

ARCHIVIO ISTITUZIONALE DELLA RICERCA

Alma Mater Studiorum Università di Bologna Archivio istituzionale della ricerca

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

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Invasive fountain grass (Pennisetum setaceum (Forssk.) Chiov.) increases its potential area of distribution in Tenerife island under future climatic scenarios / Da Re, Daniele; Tordoni, Enrico; De Pascalis, Federico; Negrín-Pérez, Zaira; Fernández-Palacios, José María; Arévalo, José Ramón; Rocchini, Duccio; Medina, Félix Manuel; Otto, Rüdiger; Arlé, Eduardo; Bacaro, Giovanni. - In: PLANT ECOLOGY. - ISSN 1385-0237. -STAMPA. - 221:10(2020), pp. 867-882. [10.1007/s11258-020-01046-9]

This version is available at: https://hdl.handle.net/11585/774515 since: 2021-02-27

Published:

DOI: http://doi.org/10.1007/s11258-020-01046-9

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

(Article begins on next page)

This item was downloaded from IRIS Università di Bologna (https://cris.unibo.it/). When citing, please refer to the published version. This is the final peer-reviewed accepted manuscript of:

Da Re, Daniele; Tordoni, Enrico; De Pascalis, Federico; Negrín-Pérez, Zaira; Fernández-Palacios, José María; Arévalo, José Ramón; Rocchini, Duccio; Medina, Félix Manuel; Otto, Rüdiger; Arlé, Eduardo; Bacaro, Giovanni: Invasive fountain grass (Pennisetum setaceum (Forssk.) Chiov.) increases its potential area of distribution in Tenerife island under future climatic scenarios

PLANT ECOLOGY VOL. 221 ISSN 1385-0237

DOI: 10.1007/s11258-020-01046-9

The final published version is available online at:

https://dx.doi.org/10.1007/s11258-020-01046-9

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<u>https://cris.unibo.it/</u>)

When citing, please refer to the published version.

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

Daniele Da Re^{1,2,*}, Enrico Tordoni¹, Federico De Pascalis^{1,3}, Zaira Negrín-Pérez⁴, José María Fernández-Palacios⁴, José Ramón Arévalo⁴, Duccio Rocchini^{5,6}, Félix Manuel Medina⁷, Rüdiger Otto⁴, Eduardo Arlé⁸ and Giovanni Bacaro¹

May 30, 2020

 1 Department of Life Sciences, University of Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy

² current address: George Lemaitre Center for Earth and Climate Research, Earth and Life Institute, UCLouvain, Place Louis Pasteur 3, 1348 Louvain-la-Neuve, Belgium.

³ current address: Department of Environmental Sciences and Policy, University of Milan, via Celoria 26, I-20133, Milano, Italy

 $^4 \rm Departamento de Botánica, Ecología y Fisiología Vegetal , Universidad de La Laguna, Avenida Astrofísico Francisco Sánchez s/n, 38206 La Laguna, Tenerife, Spain$

⁵ Alma Mater Studiorum University of Bologna, Department of Biological, Geological and Environmental Sciences, via Irnerio 42, 40126, Bologna, Italy

⁶ Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Department of Applied Geoinformatics and Spatial Planning, Kamýcka 129, Praha - Suchdol, 16500, Czech Republic

⁷ Servicio de Medio Ambiente, Cabildo Insular de La Palma, Avenida Los Indianos, 20, 38700 Santa Cruz de La Palma, Canary Islands, Spain

⁸ German Centre for Integrative Biodiversity Research (iDiv), Deutscher Platz 5e, 04103, Leipzig Halle-Jena-Leipzig, Leipzig, Germany.

* corresponding author: daniele.dare@uclouvain.be

Abstract

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

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

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

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

20 21 22

23

17

18

19

8

9

10

11

12

Keywords: Habitat suitability models, invasive alien species, Canary Archipelago, global warming

24 1 Introduction

Climate change is having strong ecological impacts on biodiversity from the polar regions 25 to the tropics, and predicting the response of biodiversity to future climate change sce-26 narios has become a primary field of research (Pereira et al., 2010; Bellard et al., 2012; 27 Matías and Jump, 2013; Dyderski et al., 2018). Global warming, along with the reduc-28 tion in precipitation during the growing season, may strongly alter species distribution 29 (Kleinbauer et al., 2010; Stocker, 2014). Furthermore, the increase in CO₂ atmospheric 30 concentration and Nitrogen deposition promote the presence of invasive species and en-31 hance the risk of biological invasions (Dukes and Mooney, 1999). In this context, special 32 attention should be paid to island systems: islands are, in fact, at the forefront against 33 global changes such as sea-level rise and biological invasions (Bellard et al., 2014; Pyšek 34 et al., 2017). Islands are well-known to host habitats rich in rare and endemic species, 35 hence more than one third of biodiversity hotspots in the world are entirely, or largely, 36 within islands (Bellard et al., 2014). 37 Biological invasions are dramatically threatening island biodiversity and ecosystem in-38 tegrity (Hulme, 2009; Scalera et al., 2012) since invasive alien species (hereafter IAS, see 39 Pyšek et al., 2004 for comprehensive definitions) may directly reduce local plant species 40 diversity (Tordoni et al., 2019). However, the deleterious effect of plant invasion is not 41 limited to competition with native species, but it could affect the whole ecosystem, espe-42 cially enclosed and fragile ones such as islands. Firstly, changes in carbon and nitrogen 43 soil dynamics, resulting from alien plants invasions (Vilà and López-Darias, 2006; Vilà 44 et al., 2011; Qian and Ricklefs, 2006) impact soil biotic community and potentially alter 45 important processes, such as mutualism. In nutrient enriched soils for example, myc-46 orrhizal populations can become antagonistic to hosts (Toby Kiers et al., 2010). The 47 balance in macroinvertebrate communities can be disrupted (Gremmen et al., 1998), 48 with potential effects on the whole ecosystems. Secondly, invasive alien plant species 49 could promote alien insect presence (Morales and Aizen, 2002), which has the potential 50 to affect entire habitats and ultimately alter ecosystem functioning and services (Kenis 51 et al., 2009). Finally, recent studies suggest that IAS may benefit from climate change 52 (e.g. Kleinbauer et al. 2010; Brundu and Richardson 2016; Dyderski et al. 2018), which 53 foster their invasion rate and, consequently, invasion-related risks. 54 Due to the high rate of endemism (Whittaker and Fernández-Palacios, 2007; Fernández-55 Palacios et al., 2016), the Canary archipelago represents an extremely vulnerable area for 56 alien species invasions (Courchamp et al., 2003; Assessment, 2005; Kueffer et al., 2010; 57 Bacaro et al., 2015). Particularly, the island of Tenerife hosts a total of 9325 species, 58 1468 of them being vascular plants with 279 local endemic plant species (Arechavaleta 59 et al., 2010). This island has been affected by an intense human activity that altered 60 the natural ecosystems, causing fragmentation and the introduction of invasive species 61 in protected areas (Delgado et al., 2004), such as fountain grass (*Pennisetum setaceum*) 62 (Forssk.) Chiov.). 63 *Pennisetum setaceum* is a perennial, wind-dispersed, apomictic, C4 bunch grass native 64 to North Africa and the Middle East (Williams et al., 1995; Poulin et al., 2007). It was in-

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

urbanized areas toward natural ones (Martín Esquivel et al., 1995; González-Rodríguez 71 et al., 2010). Elevated phenotypic plasticity, characterised by variation in functional trait 72 value according to the environment, and its resilience, makes P. setaceum well adapted 73 to different ecological conditions (Poulin et al., 2007; González-Rodríguez et al., 2010). 74 Moreover, it can establish symbiosis with different local mycorrhizal fungi (AMF) com-75 munities, further promoting a successful establishment and spread (Rodríguez-Caballero 76 et al., 2018). It is an aggressive invader of arid and semiarid coastal habitats such as 77 thermo-xerophilous grasslands and shrublands. Here it establishes almost monospecific 78 stands and causes long-lasting ecological consequences (Cordell and Sandquist, 2008) 79 González-Rodríguez et al., 2010). The species is known to have negative impacts on re-80 sources acquisitions in the dry forest plant communities and it can interact with the soil 81 bacterial community, shifting its structure and composition, which can result in severe 82 alterations of the N cycle (Rodríguez-Caballero et al., 2017). Moreover, it is a fire pro-83 moting species that can cause dramatic environmental changes, since fire is one of the 84 most important drivers of land use and atmospheric changes globally (D'Antonio and 85 Vitousek, [1992]). Finally, it can promote the presence of the alien invasive leafhopper 86 Balclutha brevis (Bella et al., 2012). It has been estimated that approximately 30% of all 87 protected areas of the Canary Islands have been invaded by fountain grass (Martín Es-88 quivel et al., 1995; González-Rodríguez et al., 2010). Considering the dramatic effects 89 that an uncontrolled increase in its distribution could create on Tenerife, understanding 90 P. setaceum future habitat distribution is particularly important both from a conserva-91 tional and ecological perspective, and it is a time-sensitive task. 92 Correlative models such as Habitat Suitability Models (HSMs) have extensively been 93 used so far to estimate the geographic distribution of a species based on an index of envi-94 ronmental similarity (Kearney, 2006; Peterson et al., 2011; Guisan et al., 2017) which, in 95 turn, is estimated starting from its occurrences in relation to its environmental determi-96 nants (Thuiller, 2007; Steiner et al., 2008; Jiménez-Valverde et al., 2011). HSMs became 97 a central tool in invasion biology, providing both interesting insight on species' ecology 98 and practical suggestions for eradication management. For invasive species, the correct 99 projection in space and time of HSMs estimates depends on different assumptions, which 100 are defined by the research questions. It is fundamental to consider niche conservatism 101 among native and invasive range when the research objective is to project the suitability 102 index estimated in the native range into the invasive one. When using the species invaded 103 range to train a HSM, the invasive species must be at quasi-equilibrium with the environ-104

ment in which it occurs (Guisan and Thuiller, 2005; Gallien et al., 2012). However, these 105 assumptions are not always met, since the naturalized climatic niche of invasive species 106 may differ from the natives climatic niches (e.g. Medley 2010; Early and Sax 2014) and 107 since an invasive species is not at equilibrium with its environment until the latest stage 108 of invasion (Barbet-Massin et al., 2018). Both cases result in a likely underestimate on 109 the species predicted habitat suitability distribution. However, in situations where as-110 sumptions cannot be met for practical reasons (e.g. impossibility to compare native and 111 invasive niche), HSMs may still provide predictions which are useful for invasive species 112 management, such as highlighting the areas of likely expansion in the near future, which 113 should be targeted and prioritized by conservation efforts (West et al., 2016). 114

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

¹²⁵ 2 Materials and Methods

$_{126}$ 2.1 Study area

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

¹³⁵ 2.2 Response variable

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

$_{144}$ 2.3 Predictors

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

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

Finally, road kernel density was selected as a proxy of propagule pressure and species dispersion, especially for *P. setaceum* (Foxcroft et al., 2019). Indeed anthropogenic activities enhance alien species' spread (Pyšek et al., 2010; Tordoni et al., 2017), and roads are known to be primary introduction pathways. Particularly, roadside may serve as invasion
epicenters for annual species with high reproductive rates (Pauchard and Alaback, 2004;
Bacaro et al., 2015; Da Re et al., 2019).

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

177 2.4 Climate change predictions

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

Cropper (2013) estimates an increase in surface air temperature of 1 °C and a decrease 183 in water availability of 15-20% due to more than 30% reduction in precipitation (Giorgi 184 2006; Somot et al., 2008). In order to get a reliable estimate of climate change effects 185 on the climatic variables considered (though deemed approximate), we apply a constant 186 correction on interpolated climatic surfaces. Specifically, we considered the two Repre-187 sentative Concentration Pathways (RCPs), namely RCP2.6 and RCP8.5, as described 188 by the 5th Intergovernmental Panel on Climate Chage (IPCC) report representing pos-189 sible ranges of radiative forcing values in the year 2100 relative to pre-industrial values 190 $(+2.6 \text{ and } +8.5 \text{ W/m}^2, \text{ respectively})$. Winter and Spring precipitation were corrected 191 by -10.6% and -36.7% (RCP2.6 and RCP8.5) according to Winter (December – January 192 - February, DJF) precipitation reduction prevision made by Cropper (2013), while for 193 Spring temperature 0.96 °C (RCP2.6) and 2.68 °C (RCP8.5) were added. 194

¹⁹⁵ 2.5 Habitat Suitability Modelling

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

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

226 3 Results

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

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

In warmer and drier climatic conditions, *P. setaceum* is likely to shift from lower to higher elevations, increasing the total area occupied by the species (Figure 3). Indeed, estimates of habitat suitability indicate the preference of the species for climatic conditions with a mean spring temperature higher than 10° C (Figure 4).

²⁵⁰ 4 Discussion

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

²⁶² 4.1 Invaded habitats

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

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

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

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

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

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

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

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

364 5 Conclusions

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

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

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

408 6 Acknowledgements

We would like to thank the Teno Rural Park for having shared its IAS database. We are grateful to the anonymous reviewers for the constructive and positive suggestions. D.D.R. was supported by an ERASMUS+ 2015-2016 grant provided by the European Commission.

413 References

Adkins, E., Cordell, S., and Drake, D. R. (2011). Role of fire in the germination ecology
of fountain grass (*Pennisetum setaceum*), an invasive african bunchgrass in Hawai'i. *Pacific Science*, 65(1):17–26.

- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., and Anderson, R. P.
 (2015). spthin: an r package for spatial thinning of species occurrence records for use
 in ecological niche models. *Ecography*, 38(5):541–545.
- Arechavaleta, M., Rodríguez, S., Zurita, N., and García, A. (2010). Lista de especies silvestres de canarias. Hongos, plantas y animales terrestres. 2009. *Gobierno de Canarias, Tenerife*.

Arévalo, J., Otto, R., Escudero, C., Fernández-Lugo, S., Arteaga, M., Delgado, J., and
Fernández-Palacios, J. (2010). Do anthropogenic corridors homogenize plant communities at a local scale? a case studied in Tenerife (Canary Islands). *Plant Ecology*,
209(1):23–35.

- 427 Arteaga, M. A., Delgado, J. D., Otto, R., Fernández-Palacios, J. M., and Arévalo, J. R.
- (2009). How do alien plants distribute along roads on oceanic islands? A case study in

⁴²⁹ Tenerife, Canary Islands. *Biological Invasions*, 11(4):1071–1086.

430 Assessment, M. E. (2005). Ecosystems and human well-being: synthesis.

Bacaro, G., Maccherini, S., Chiarucci, A., Jentsch, A., Rocchini, D., Torri, D., Gioria,
M., Tordoni, E., Martellos, S., Altobelli, A., et al. (2015). Distributional patterns
of endemic, native and alien species along a roadside elevation gradient in Tenerife,
Canary Islands. *Community ecology*, 16(2):223–234.

- Barbet-Massin, M., Rome, Q., Villemant, C., and Courchamp, F. (2018). Can species
 distribution models really predict the expansion of invasive species? *PloS one*, 13(3).
- Barni, E., Bacaro, G., Falzoi, S., Spanna, F., and Siniscalco, C. (2012). Establishing
 climatic constraints shaping the distribution of alien plant species along the elevation
 gradient in the Alps. *Plant Ecology*, 213(5):757–767.
- Bella, S., D'Urso, V., et al. (2012). First record in the Mediterranean basin of the
 alien leafhopper *Balclutha Brevis* living on invasive *Pennisetum setaceum*. *Bulletin of Insectology*, 65(2):195–198.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology letters*, 15(4):365–377.
- Bellard, C., Leclerc, C., and Courchamp, F. (2014). Impact of sea level rise on the 10 insular biodiversity hotspots. *Global Ecology and Biogeography*, 23(2):203–212.
- Benedetti, Y. and Morelli, F. (2017). Spatial mismatch analysis among hotspots of
 alien plant species, road and railway networks in Germany and Austria. *PloS one*,
 12(8):e0183691.

Brundu, G. and Richardson, D. M. (2016). Planted forests and invasive alien trees in
Europe: a code for managing existing and future plantings to mitigate the risk of
negative impacts from invasions.

⁴⁵³ Chuine, I., Morin, X., Sonié, L., Collin, C., Fabreguettes, J., Degueldre, D., Salager,
⁴⁵⁴ J.-L., and Roy, J. (2012). Climate change might increase the invasion potential of the
⁴⁵⁵ alien C4 grass Setaria parviflora (Poaceae) in the Mediterranean Basin. Diversity and
⁴⁵⁶ Distributions, 18(7):661-672.

- 457 Cordell, S. and Sandquist, D. (2008). The impact of an invasive African bunchgrass
 458 (*Pennisetum setaceum*) on water availability and productivity of canopy trees within
 459 a tropical dry forest in Hawaii. *Functional Ecology*, 22(6):1008–1017.
- Courchamp, F., Chapuis, J.-L., and Pascal, M. (2003). Mammal invaders on islands:
 impact, control and control impact. *Biological Reviews*, 78(3):347–383.
- 462 Cropper, T. (2013). The weather and climate of Macaronesia: past, present and future.
 463 Weather, 68(11):300-307.
- Cropper, T. E. and Hanna, E. (2014). An analysis of the climate of Macaronesia, 1865–
 2012. International Journal of Climatology, 34(3):604–622.
- ⁴⁶⁶ Da Re, D., Tordoni, E., Pérez, Z. N., Fernández-Palacios, J. M., Arévalo, J. R., Otto, R.,
 ⁴⁶⁷ Rocchini, D., and Bacaro, G. (2019). A spatially-explicit model of alien plant richness
 ⁴⁶⁸ in Tenerife (Canary Islands). *Ecological Complexity*, 38:75–82.
- ⁴⁶⁹ D'Antonio, C. M. and Vitousek, P. M. (1992). Biological invasions by exotic grasses,
 ⁴⁷⁰ the grass/fire cycle, and global change. Annual review of ecology and systematics,
 ⁴⁷¹ 23(1):63-87.
- ⁴⁷² Davis, M. A., Grime, J. P., and Thompson, K. (2000). Fluctuating resources in plant ⁴⁷³ communities: a general theory of invasibility. *Journal of ecology*, 88(3):528–534.
- ⁴⁷⁴ Davis, S. J. and Socolow, R. H. (2014). Commitment accounting of co₂ emissions. *Envi*-⁴⁷⁵ ronmental Research Letters, 9(8):084018.
- ⁴⁷⁶ de Paz, P. L. P., Gallo, A. G., and Heene, A. (1999). Control y erradicación del" Rabo-⁴⁷⁷ Gato" ('Pennisetum setaceum') en la Isla de Palma. Universidad de la Laguna.
- ⁴⁷⁸ Delgado, J. D., Arévalo, J. R., and Fernández-Palacios, J. (2004). Consecuencias de la fragmentación viaria: efectos de borde de las carreteras en la laurisilva y el pinar de Tenerife. Ecología Insular/Island Ecology. Asociación Española de Ecología Terrestre (AEET)-Cabildo Insular de la Palma, pages 181–225.
- ⁴⁸² Devesa Alcaraz, J. A., Arnelas, I., et al. (2006). *Pennisetum setaceum* (forssk.) Chiov.
 ⁴⁸³ (Poaceae), nueva localidad para la flora ibérica.
- ⁴⁸⁴ Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'amen, M., Randin, C.,
 ⁴⁸⁵ Engler, R., Pottier, J., Pio, D., Dubuis, A., et al. (2017). ecospat: an r package to
 ⁴⁸⁶ support spatial analyses and modeling of species niches and distributions. *Ecography*,
 ⁴⁸⁷ 40(6):774–787.

- ⁴⁸⁸ Dukes, J. S. and Mooney, H. A. (1999). Does global change increase the success of ⁴⁸⁹ biological invaders? *Trends in Ecology & Evolution*, 14(4):135–139.
- ⁴⁹⁰ Dyderski, M. K., Paź, S., Frelich, L. E., and Jagodziński, A. M. (2018). How much does
 ⁴⁹¹ climate change threaten European forest tree species distributions? *Global change*⁴⁹² *biology*, 24(3):1150–1163.
- Early, R. and Sax, D. F. (2014). Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change.
 Global ecology and biogeography, 23(12):1356–1365.
- Ehleringer, J. and Björkman, O. (1977). m yields for CO2 uptake in C3 and C4 plants:
 dependence on temperature, CO2, and O2 concentration. *Plant Physiology*, 59(1):86–90.
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., and Yates, C. J. (2011). A
 statistical explanation of maxent for ecologists. *Diversity and distributions*, 17(1):43–57.
- Fernández-Palacios, J. M., Rijsdijk, K. F., Norder, S. J., Otto, R., de Nascimento, L.,
 Fernández-Lugo, S., Tjørve, E., and Whittaker, R. J. (2016). Towards a glacial-sensitive
 model of island biogeography. *Global Ecology and Biogeography*, 25(7):817–830.
- Follak, S., Eberius, M., Essl, F., Fürdös, A., Sedlacek, N., and Trognitz, F. (2018).
 Invasive alien plants along roadsides in Europe. *EPPO Bulletin*, 48(2):256–265.
- Foxcroft, L. C., Spear, D., van Wilgen, N. J., and McGeoch, M. A. (2019). Assessing the
 association between pathways of alien plant invaders and their impacts in protected
 areas. *NeoBiota*, 43:1.
- Francisco-Ortega, J., Santos-Guerra, A., and Bacallado, J. J. (2009). Canary Islands,
 biology. *Encyclopedia of islands*, pages 127–133.
- Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., and Thuiller, W. (2012). Invasive
 species distribution models-how violating the equilibrium assumption can create new
 insights. *Global Ecology and Biogeography*, 21(11):1126–1136.
- García-Herrera, R., Gallego, D., Hernández, E., Gimeno, L., Ribera, P., and Calvo, N.
 (2003). Precipitation trends in the Canary Islands. *International Journal of Climatol*ogy, 23(2):235–241.
- Garzón-Machado, V., Otto, R., and del Arco Aguilar, M. J. (2014). Bioclimatic and
 vegetation mapping of a topographically complex oceanic island applying different
 interpolation techniques. *International Journal of Biometeorology*, 58(5):887–899.
- ⁵²¹ Giorgi, F. (2006). Climate change hot-spots. *Geophysical research letters*, 33(8).
- ⁵²² Gobierno de Canarias, G. (2015). Banco de datos de biodiversidad de Canarias.
- Goergen, E. and Daehler, C. C. (2002). Factors affecting seedling recruitment in an invasive grass (*Pennisetum setaceum*) and a native grass (*Heteropogon contortus*) in the Hawaiian Islands. *Plant Ecology*, 161(2):147–156.

- González-Rodríguez, A. M., Baruch, Z., Palomo, D., Cruz-Trujillo, G., Jiménez, M. S.,
 and Morales, D. (2010). Ecophysiology of the invader *Pennisetum setaceum* and three
- native grasses in the Canary Islands. *Acta Oecologica*, 36(2):248–254.

Gremmen, N., Chown, S., and Marshall, D. (1998). Impact of the introduced grass
 Agrostis stolonifera on vegetation and soil fauna communities at Marion Island, sub Antarctic. Biological Conservation, 85(3):223–231.

- Guevara, L., Gerstner, B. E., Kass, J. M., and Anderson, R. P. (2018). Toward ecologically realistic predictions of species distributions: A cross-time example from tropical montane cloud forests. *Global change biology*, 24(4):1511–1522.
- Guisan, A. and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology letters*, 8(9):993–1009.
- ⁵³⁷ Guisan, A., Thuiller, W., and Zimmermann, N. E. (2017). *Habitat suitability and distri-*⁵³⁸ *bution models: with applications in R.* Cambridge University Press.
- Hansen, A. et al. (1970). Contributions to the flora of the Canary Islands (especially
 Tenerife). Cuad. Bot. Canar, 9:37–59.
- Hernandez, R. R. and Sandquist, D. R. (2011). Disturbance of biological soil crust
 increases emergence of exotic vascular plants in California sage scrub. *Plant Ecology*,
 212(10):1709.
- Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., and Hijmans, M. R. J. (2017).
 Package 'dismo'. *Circles*, 9(1):1–68.
- Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., and Guisan, A. (2006). Evaluating the
 ability of habitat suitability models to predict species presences. *Ecological modelling*,
 199(2):142–152.
- Hobi, S. (2008). Analyse der faktoren klima und störung als höhenlimite des neophyten
 Pennisetum setaceum auf Teneriffa.
- ⁵⁵¹ Hulme, P. E. (2009). Handbook of alien species in Europe, volume 569. Springer.
- Jacobi, J. D. and Warshauer, F. R. (1992). Distribution of six alien plant species in upland habitats on the island of Hawaii. Alien plant invasions in native ecosystems of Hawaii. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu, pages 155–188.
- Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J., Aragón, P., and Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. *Biological invasions*, 13(12):2785–2797.
- Kalwij, J. M., Robertson, M. P., and van Rensburg, B. J. (2015). Annual monitoring
 reveals rapid upward movement of exotic plants in a montane ecosystem. *Biological invasions*, 17(12):3517–3529.
- Kearney, M. (2006). Habitat, environment and niche: what are we modelling? Oikos,
 115(1):186-191.

Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Péré, C., Cock, M. J.,
Settele, J., Augustin, S., and Lopez-Vaamonde, C. (2009). Ecological effects of invasive
alien insects. *Biological Invasions*, 11(1):21–45.

Khalyani, A. H., Gould, W. A., Harmsen, E., Terando, A., Quinones, M., and Collazo,
J. A. (2016). Climate change implications for tropical islands: Interpolating and interpreting statistically downscaled gcm projections for management and planning. *Journal*of Applied Meteorology and Climatology, 55(2):265–282.

Kleinbauer, I., Dullinger, S., Peterseil, J., and Essl, F. (2010). Climate change might drive
the invasive tree *Robinia pseudacacia* into nature reserves and endangered habitats.

Biological conservation, 143(2):382-390.

Kueffer, C., Daehler, C. C., Torres-Santana, C. W., Lavergne, C., Meyer, J.-Y., Otto,
R., and Silva, L. (2010). A global comparison of plant invasions on oceanic islands.

Perspectives in Plant Ecology, Evolution and Systematics, 12(2):145–161.

Luque, A., Martín, J. L., Dorta, P., Mayer, P., et al. (2014). Temperature trends on
Gran Canaria (Canary Islands). an example of global warming over the subtropical
Northeastern Atlantic. Atmospheric and Climate Sciences, 4(1):20–28.

Martín, J. L., Bethencourt, J., and Cuevas-Agulló, E. (2012). Assessment of global warm ing on the island of Tenerife, Canary Islands (Spain). trends in minimum, maximum

and mean temperatures since 1944. *Climatic Change*, 114(2):343–355.

Martín Esquivel, J., García, H., Redondo, C., García, I., and Carralero, I. (1995). La
 red canaria de espacios naturales protegidos. *Gobierno de Canarias. Viceconsejería de Medio Ambiente, Santa Cruz.*

Matías, L. and Jump, A. S. (2013). Impacts of predicted climate change on recruitment at the geographical limits of Scots pine. *Journal of experimental botany*, 65(1):299–310.

Medley, K. A. (2010). Niche shifts during the global invasion of the Asian tiger mosquito,
 Aedes albopictus skuse (Culicidae), revealed by reciprocal distribution models. *Global ecology and biogeography*, 19(1):122–133.

Merow, C., Smith, M. J., and Silander, J. A. (2013). A practical guide to MaxEnt for
 modeling species' distributions: what it does, and why inputs and settings matter.
 Ecography, 36:1058–1069.

Morales, C. L. and Aizen, M. A. (2002). Does invasion of exotic plants promote invasion
of exotic flower visitors? A case study from the temperate forests of the southern andes. *Biological Invasions*, 4(1):87–100.

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M.,
and Anderson, R. P. (2014). Enm eval: An r package for conducting spatially independent evaluations and estimating optimal model complexity for maxent ecological niche
models. *Methods in Ecology and Evolution*, 5(11):1198–1205.

Myers, D. E. (1984). *Co-Kriging — New Developments*, pages 295–305. Springer Netherlands, Dordrecht.

Pasta, S., Badalamenti, E., and Mantia, T. L. (2010). Tempi e modi di un'invasione
incontrastata: *Pennisetum setaceum* (Forssk.) Chiov. (Poaceae) in sicilia.

Pauchard, A. and Alaback, P. B. (2004). Influence of elevation, land use, and landscape
 context on patterns of alien plant invasions along roadsides in protected areas of South Central Chile. *Conservation Biology*, 18(1):238–248.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W.,
Fernández-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L.,
Chini, L. P., Cooper, H. A., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington,
H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P. P., Scholes, R. J.,
Sumaila, U. R., and Walpole, M. (2010). Scenarios for global biodiversity in the 21st
century. *Science*, 330 6010:1496–501.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E.,
Nakamura, M., and Araújo, M. B. (2011). *Ecological niches and geographic distributions*(MPB-49), volume 56. Princeton University Press.

- Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., and Blair, M. E. (2017).
 Opening the black box: an open-source release of maxent. *Ecography*, 40(7):887–893.
- Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling
 of species geographic distributions. *Ecological modelling*, 190(3-4):231–259.
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., and
 Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological applications*, 19(1):181–197.
- Potgieter, L. J., Gaertner, M., O'Farrell, P. J., and Richardson, D. M. (2019). Perceptions
 of impact: invasive alien plants in the urban environment. *Journal of environmental management*, 229:76–87.
- Poulin, J., Sakai, A. K., Weller, S. G., and Nguyen, T. (2007). Phenotypic plasticity, precipitation, and invasiveness in the fire-promoting grass *Pennisetum setaceum*(Poaceae). *American Journal of Botany*, 94(4):533–541.

Pyšek, P., Jarošík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S.,
Chiron, F., Didžiulis, V., Essl, F., et al. (2010). Disentangling the role of environmental
and human pressures on biological invasions across europe. *Proceedings of the National Academy of Sciences*, 107(27):12157–12162.

Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Winter, M., 634 Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabesaz, F. J., Cárdenas, 635 D., Cárdenas-Toro, J., Castaño, N., Chacón, E. L., Chatelain, C., Dullinger, S., Ebel, 636 A. L., Figueiredo, E., Fuentes, N. J., Genovesi, P., Groom, Q. J., Henderson, L. M., 637 Inderjit, Kupriyanov, A., Masciadri, S., Maurel, N., Meerman, J. C., Morozova, O. V., 638 Moser, D., Nickrent, D. L., Nowak, P. M., Pagad, S., Patzelt, A., Pelser, P. B., Seebens, 639 H., Shu, W., Thomas, J. J., Velayos, M., Weber, E., Wieringa, J. J., Baptiste, M. P., 640 and van Kleunen, M. (2017). Naturalized alien flora of the world: species diversity, 641 taxonomic and phylogenetic patterns, geographic distribution and global hotspots of 642 plant invasion. volume 89, pages 203–274. Czech Botanical Society. 643

- Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M., and
 Kirschner, J. (2004). Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. volume 53, pages 131–143. Wiley Online
 Library.
- Qian, H. and Ricklefs, R. E. (2006). The role of exotic species in homogenizing the North
 American flora. *Ecology letters*, 9 12:1293–8.
- Rahlao, S. J., Esler, K. J., Milton, S. J., and Barnard, P. (2010). Nutrient addition and
 moisture promote the invasiveness of crimson fountaingrass (*Pennisetum setaceum*). *Weed Science*, 58(2):154–159.
- Ribeiro Jr, P. J., Diggle, P. J., et al. (2001). geor: a package for geostatistical analysis. R news, 1(2):14–18.

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., et al. (2017). Crossvalidation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, 40(8):913–929.

- Rodríguez-Caballero, G., Caravaca, F., del Mar Alguacil, M., Fernández-López, M.,
 Fernández-González, A. J., and Roldán, A. (2017). Striking alterations in the soil
 bacterial community structure and functioning of the biological N cycle induced by *Pennisetum setaceum* invasion in a semiarid environment. Soil Biology and Biochem-*istry*, 109:176–187.
- Rodríguez-Caballero, G., Caravaca, F., and Roldán, A. (2018). The unspecificity of
 the relationships between the invasive *Pennisetum setaceum* and mycorrhizal fungi
 may provide advantages during its establishment at semiarid mediterranean sites. *The Science of the total environment*, 630:1464–1471.
- Saavedra, M. and Alcántara, C. (2017). Pennisetum setaceum, planta invasora en expansión. In Mercedes Royuela Hernando y Ana Zabalza Aznárez (editoras): XVI Congreso
 de la Sociedad Española de Malherbología: actas. Pamplona-Iruña, 25-27 octubre, 2017.
 Universidad Pública de Navarra Nafarroako Unibertsitate Publikoa, 2017. Universidad
 Pública de Navarra/Nafarroako Unibertsitate Publikoa.
- Sage, R. F. and Kubien, D. S. (2003). Quo vadis C4? an ecophysiological perspective on
 global change and the future of C4 plants. *Photosynthesis research*, 77(2-3):209–225.

Sánchez-Benítez, A., García-Herrera, R., and Vicente-Serrano, S. M. (2017). Revisiting
 precipitation variability, trends and drivers in the Canary Islands. *International Journal* of Climatology, 37(9):3565–3576.

- Scalera, R., Genovesi, P., Essl, F., and Rabitsch, W. (2012). The impacts of invasive
 alien species in Europe. European Environment Agency Technical Report, 16:114.
- Schuster, M. J., Wragg, P. D., and Reich, P. B. (2018). Using revegetation to suppress
 invasive plants in grasslands and forests. *Journal of Applied Ecology*, 55(5):2362–2373.
- Sladonja, B. and Poljuha, D. (2018). Citizen science as a tool in biological recording–A case study of *Ailanthus altissima* (Mill.) Swingle. *Forests*, 9(1):31.

Somot, S., Sevault, F., Déqué, M., and Crépon, M. (2008). 21st century climate change
scenario for the Mediterranean using a coupled atmosphere-ocean regional climate
model. *Global and Planetary Change*, 63(2-3):112–126.

Steinbauer, M. J., Irl, S. D. H., González-Mancebo, J. M., Breiner, F. T., Hernández-Hernández, R., Hopfenmüller, S., Kidane, Y. M., Jentsch, A., and Beierkuhnlein, C.
(2017). Plant invasion and speciation along elevational gradients on the oceanic island La Palma, Canary Islands. In *Ecology and evolution*.

- Steiner, F. M., Schlick-Steiner, B. C., VanDerWal, J., Reuther, K. D., Christian, E.,
 Stauffer, C., Suarez, A. V., Williams, S. E., and Crozier, R. H. (2008). Combined
 modelling of distribution and niche in invasion biology: a case study of two invasive
 tetramorium ant species.
- Stephenson, N. L. (1990). Climatic control of vegetation distribution: the role of the
 water balance. *The American Naturalist*, 135(5):649–670.

Stocker, T. (2014). Climate change 2013: the physical science basis: Working Group I
 contribution to the Fifth assessment report of the Intergovernmental Panel on Climate
 Change. Cambridge University Press.

- Sweet, L. C. and Holt, J. S. (2015). Establishment stage competition between exotic Crim son fountaingrass (*Pennisetum setaceum*, C4) and native Purple Needlegrass (*Stipa pulchra*, C3). Invasive Plant Science and Management, 8(2):139–150.
- Syfert, M. M., Smith, M. J., and Coomes, D. A. (2013). The effects of sampling bias
 and model complexity on the predictive performance of maxent species distribution
 models. *PloS one*, 8(2):e55158.
- Thuiller, W. (2007). Biodiversity: Climate change and the ecologist. *Nature*, 448:550–552.
- Toby Kiers, E., Palmer, T. M., Ives, A. R., Bruno, J. F., and Bronstein, J. L. (2010). Mutualisms in a changing world: an evolutionary perspective. *Ecology letters*, 13(12):1459–
 1474.
- Tordoni, E., Napolitano, R., Nimis, P., Castello, M., Altobelli, A., Da Re, D., Zago, S.,
 Chines, A., Martellos, S., Maccherini, S., and Bacaro, G. (2017). Diversity patterns of
 alien and native plant species in trieste port area: exploring the role of urban habitats
 in biodiversity conservation. Urban ecosystems, 20(5):1151–1160.
- Tordoni, E., Petruzzellis, F., Nardini, A., and Bacaro, G. (2020). Functional divergence drives invasibility of plant communities at the edges of a resource availability gradient. *Diversity*, 12(4):148.
- Tordoni, E., Petruzzellis, F., Nardini, A., Savi, T., and Bacaro, G. (2019). Make it simpler: Alien species decrease functional diversity of coastal plant communities. *Journal of Vegetation Science*, 30(3):498–509.
- Tunison, J. T. (1992). Fountain grass control in Hawaii Volcanoes National Park: management considerations and strategies. Alien plant invasions in native ecosystems of Hawai 'i: Management and research. Cooperative National Parks Resources Studies Unit, University of Hawai 'i at Manoa, Honolulu, pages 376–393.

Vilà, M., Espinar, J. A. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl,
J., Schaffner, U., Sun, Y., and Pyšek, P. (2011). Ecological impacts of invasive alien
plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology letters*, 14 7:702–8.

- Vilà, M. and López-Darias, M. (2006). Contrasting biogeography of endemic and alien
 terrestrial species in the canary islands. Orsis: organismes i sistemes, 21:91–101.
- Walentowitz, A. J., Irl, S. D., Acevedo Rodríguez, A. J., Palomares-Martínez, Á., Vetter,
 V., Zennaro, B., Medina, F. M., and Beierkuhnlein, C. (2019). Graminoid invasion in
 an insular endemism hotspot and its protected areas. *Diversity*, 11(10):192.
- Warren, D. L. and Seifert, S. N. (2011). Ecological niche modeling in maxent: the importance of model complexity and the performance of model selection criteria. *Ecological applications*, 21(2):335–342.
- West, A. M., Kumar, S., Brown, C. S., Stohlgren, T. J., and Bromberg, J. (2016). Field
 validation of an invasive species maxent model. *Ecological Informatics*, 36:126–134.
- Whittaker, R. J. and Fernández-Palacios, J. M. (2007). Island biogeography: ecology,
 evolution, and conservation. Oxford University Press.
- Williams, D. and Black, R. (1993). Phenotypic variation in contrasting temperature environments: growth and photosynthesis in *Pennisetum setaceum* from different altitudes
 on Hawaii. *Functional Ecology*, pages 623–633.
- Williams, D. G., Mack, R. N., and Black, R. A. (1995). Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology*, 76(5):1569–1580.
- ⁷⁴⁶ Wilson, A. M. and Silander, J. A. (2014). Estimating uncertainty in daily weather inter-
- 747 polations: a bayesian framework for developing climate surfaces. International Journal
- ⁷⁴⁸ of Climatology, 34(8):2573–2584.

$_{749}$ 7 Tables

	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 1: Predictors summary statistics at the occurrences locations.

parameters	3.00	5.00	4.00	30.00	3.00	4.00	4.00	23.00	3.00	4.00	3.00	11.00	3.00	3.00	3.00	12.00	3.00	3.00	2.00	9.00	3.00	3.00	2.00	6.00	3.00	3.00	1.00	1.00	3.00	3.00	1.00	1.00	3.00	2.00	1.00	1.00	3.00	2.00	1.00	1.00
w.AIC	0.05	0.10	0.23	0.00	0.04	0.07	0.02	0.00	0.04	0.01	0.03	0.00	0.03	0.03	0.01	0.00	0.03	0.02	0.02	0.00	0.02	0.02	0.01	0.00	0.02	0.01	0.02	0.02	0.01	0.01	0.02	0.02	0.01	0.01	0.02	0.02	0.00	0.01	0.01	0.01
delta.AICc	3.22	1.62	0.00	162.82	3.36	2.52	4.91	81.48	3.60	6.00	4.14	19.68	3.92	4.15	5.68	26.15	4.34	4.70	4.75	19.21	4.85	5.36	5.88	13.76	5.45	6.15	4.68	4.68	6.13	7.06	4.98	4.94	6.91	5.64	5.22	5.29	7.78	6.26	5.52	5.52
pet AlCc	0.05 787.33	0.07 785.73	0.04 784.11	0.02 946.93	0.05 787.47	0.07 786.63	0.05 789.02	0.02 865.59	0.05 787.71	0.05 790.11	0.04 788.25	0.02 803.79	0.05 788.03	0.04 788.26	0.04 789.79	0.02 810.26	0.04 788.45	0.04 788.81	0.02 788.86	0.02 803.32	0.04 788.96	0.04 789.47	0.01 789.99	0.01 797.87	0.04 789.55	0.04 790.26	0.01 788.79	0.01 788.79	0.04 790.24	0.02 791.17	0.01 789.09	0.01 789.05	0.04 791.02	0.01 789.75	0.01 789.33	0.01 789.39	0.02 791.88	0.01 790.37	0.01 789.63	0.01 789.63
var.test.or10)))	0)))))))	0)))	0)))	0))	0	0	0	0	0	0	0	0	0	0	0))	0)))	0
avg.test.or10pct	0.13	0.16	0.16	0.28	0.16	0.16	0.16	0.16	0.16	0.16	0.18	0.16	0.16	0.18	0.18	0.16	0.18	0.18	0.16	0.18	0.18	0.18	0.13	0.13	0.18	0.18	0.11	0.11	0.18	0.16	0.09	0.11	0.18	0.13	0.09	0.09	0.16	0.13	0.09	0.09
ar.test.orMTP	0.01	0.03	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
avg.test.orMTP v	0.05	0.09	0.02	0.02	0.02	0.07	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.05	0.02	0.02	0.02	0.05	0.02	0.05	0.02	0.02	0.02	0.02	0.02	0.02	0.05	0.02	0.02	0.02	0.02	0.02	0.02	0.02
var.diff.AUC	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.00	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00
avg.diff.AUC	0.04	0.05	0.05	0.08	0.04	0.04	0.04	0.07	0.03	0.04	0.04	0.06	0.03	0.03	0.03	0.05	0.03	0.03	0.03	0.05	0.03	0.03	0.03	0.05	0.03	0.03	0.03	0.04	0.03	0.03	0.02	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.02	0.02
ar.test.AUC 8	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
vg.test.AUC v	0.77	0.76	0.77	0.75	0.77	0.76	0.77	0.76	0.76	0.76	0.76	0.75	0.76	0.76	0.75	0.74	0.76	0.75	0.75	0.74	0.76	0.75	0.74	0.73	0.75	0.75	0.74	0.73	0.75	0.74	0.75	0.74	0.75	0.74	0.75	0.75	0.74	0.74	0.75	0.75
train.AUC a	0.76	0.78	0.78	0.81	0.76	0.77	0.76	0.80	0.76	0.76	0.76	0.79	0.76	0.76	0.76	0.78	0.76	0.76	0.75	0.77	0.76	0.76	0.75	0.75	0.76	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75
	0.50	0.50	0.50	0.50	1.00	1.00	1.00	1.00	1.50	1.50	1.50	1.50	2.00	2.00	2.00	2.00	2.50	2.50	2.50	2.50	3.00	3.00	3.00	3.00	3.50	3.50	3.50	3.50	4.00	4.00	4.00	4.00	4.50	4.50	4.50	4.50	5.00	5.00	5.00	5.00
Ieatures	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH	L	LQ	LQP	LQPH
settings	$L_{-0.5}$	$LQ_0.5$	$LQP_{0.5}$	$LQPH_0.5$	${ m L}_{-1}$	LQ_{-1}	LQP_{-1}	$LQPH_1$	$L_{-1.5}$	$LQ_{-}1.5$	$LQP_{-1.5}$	$LQPH_{-1.5}$	L_2	LQ_2	LQP_2	$LQPH_2$	$L_2.5$	$LQ_2.5$	$LQP_{-2.5}$	$LQPH_{2.5}$	L_{-3}	LQ_{-3}	LQP_{-3}	$LQPH_3$	$L_{-3.5}$	$LQ_{-3.5}$	$LQP_{3.5}$	$LQPH_{3.5}$	L_{-4}	LQ_4	LQP_{-4}	$LQPH_4$	$L_{-4.5}$	$LQ_{-4.5}$	$LQP_{-4.5}$	$LQPH_{-4.5}$	L_{-5}	LQ_{-5}	LQP_5	LQPH 5
	-	0	ŝ	4	5	9	2	×	6	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40

Table 2: Results of the Maxent model selection via AICc

750 8 Figures



Figure 1: P. setaceum thinned occurences 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 \boldsymbol{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

(2) opposed by $R^2 = 0.97$ (2)

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

Occurences cumulative distribution



Presence cumulative density distribution

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

 R codes
 The R codes used in the present study are available at the following gitLab repositories
 cokriging repository: https://gitlab.com/danidr/cokriging Occurence filtering and Maxent Modelling: https://gitlab.com/danidr/pennisetum_ hsm_tfe