaluation dataset), and values close to zero mean that the model is not
222 different from random expectations (Hirzel et al., 2006). Finally the model was projected
223 onto current, RCP2.6 and RCP8.5 climatic scenarios using unconstrained extrapolation
224 (Guevara et al., 2018). The R codes used are available in the gitLab repository presented
225 in the Supplementary Materials.

226 3 Results

227 *P. setaceum* is mainly present in coastal areas, especially on the North-Western side of
228 the island and near the largest cities (Santa Cruz de Tenerife, San Cristobal de La Laguna
229 and Güímar on the N-E coast; Bajamar, Punta del Hidalgo and Puerto de La Cruz on
230 the N-W coast, Los Gigantes and Las Americas on the south; Fig. 2 and 2a).

231 48 occurrences (out of the original 227) were produced using the spatial thinning ap-
232 proach and then these were used to train the model. Model selection based on the AICc
233 criteria pointed out that the most appropriate model was the one having linear, quadratic
234 and product features and a beta regularization multiplier equal to 0.5 (Tab. 2). For this
235 model, both Boyce's Index and AUC suggested good performance in predicting species'
236 environmental suitability (AUC = 0.757; Boyce's Index = 0.855, respectively). Temper-
237 ature was the most important variable (88.6% of variable importance) followed by pre-
238 cipitation and roads density (8.7 and 2.7% of variable importance respectively). Current
239 suitable areas for *P. setaceum* mirrored occurrences' distribution appearing prevalently
240 below 800 m (Fig. 2). Model prediction based on the RCP2.6 scenario substantially con-
241 firmed as highly suitable areas the current suitable ones, though a shift to higher values
242 of habitat suitability can also be observed at higher elevation (Fig. 2b). An elevational
243 shift is emphasized by the model prediction based on the RCP8.5 scenario (Fig. 2c),
244 where *P. setaceum* seems to climb up along elevation (especially in the northern part of
245 the island on the Anaga mountains).

246 In warmer and drier climatic conditions, *P. setaceum* is likely to shift from lower to
247 higher elevations, increasing the total area occupied by the species (Figure 3). Indeed, es-
248 timates of habitat suitability indicate the preference of the species for climatic conditions

249 with a mean spring temperature higher than 10°C (Figure 4).

250 4 Discussion

251 We investigated here the present and future spread of the invasive *P. setaceum* under
252 different climatic scenarios, highlighting the current suitability of areas below 800 m
253 asl (mirroring its current distribution; Supplementary Material Fig. 5), and predicting
254 an increase in habitat suitability at higher elevations (~ 1000 m asl) for both future
255 scenarios considered. Specifically, the predicted increase resulted particularly pronounced
256 for the RCP8.5 scenario. Our predictions are quite alarming, considering that 800 m asl
257 represents the current upper distribution limit of *P. setaceum* in Tenerife (Hobi, 2008).
258 *P. setaceum* is one of the most invasive species in Tenerife and it is currently spreading
259 around the Mediterranean basin (Devesa Alcaraz et al., 2006; Pasta et al., 2010; Saavedra
260 and Alcántara, 2017). Our work is therefore particularly valuable to halt its spread via
261 an effective monitoring of these areas that are under high invasion risk in the future.

262 4.1 Invaded habitats

263 *P. setaceum* spread below 800 m asl is likely to be enhanced by anthropic disturbance (e.g.
264 land-cover change and consequent habitat fragmentation), rather than global warming.
265 However, due to the year-by-year increase in anthropic disturbance and temperature at
266 higher elevations, its present distribution is still expanding above 800 m asl (see for
267 instance Kalwij et al., 2015). It has also been observed that *P. setaceum* can reach up to
268 2000 m asl in other islands contexts such as Hawaii (Williams et al., 1995). Moreover,
269 *P. setaceum* has been recently observed at altitudes of 1500 m in the Barranco Risco
270 Liso, located within the Caldera de Taburiente in La Palma island (Walentowitz et al.,
271 2019). Around Tenerife island, *P. setaceum* has rapidly colonized mainly areas that
272 were already experiencing anthropic disturbance, such as agricultural and rural areas,
273 spreading at higher altitudinal belts using the road network as the main propagation
274 pathway like other IAS (Arteaga et al., 2009; Arévalo et al., 2010; Benedetti and Morelli,
275 2017; Follak et al., 2018). In fact, in the area near Arafo, which has a long land-use history
276 for agriculture, the species has climbed up approximately 100 m in elevation in three years
277 (from 655 to 740 m asl, personal observation of DDR and ZNP in April 2019). *P. setaceum*
278 established firstly along the roadside, and then it spread deeper into the surrounding
279 landscapes, confirming that roads remain a crucial dispersion pathway for this species
280 and could promote its spread into protected areas (Foxcroft et al., 2019; Walentowitz
281 et al., 2019). However its ability to compete and outstand native plant communities
282 could be questioned in areas characterized by a high degree of biotic resistance and where
283 the native community has sufficient propagule pressure for new colonization (Schuster
284 et al., 2018).

285 *P. setaceum* also spread into many ravines within the lowlands in the South of Tenerife
286 as well as into the lower parts of the National Park Caldera de Taburiente (Barranco
287 de las Angustias), settling in semi natural communities (personal observations of RO).
288 In ravines, called *barrancos* in Tenerife, temporary water flow during the rainy season
289 facilitates the spread of seeds downriver, improving also the water supply in semiarid
290 areas. However, in the southernmost part of Tenerife, *P. setaceum* probably is still
291 limited by soil water conditions and at the highest sites of its distribution (currently at
292 about 1000 m asl) low temperature might limit its growth. A still unanswered question

293 is if *P. setaceum* will be able to grow and spread in open Canary pine forests growing
294 above 800 to 1000 m asl, which might have serious consequences for natural regeneration
295 and fire dynamics. However, according to Walentowitz et al. (2019), the dense canopy of
296 forest ecosystems should prevent *P. setaceum* spread due to its heliophilous nature.

297 4.2 Limiting factors, functional traits and competitive advan- 298 tages

299 Generally, rainfall and temperature patterns are among the most important limiting
300 factors determining plant distribution and abundance (Stephenson, 1990), affecting re-
301 production and other life-history traits. Temperature is a strong limiting factor for the
302 species, which usually prefers areas with temperature higher than 10°C (Fig. 4). Under
303 the current conditions, these areas are located under 1000 m asl, but they are expected
304 to rise under both the climate change scenarios analysed (RCP2.6 and RCP8.5). The
305 geographic distribution of the species in both scenarios showed an elevation shift, partic-
306 ularly pronounced in the RCP8.5 scenario. The species could move to higher elevation
307 probably benefitting from the effect of orographic precipitations, and it could migrate in
308 the north-western part of the island, where the trade winds enhance water availability
309 (Figures 2 and 3). The ecophysiological traits of *P. setaceum* support its large size, exten-
310 sive canopy, shorter leaf senescence period and the capacity to buffer seasonal and local
311 water shortages (González-Rodríguez et al., 2010). Indeed, they confer considerable com-
312 petitive advantages to the invader, and this can partially explain its invasion success in
313 the Canary archipelago, considering local environmental and climatic conditions. On the
314 other hand, seedlings growth could be a limiting factor of *P. setaceum* invasion success:
315 despite their relatively broad germination requirements, seedling cannot cope with low
316 soil moisture or drought conditions (Adkins et al., 2011; Goergen and Daehler, 2002), and
317 it has been suggested that they do not tolerate more than one month of drought (Rahlao
318 et al., 2010). Interestingly, once the seedlings are established, the amount of water does
319 not seem to affect their performance, even under higher temperature regimes. When
320 favourable conditions occur, *P. setaceum* can quickly thrive (already under sub-optimal
321 ecological conditions) and overcome native coexisting species through rapid exploitation
322 of available resources (such as water and nutrients), thanks to its broad ecological toler-
323 ance and high phenotypic plasticity (Williams and Black, 1993; Poulin et al., 2007; Rahlao
324 et al., 2010). Furthermore, under drought or limited resources availability, the alteration
325 of biomass allocation patterns in favour of roots seems to be a conservative strategy
326 (Williams et al., 1995; Rahlao et al., 2010). This may explain why *P. setaceum* is an
327 excellent invader of habitats characterized by fluctuating resources, frequently disturbed
328 or with an irregular rainfall pattern, in agreement with Davis' theory of community inva-
329 sibility (Davis et al., 2000). Compared to native species, the higher nitrogen and water
330 use efficiency (González-Rodríguez et al., 2010) allow *P. setaceum* to compete effectively
331 in warmer, drier areas, conferring it a considerable competitive advantage (Tordoni et al.,
332 2020). Recently, Rodríguez-Caballero et al. (2017, 2018) have shown how *P. setaceum*
333 could establish symbiosis with different mycorrhizal fungi and act as a transformer (Pyšek
334 et al., 2004) modifying the soil bacterial community related to N cycle. As a consequence,
335 it also tends to increase the risk of intense wildfires (to which it is well adapted), thus
336 posing a further threat to resident native communities (Tunison, 1992).

337 Other studies on *P. setaceum* ecophysiology have confirmed the broad ecological toler-
338 ance of the species in other environments. Specifically, Jacobi and Warshauer (1992)

339 reported that in the Hawaiian Islands, *P. setaceum* has a relatively wide elevation range
340 (500-2900 m) but is limited to areas with median annual rainfall less than 1250 mm, hence
341 only dry and mesic habitats are colonized by this species. In southern California, Sweet
342 and Holt (2015) reported that *P. setaceum* might benefit from dampened temperatures
343 and additional moisture through fog drip, becoming competitive in the cooler season due
344 to phenotypic plasticity in response to temperature and water. Finally, since *P. setaceum*
345 is endowed of C4 metabolism, it is likely that climate change may have positive effects
346 on its performance, further promoting its invasion success, as already observed for other
347 C4 invaders (e.g. Chuine et al. 2012 for *Setaria parviflora*). Indeed, C4 plants are intrin-
348 sically adapted to elevated temperatures and to tolerate heat stress (Sage and Kubien,
349 2003) thanks to higher effective quantum yield of CO2 fixation, which increases photo-
350 synthetic rates, especially at higher temperatures (Ehleringer and Björkman, 1977; Sage
351 and Kubien, 2003).

352 For the sake of clarity, we would like to highlight that a possible drawback of our
353 predictions is the violation of the equilibrium assumption. In fact, it was not possible
354 to consider the whole climatic range of the species and train the model including also
355 occurrences present in native range: only 52 *P. setaceum* occurrences are available in an
356 area covering mostly the East Africa and the Arabian peninsula (Sudan, Ethiopia, Eritrea,
357 Kenya, Somalia, Saudi Arabia, Yemen and Oman, GBIF accessed on 26th May 2020).
358 Considering, however, the invasion pressure that the delicate ecosystem of Tenerife is
359 undergoing, predicting the areas that are more prone to invasion in the near future is more
360 valuable (from a conservation and management perspective and under the precautionary
361 principle; West et al., 2016) than modelling the full potential invasive range of *P. setaceum*
362 at equilibrium. Nonetheless, considering the possible violation of this assumption, care
363 must be taken when interpreting the model outputs.

364 5 Conclusions

365 Our model predictions highlight that the distribution of *P. setaceum* in Tenerife will
366 be strongly affected by climate change, and particularly by the predicted increase in
367 aridity on the island. Our model (particularly RCP8.5) foresees that the species would
368 move to higher elevation and to the north-western part of the island, likely to benefit
369 both from orographic precipitations and enhanced water availability promoted by trade
370 winds. Moreover, under the current socio-economic perspectives, the RCP2.6 scenario
371 is becoming year after year less feasible (Davis and Socolow, 2014), making the RCP8.5
372 one even more likely. The species may consequently have negative impacts on entire
373 ecosystems, due to its strong competitive capacities and being a driver of other invasive
374 species. Particularly, the predicted invasion of areas at higher elevation pose the question
375 of its ability to penetrate the pine forests (especially the more xeric ones in the southern
376 part of the island). Its establishment could drastically affect the dynamics of this unique
377 ecosystem (e.g. natural regeneration, fire regime), if proper conservation plans will not
378 be developed to support ecosystem health and diversity. However, even though our pre-
379 dictions are coherent with the auto-ecology of the species, climate change predictions
380 are extremely simplified, and should be therefore interpreted with care. More powerful
381 outcomes may be obtained downscaling climatic data from global models such as Global
382 Circulation Model (GCM), but to our knowledge spatially interpolated fine scale GCM
383 projections for the Canary Islands are still lacking. Moreover, it has been showed that

384 whereas global scale products are generally applicable at broad geographical scale, mod-
385 elling climate surface on islands need to consider fine scale spatial variation due to spatial
386 variability and steep climatic gradient variation (Garzón-Machado et al., 2014; Khalyani
387 et al., 2016). In a global warming scenario, a modelling approach as the one proposed
388 here could play a key-role in alien species monitoring, highlighting the portions of the
389 territory that are more prone to biological invasions.

390 To our knowledge, Walentowitz et al. (2019) and ours results are the first *P. setaceum*
391 niche model outputs presented. Such cartographic products provide an immediate tool
392 for understanding potential changes in species distributions, and they can be used to
393 disseminate and increase the awareness of biological invasion outside the academia. Con-
394 sidering the dramatic effects that an uncontrolled increase of *P. setaceum* may have on
395 Tenerife, understanding its future potential habitat distribution is therefore crucial from
396 a conservational perspective. Immediate control measures (e.g., manual and chemical
397 species removal efforts) should be carried out from the border of *P. setaceum* current
398 distribution, focusing especially along invasion pathways (Walentowitz et al., 2019). Fur-
399 thermore, prohibiting the commercial use of *P. setaceum* propagules could be another
400 tool to control the species further spread. In fact, Potgieter et al. (2019) showed that
401 ornamental plants are still perceived as having aesthetic benefits when confined to pri-
402 vate gardens; however, shifts in perceptions may occur when they become widespread in
403 the wild, leading to economic and environmental costs. Finally, specific Citizen Science
404 projects have been shown to be effective to raise the awareness about biological invasions
405 and to engage both public administrations and citizens in monitoring and controlling
406 invasive species, and therefore could be a valuable tool to help controlling the species
407 invasion and its deleterious effect on Canary Islands (e.g. Sladonja and Poljuha, 2018).

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7 Tables

Table 1: Predictors summary statistics at the occurrences locations.

	mean	sd	median	min	max
October-March mean monthly precipitation	266.48	87.42	263.22	140.47	460.07
Mean spring temperature	18.00	1.00	18.24	15.54	19.93
Road kernel density	0.06	0.07	0.04	0.00	0.40
RCP2.6 October-March mean monthly precipitation	223.85	73.43	221.10	118.00	386.46
RCP2.6 Mean spring temperature	18.96	1.00	19.20	16.50	20.89
RCP8.5 October-March mean monthly precipitation	168.68	55.33	166.62	88.92	291.22
RCP8.5 Mean spring temperature	20.68	1.00	20.92	18.22	22.61

Table 2: Results of the Maxent model selection via AICc

	settings	features	rm	train.AUC	avg.test.AUC	var.test.AUC	avg.diff.AUC	var.diff.AUC	avg.test.orMTP	var.test.orMTP	avg.test.or10pct	var.test.or10pct	AICc	delta.AICc	w.AIC	parameters
1	L_0.5	L	0.50	0.76	0.77	0.02	0.04	0.01	0.01	0.05	0.13	0.05	787.33	3.22	0.05	3.00
2	LQ_0.5	LQ	0.50	0.78	0.76	0.02	0.05	0.02	0.03	0.09	0.16	0.07	785.73	1.62	0.10	5.00
3	LQP_0.5	LQP	0.50	0.78	0.77	0.02	0.05	0.02	0.00	0.02	0.16	0.04	784.11	0.00	0.23	4.00
4	LQPH_0.5	LQPH	0.50	0.81	0.75	0.02	0.08	0.02	0.00	0.02	0.28	0.02	946.93	162.82	0.00	30.00
5	L_1	L	1.00	0.76	0.77	0.01	0.04	0.01	0.00	0.02	0.16	0.05	787.47	3.36	0.04	3.00
6	LQ_1	LQ	1.00	0.77	0.76	0.02	0.04	0.02	0.02	0.07	0.16	0.07	786.63	2.52	0.07	4.00
7	LQP_1	LQP	1.00	0.76	0.77	0.02	0.04	0.01	0.00	0.02	0.16	0.05	789.02	4.91	0.02	4.00
8	LQPH_1	LQPH	1.00	0.80	0.76	0.02	0.07	0.02	0.00	0.02	0.16	0.02	865.59	81.48	0.00	23.00
9	L_1.5	L	1.50	0.76	0.76	0.01	0.03	0.01	0.00	0.02	0.16	0.05	787.71	3.60	0.04	3.00
10	LQ_1.5	LQ	1.50	0.76	0.76	0.01	0.04	0.01	0.00	0.02	0.16	0.05	790.11	6.00	0.01	4.00
11	LQP_1.5	LQP	1.50	0.76	0.76	0.01	0.04	0.01	0.00	0.02	0.18	0.04	788.25	4.14	0.03	3.00
12	LQPH_1.5	LQPH	1.50	0.79	0.75	0.02	0.06	0.02	0.00	0.02	0.16	0.02	803.79	19.68	0.00	11.00
13	L_2	L	2.00	0.76	0.76	0.01	0.03	0.01	0.00	0.02	0.16	0.05	788.03	3.92	0.03	3.00
14	LQ_2	LQ	2.00	0.76	0.76	0.01	0.03	0.01	0.00	0.02	0.18	0.04	788.26	4.15	0.03	3.00
15	LQP_2	LQP	2.00	0.78	0.75	0.01	0.03	0.01	0.00	0.02	0.18	0.04	789.79	5.68	0.01	3.00
16	LQPH_2	LQPH	2.00	0.78	0.74	0.01	0.05	0.02	0.00	0.02	0.16	0.02	810.26	26.15	0.00	12.00
17	L_2.5	L	2.50	0.76	0.76	0.01	0.03	0.01	0.00	0.02	0.18	0.04	788.45	4.34	0.03	3.00
18	LQ_2.5	LQ	2.50	0.76	0.75	0.01	0.03	0.01	0.00	0.02	0.18	0.04	788.81	4.70	0.02	3.00
19	LQP_2.5	LQP	2.50	0.75	0.75	0.01	0.03	0.01	0.00	0.02	0.16	0.02	788.86	4.75	0.02	2.00
20	LQPH_2.5	LQPH	2.50	0.77	0.74	0.01	0.05	0.02	0.00	0.02	0.18	0.02	803.32	19.21	0.00	9.00
21	L_3	L	3.00	0.76	0.76	0.01	0.03	0.01	0.00	0.02	0.18	0.04	788.96	4.85	0.02	3.00
22	LQ_3	LQ	3.00	0.76	0.75	0.01	0.03	0.01	0.00	0.02	0.18	0.04	789.47	5.36	0.02	3.00
23	LQP_3	LQP	3.00	0.75	0.74	0.00	0.03	0.00	0.00	0.02	0.13	0.01	789.99	5.88	0.01	2.00
24	LQPH_3	LQPH	3.00	0.75	0.73	0.01	0.05	0.01	0.00	0.02	0.13	0.01	797.87	13.76	0.00	6.00
25	L_3.5	L	3.50	0.76	0.75	0.01	0.03	0.01	0.00	0.02	0.18	0.04	789.55	5.45	0.02	3.00
26	LQ_3.5	LQ	3.50	0.75	0.75	0.01	0.03	0.01	0.00	0.05	0.18	0.04	790.26	6.15	0.01	3.00
27	LQP_3.5	LQP	3.50	0.75	0.74	0.00	0.03	0.00	0.00	0.02	0.11	0.01	788.79	4.68	0.02	1.00
28	LQPH_3.5	LQPH	3.50	0.75	0.73	0.01	0.04	0.01	0.00	0.02	0.11	0.01	788.79	4.68	0.02	1.00
29	L_4	L	4.00	0.75	0.75	0.01	0.03	0.01	0.00	0.02	0.18	0.04	790.24	6.13	0.01	3.00
30	LQ_4	LQ	4.00	0.75	0.74	0.00	0.03	0.01	0.00	0.02	0.16	0.02	791.17	7.06	0.01	3.00
31	LQP_4	LQP	4.00	0.75	0.75	0.00	0.02	0.00	0.00	0.02	0.09	0.01	789.09	4.98	0.02	1.00
32	LQPH_4	LQPH	4.00	0.75	0.74	0.00	0.03	0.00	0.00	0.02	0.11	0.01	789.05	4.94	0.02	1.00
33	L_4.5	L	4.50	0.75	0.75	0.01	0.03	0.01	0.00	0.05	0.18	0.04	791.02	6.91	0.01	3.00
34	LQ_4.5	LQ	4.50	0.75	0.74	0.00	0.03	0.00	0.00	0.02	0.13	0.01	789.75	5.64	0.01	2.00
35	LQP_4.5	LQP	4.50	0.75	0.75	0.00	0.02	0.00	0.00	0.02	0.09	0.01	789.33	5.22	0.02	1.00
36	LQPH_4.5	LQPH	4.50	0.75	0.75	0.00	0.02	0.00	0.00	0.02	0.09	0.01	789.39	5.29	0.02	1.00
37	L_5	L	5.00	0.75	0.74	0.00	0.03	0.00	0.00	0.02	0.16	0.02	791.88	7.78	0.00	3.00
38	LQ_5	LQ	5.00	0.75	0.74	0.00	0.03	0.00	0.00	0.02	0.13	0.01	790.37	6.26	0.01	2.00
39	LQP_5	LQP	5.00	0.75	0.75	0.00	0.02	0.00	0.00	0.02	0.09	0.01	789.63	5.52	0.01	1.00
40	LQPH_5	LQPH	5.00	0.75	0.75	0.00	0.02	0.00	0.00	0.02	0.09	0.01	789.63	5.52	0.01	1.00

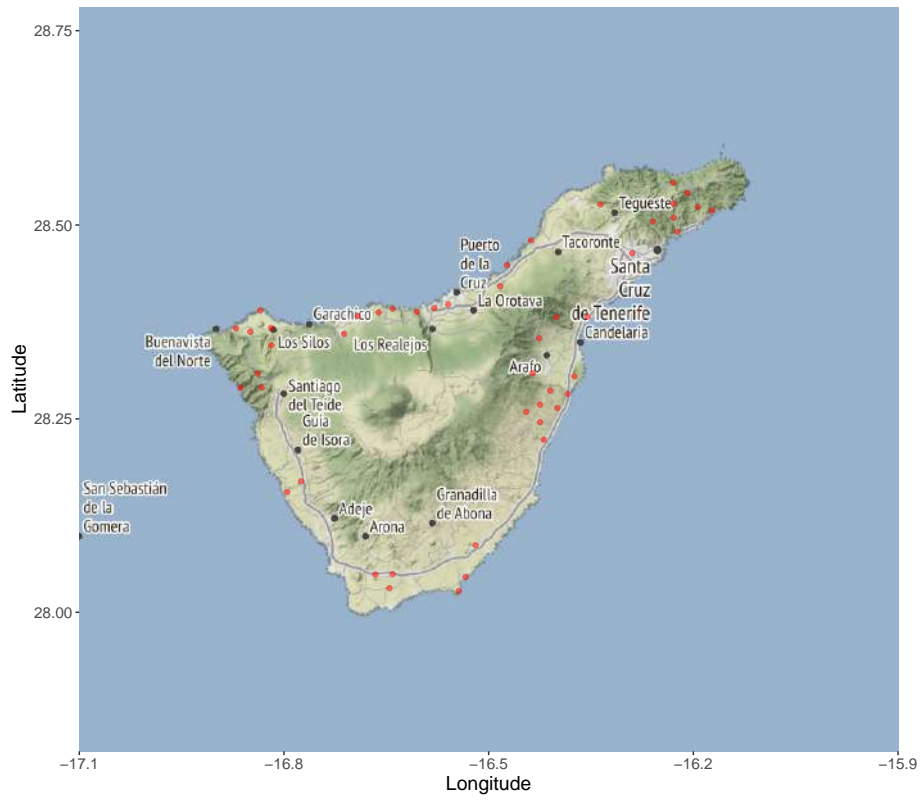


Figure 1: *P. setaceum* thinned occurrences distribution on Tenerife

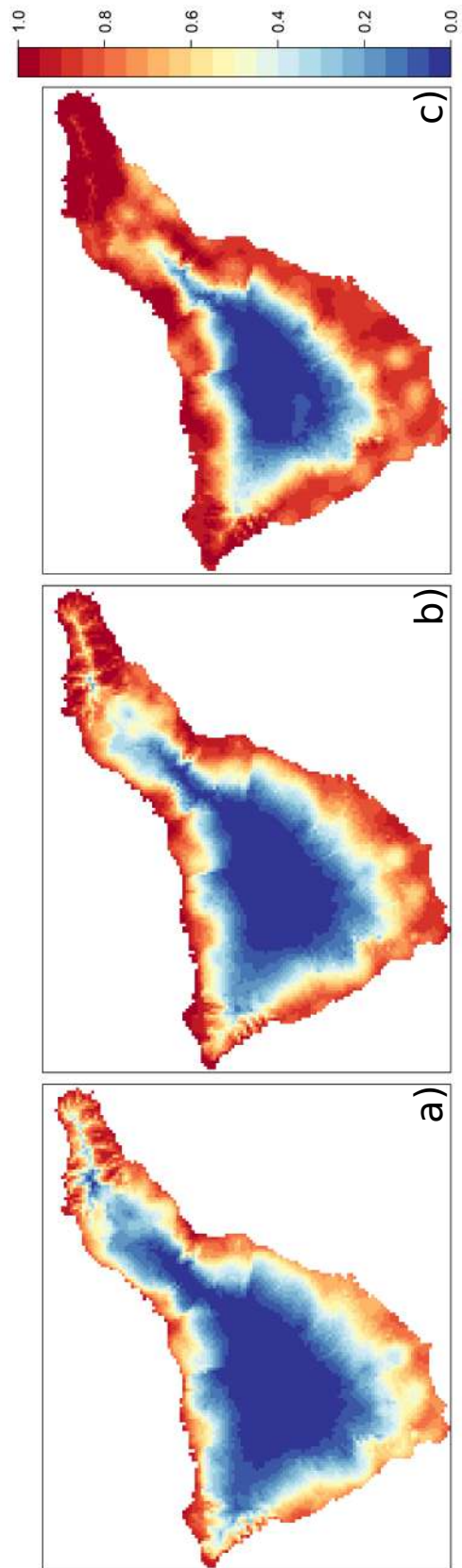


Figure 2: *P. setaceum* HSM predictions: a) current climatic conditions, b) RCP2.6 climatic conditions c) RCP8.5 climatic conditions

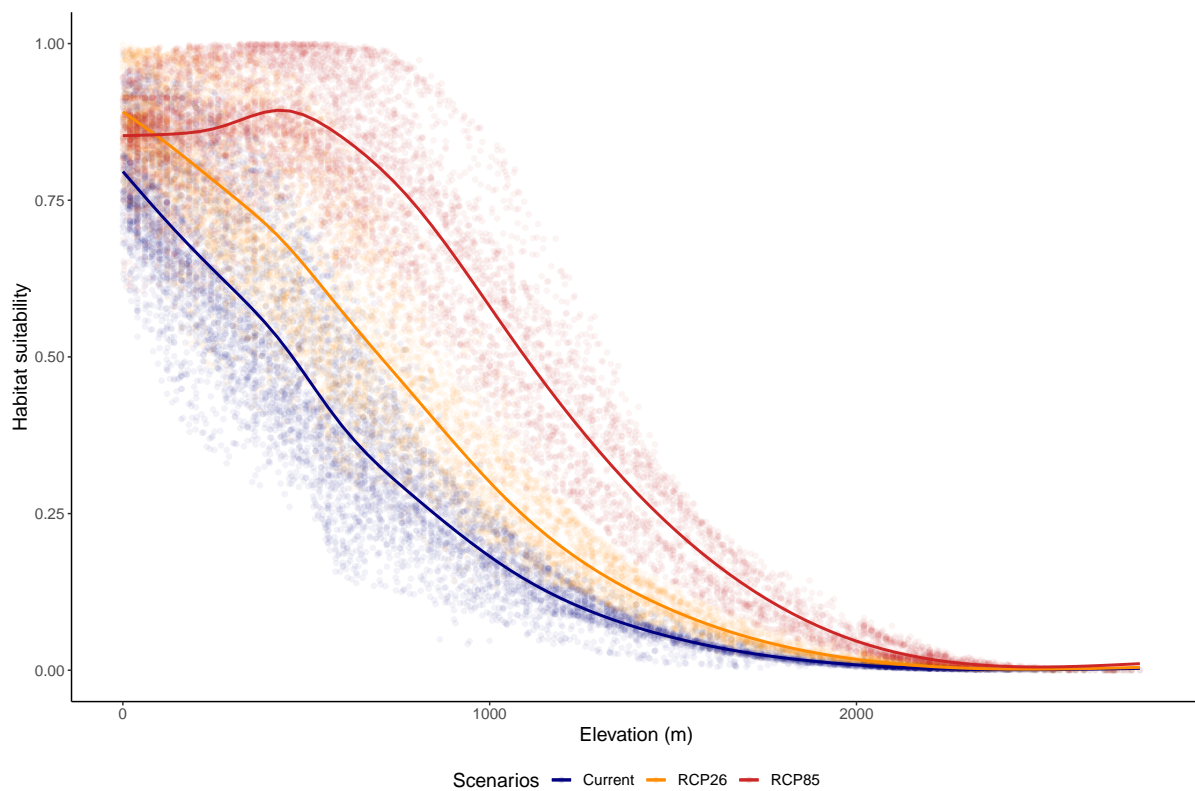


Figure 3: Relationships between *P. setaceum* HSM predictions and elevation: blue dots and line, current climatic conditions; orange dots and line, RCP2.6 climatic conditions; red dots and line, RCP8.5 climatic conditions

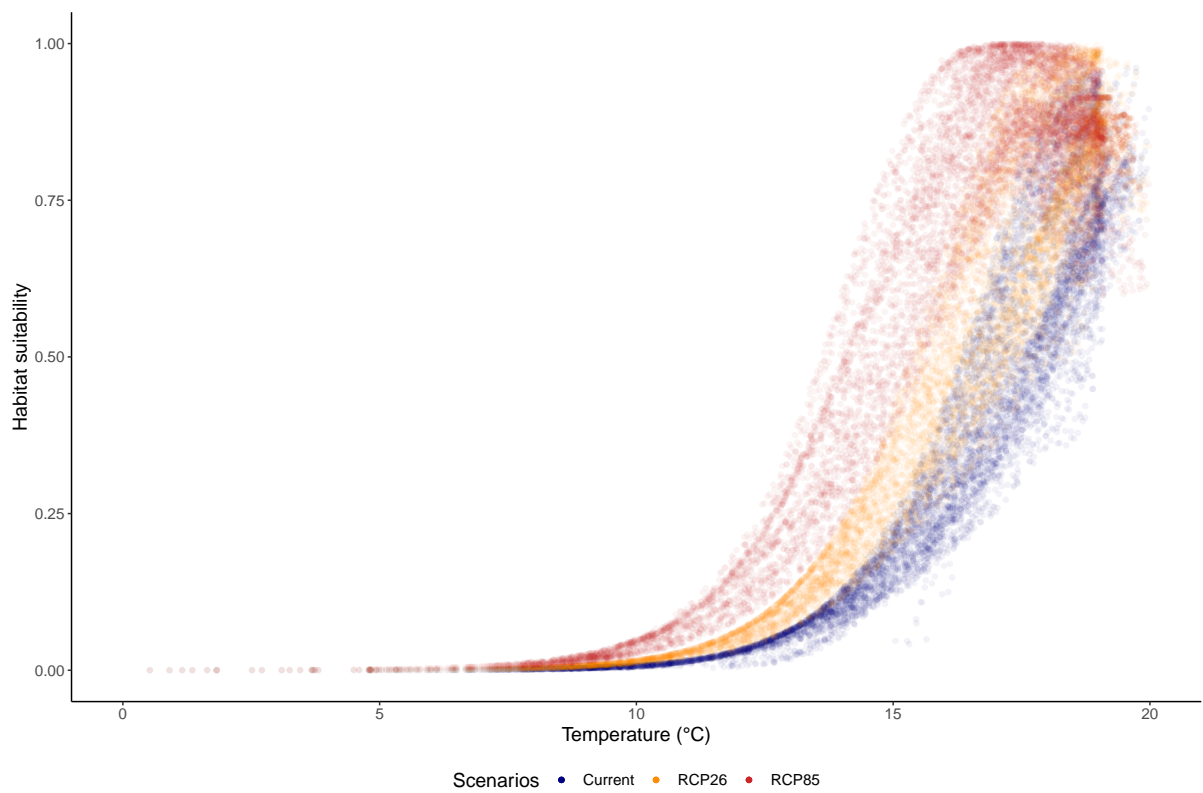
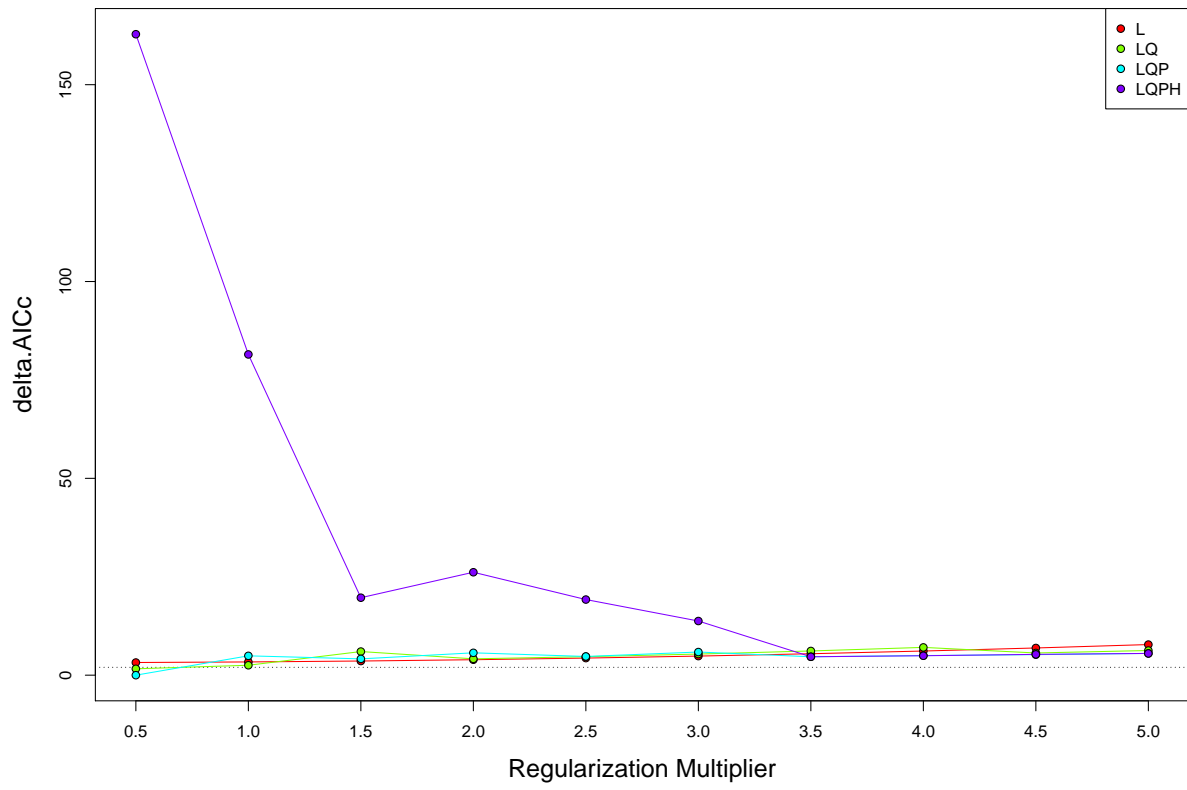


Figure 4: Relationships between *P. setaceum* HSM predictions and temperatures: blue dots, current climatic conditions; orange dots, RCP2.6 climatic conditions; red dots, RCP8.5 climatic conditions

751 9 Supplementary Materials

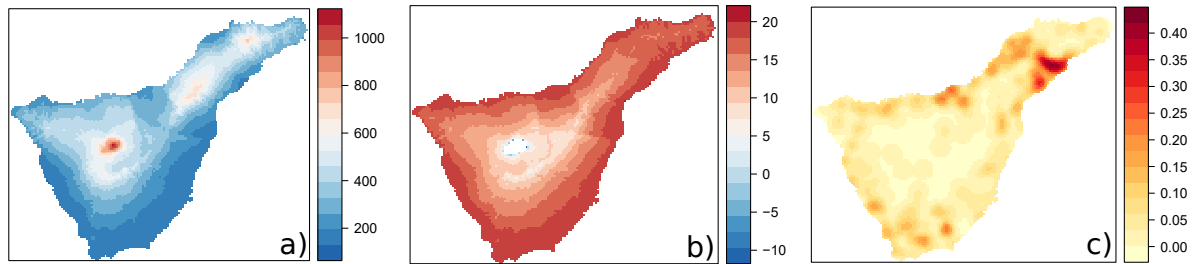
ENMeval plot



Supplementary Figure 1: ENMeval AICc output

752

Predictors plot



Supplementary Figure 2: Predictors used to train the model: a) October-March 2005-2014 mean precipitation, b) March-April-May 2005-2014 mean temperatures, c) Roads kernel density.

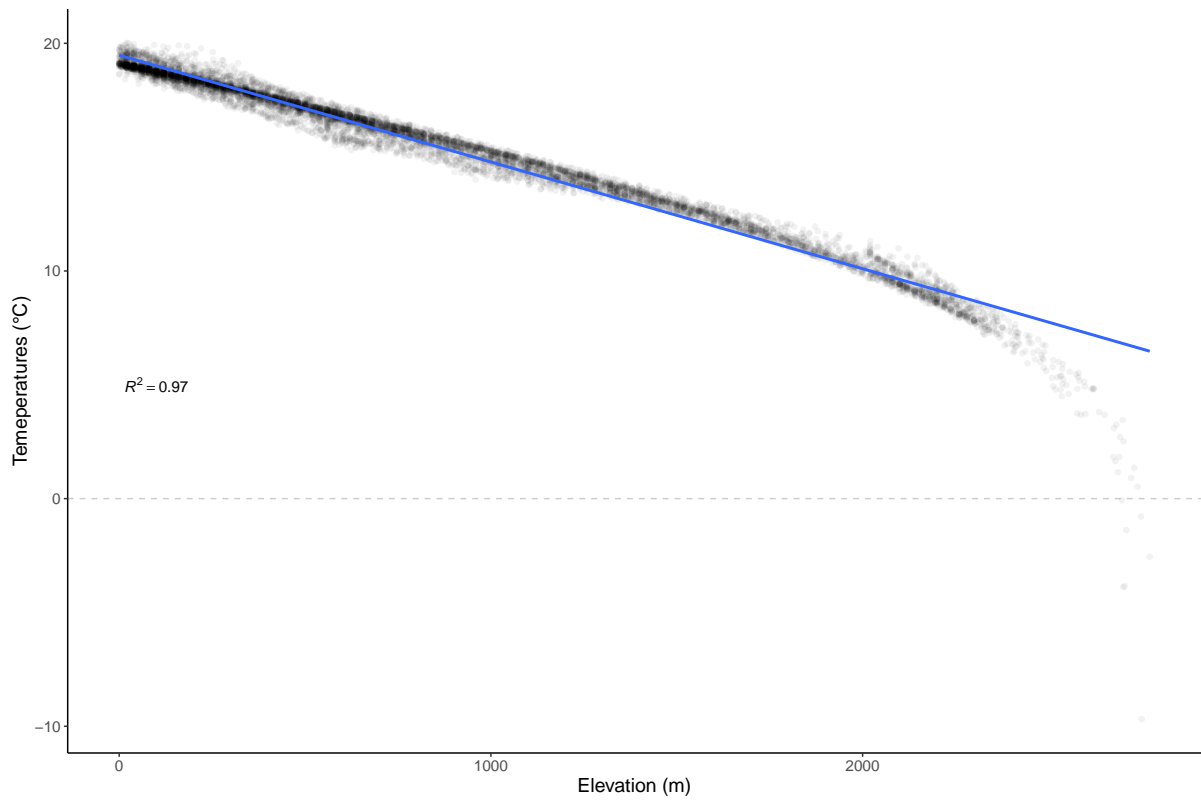
Correlation Matrix

Supplementary Table 1: Predictors Pearson's r correlation matrix

	October-March mean monthly precipitation	Road kernel density	Mean spring temperature
October-March mean monthly precipitation	1.00	-0.17	-0.64
Road kernel density	-0.17	1.00	0.38
Mean spring temperature	-0.64	0.38	1.00

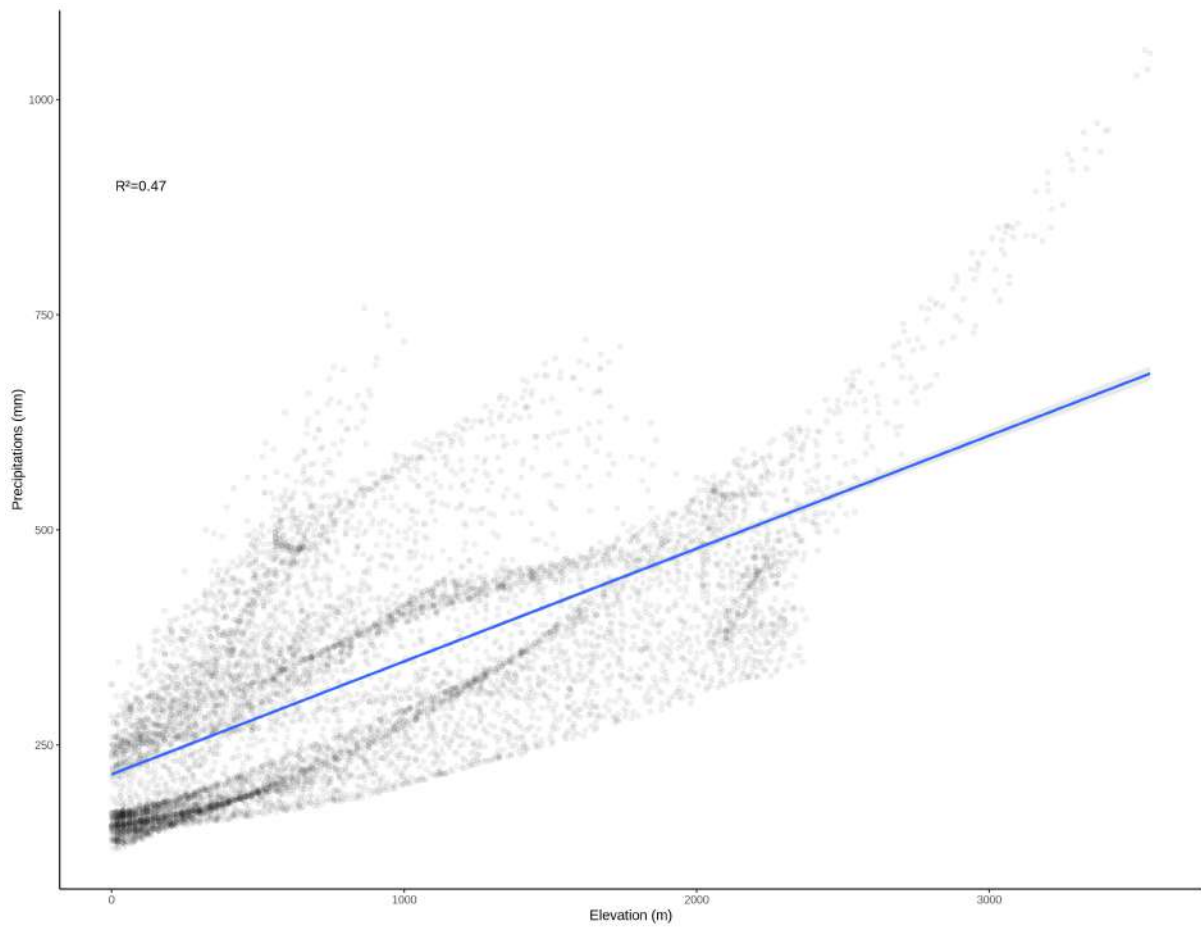
754

Temperature-Elevation relationship



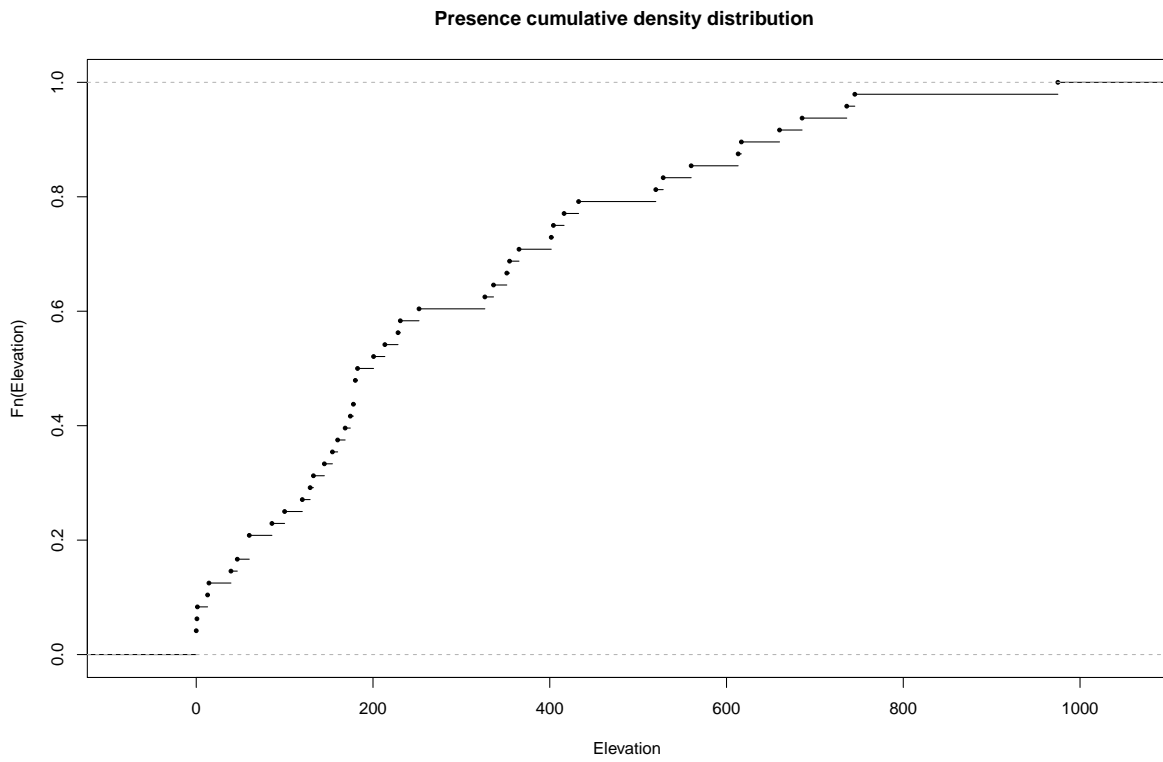
Supplementary Figure 3: Relationship between March-April-May 2005-2014 mean temperatures and elevation in Tenerife island

Precipitation-Elevation relationship



Supplementary Figure 4: Relationship between October-March 2005-2014 mean precipitation and elevation in Tenerife island

Occurrences cumulative distribution



Supplementary Figure 5: Cumulative distribution along the elevation of the Presence occurrences used to train the model

R codes

758

759 The R codes used in the present study are available at the following gitLab repositories

760

- cokriging repository: <https://gitlab.com/danidr/cokriging->

761

- Occurence filtering and Maxent Modelling: https://gitlab.com/danidr/pennisetum_hsm_tfe

762