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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 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.*

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setaceum suitable areas is characterized by an elevational shift, which is more pronounced in the RCP8.5 AQ1 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.

Keywords Habitat suitability models · Invasive alien species · Canary Archipelago · Global warming

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 CO_2 atmospheric concentration and Nitrogen deposition promotes the presence of invasive species and enhances 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; Millennium Ecosystem 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 urbanized areas toward natural ones (Martín Esquivel et al. 1995; González-Rodríguez et al. 2010). Elevated phenotypic plasticity, characterised by variation in functional trait value according to the environment, and its resilience, makes *P. setaceum* well adapted to different ecological conditions (Poulin et al. 2007; González-Rodríguez et al. 2010). Moreover, it can establish symbiosis with different local mycorrhizal fungi (AMF) communities, further promoting a successful establishment and spread (Rodríguez-Caballero et al. 2018). It is an aggressive invader of arid and semiarid coastal habitats such as thermo-xerophilous grasslands and shrublands. Here, it establishes almost monospecific stands and causes long-lasting ecological consequences (Cordell and Sandquist 2008; González-Rodríguez et al. 2010). The species is known to have negative impacts on resources acquisitions in the dry forest plant communities and it can interact with the soil bacterial community, shifting its structure and composition, which can result in severe alterations of the N cycle (Rodríguez-Caballero et al. 2017). Moreover, it is a fire promoting species that can cause dramatic environmental changes, since fire is one of the most important drivers of land use and atmospheric changes globally (D'Antonio and Vitousek 1992). Finally, it can promote the presence of the alien invasive leafhopper *Balclutha brevis* (Bella et al. 2012). It has been estimated that approximately 30% of all protected areas of the Canary Islands have been invaded by fountain grass (Martín Esquivel et al. 1995; González-Rodríguez et al. 2010). Considering the dramatic effects that an uncontrolled increase in its distribution could create on Tenerife, understanding *P. setaceum* future habitat distribution is particularly important both from a conservational and ecological perspective, and it is a time-sensitive task.

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

Considering the importance of predictive tools to halt the loss of biodiversity, especially in relation to the spread of IAS fostered by climate change, here we aimed at (i) estimating *P. setaceum*'s current habitat distribution through HSM, across its' invaded 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.

Materials and methods

Study area

The study was carried out in Tenerife (27°–29°N, 13°–18°W; Fig. 1), the largest island of the Canary archipelago and the one with the highest elevation within Macaronesia (Mount Teide, 3718 m asl). Strong variations in elevation and aspect define local mesoclimatic zones and land uses that are primary

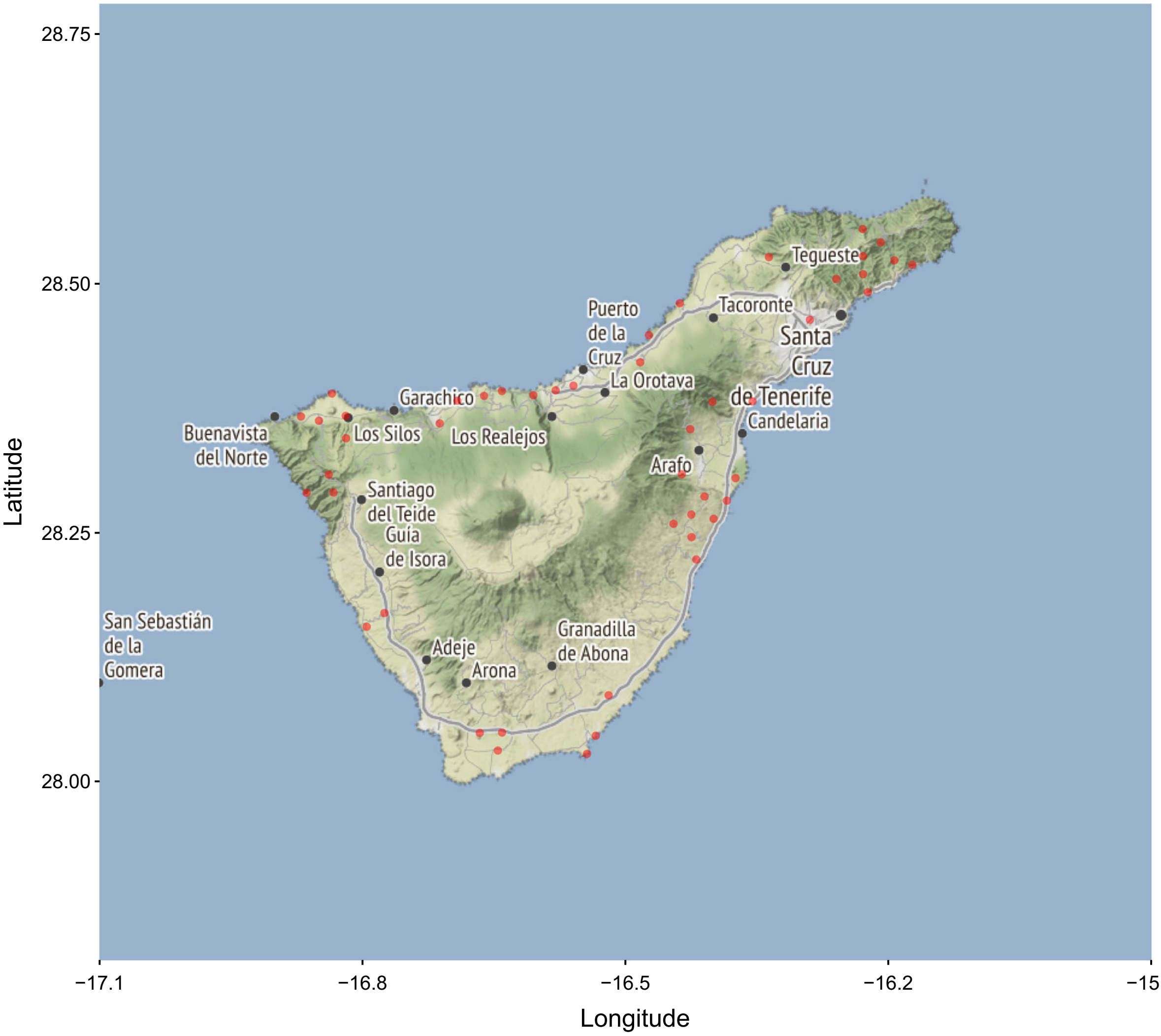

Fig. 1 *Pennisetum setaceum* thinned occurrences distribution on Tenerife

factors in structuring both native and alien plant communities on the Canary Islands (Whittaker and Fernández-Palacios 2007). Mesoclimate is affected by the trade winds that create a contrast between the northern or windward aspect (more humid and cloudier) and the southern or leeward aspect (more arid and cloudless).

Response variable

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

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 October–March concentrates the 87.3 % of Canary Islands' annual precipitation (Sánchez-Benítez et al. 2017). Moreover, it has been reported that in Mediterranean-type climate areas, *P. setaceum* germination occurs primarily in the Winter–Spring period (especially in December–January), followed by a constant decline towards the Summer due to moisture reduction (Hernandez and Sandquist 2011). Mean spring temperature was also selected, since it is known to be a limiting factor for alien species colonization along an elevational gradient, being usually correlated to elevation (Barni et al. 2012; Bacaro et al. 2015; Steinbauer et al. 2017) and because the species has a maximum growth in warmer conditions (Sweet and Holt 2015).

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 epicentres 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–May periods, spanning from 2005 to 2014, were obtained from Agencia Estatal de Meteorología (AEMET, accessed on April 2016). The methodology presented in Da Re et al. (2019) was used for filtering and the processing of the meteorological data in order to obtain continuous climatic interpolated surfaces through a co-Kriging procedure, using elevation as covariate (Myers 1984; Garzón-Machado et al. 2014; Wilson and Silander 2014) and the R-package "geoR" (Ribeiro et al. 2001). Road kernel density, calculated on the road network using 10 km regularly distributed sample points, was used here as a proxy of human disturbance and as a source of propagule pressure (Bacaro et al. 2015; Da Re et al. 2019). The digital elevation model (DEM, 10 m of spatial resolution) and road network of Tenerife Island were downloaded from Cartográfica de Canarias S.A. (GRAFCAN, https://www.grafcan.es/, accessed on March 2016), all the derived variables were calculated using the grid spatial resolution as for the IAS occurrences (500 m) (Table 1).

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). With 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 in water availability of 15–20% due to more than 30% reduction in precipitation (Giorgi 2006; Somot et al. 2008). In order to get a reliable estimate of climate change effects on the climatic variables considered (though deemed approximate), we apply a constant correction on interpolated climatic surfaces. Specifically, we considered the two Representative Concentration Pathways (RCPs), namely RCP2.6 and RCP8.5, as described by the 5th Intergovernmental Panel on Climate Chage (IPCC) report representing possible ranges of radiative forcing values in the year 2100 relative to pre-industrial values (+ 2.6 and + 8.5 W/m^2, respectively). Winter and Spring precipitations were corrected by − 10.6% and − 36.7% (RCP2.6 and RCP8.5) according to Winter (December–January–February, DJF) precipitation reduction prevision made by Cropper (2013), while for Spring, temperature values 0.96 °C (RCP2.6) and 2.68 °C (RCP8.5) were added.

Habitat suitability modelling

HSMs were performed using Maxent v3.4.1 (Phillips et al. 2017) through the R-package "dismo" (Hijmans et al. 2017). Maxent estimates the relationship between species occurrences and various environmental predictors, identifying areas with suitable environmental conditions for the species, given a background uniform probability of 0.5 (Elith et al. 2011). To reduce the effects of sampling bias and thus avoiding a possible source of model inaccuracy (Phillips et al.

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

2006, 2009; Syfert et al. 2013), spatial filtering with a thinning distance of 2 km was applied to the *P. setaceum* occurrence dataset using the R-package “spThin” (Aiello-Lammens et al. 2015). The thinned occurrence data were then randomly divided into a training set and testing dataset applying a spatial block approach (Guevara et al. 2018; Roberts et al. 2017). Models with different combinations of feature classes (FC: Linear; Quadratic; Linear and Quadratic; Hinge; Linear, Quadratic, and Hinge) and beta regularization multipliers (RM: 0.5–5.0 with 0.5 intervals) were computed in order to avoid overfitting and to approximate optimal levels of complexity. The best model was then chosen based on Akaike Information Criterion corrected for small sample sizes (AICc, Warren and Seifert 2011; Muscarella et al. 2014). Following Guevara et al. (2018), we used all 8134-island pixel as background point to ensure a full representation of environments available for the species. The optimal settings obtained from above were used to train the final models using maxent.jar software. Model outputs were set as logistic response of the predicted distribution. The logistic output was then interpreted conservatively as a suitability index rather than as a probability (Merow et al. 2013) and it was evaluated using both the area under the curve (AUC) provided for the test data (Phillips et al. 2006), and the Boyce’s Index (Hirzel et al. 2006). The Boyce’s Index, computed through the “ecospat” R-package (Di Cola et al. 2017), ranges between − 1 (the model predict areas where presences are more frequent as being highly suitable for the species) and + 1 (the model predictions are consistent with the distribution of presences in the evaluation dataset), and values close to zero mean that the model is not different from random expectations (Hirzel et al. 2006). Finally, the model was projected onto current, RCP2.6, and RCP8.5 climatic scenarios using unconstrained extrapolation (Guevara et al. 2018). The R codes used are available in the gitLab repository presented in the Supplementary Materials.

Results

Pennisetum 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 approach and then these were used to train the model. Model selection based on the AICc criteria pointed out that the most appropriate model was the one having linear, quadratic and product features and a beta regularization multiplier equal to 0.5 (Table 2). For this model, both Boyce’s Index and AUC suggested good performance in predicting species’ environmental suitability (AUC = 0.757; Boyce’s Index = 0.855, respectively). Temperature was the most important variable (88.6% of variable importance) followed by precipitation and roads density (8.7 and 2.7% of variable importance, respectively). Current suitable areas for *P. setaceum* mirrored occurrences’ distribution appearing prevalently below 800 m (Fig. 2). Model prediction based on the RCP2.6 scenario substantially confirmed as highly suitable areas, the current suitable ones, though a shift to higher values of habitat suitability can also be observed at higher elevation (Fig. 2b). An elevational

shift is emphasized by the model prediction based on the RCP8.5 scenario (Fig. 2c), where *P. setaceum* seems to climb up along elevation (especially in the northern part of the island on the Anaga mountains).

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 (Fig. 3). Indeed, estimates of habitat suitability indicate the preference of the species for climatic conditions with a mean spring temperature higher than 10 °C (Fig. 4).

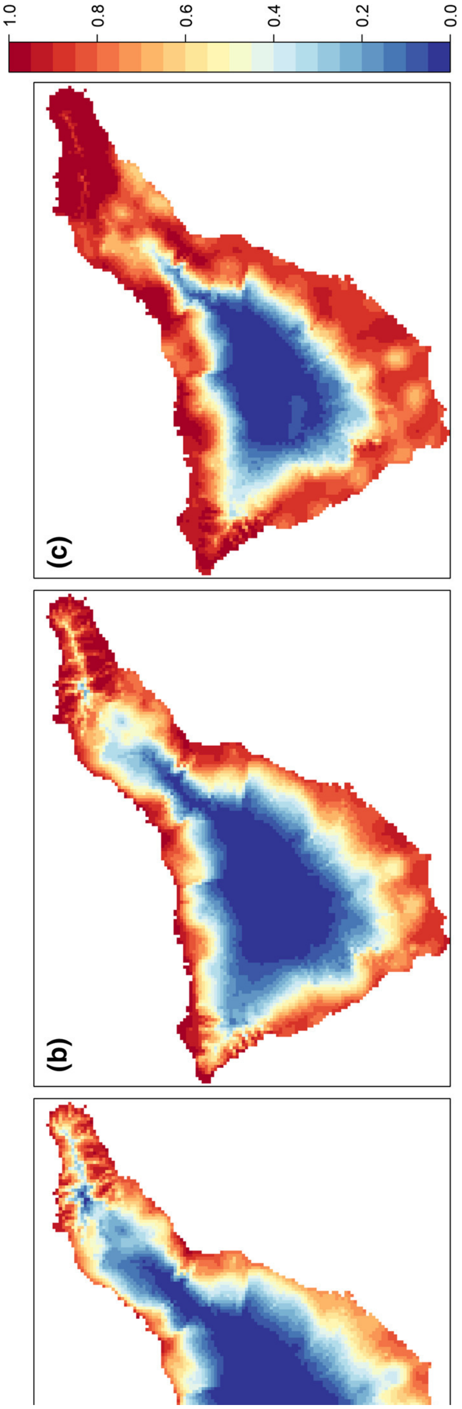

Fig. 2 *Pennisetum setaceum* HSM predictions: **a** current climatic conditions, **b** RCP2.6 climatic conditions, **c** RCP8.5 climatic conditions

Discussion

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

Invaded habitats

Pennisetum setaceum spread below 800 m asl is likely to be enhanced by anthropic disturbance (e.g. land-cover change and consequent habitat fragmentation), rather than global warming. However, due to the year-by-year increase in anthropic disturbance and temperature at higher elevations, its present distribution is still expanding above 800 m asl (see for instance Kalwij et al. 2015). It has also been observed that *P. setaceum* can reach up to 2000 m asl in other islands contexts such as Hawaii (Williams et al. 1995). Moreover, *P. setaceum* has been recently observed at altitudes of 1500 m in the Barranco Risco Liso, located

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	0.05	0.01	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	0.09	0.03	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.07	0.02	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	0.18	0.04	788.26	4.15	0.03	3.00
15	LQP_2	LQP	2.00	0.76	0.75	0.01	0.03	0.01	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.05	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.05	0.00	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	0.02	0.00	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	0.05	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.05	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	0.09	0.01	789.39	5.29	0.02	1.00

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Table 2 continued

	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
37	L_5	L	5.00	0.75	0.74	0.00	0.03	0.01	0.02	0.00	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	0.02	0.00	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	0.02	0.00	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	0.02	0.00	0.09	0.01	789.63	5.52	0.01	1.00

within the Caldera de Taburiente in La Palma island (Walentowitz et al. 2019). Around Tenerife island, *P. setaceum* has rapidly colonized mainly areas that were already experiencing anthropic disturbance, such as agricultural and rural areas, spreading at higher altitudinal belts using the road network as the main propagation pathway like other IAS (Arteaga et al. 2009; Arévalo et al. 2010; Benedetti and Morelli 2017; Follak et al. 2018). In fact, in the area near Arafo, which has a long land-use history for agriculture, the species has climbed up approximately 100 m in elevation in three years (from 655 to 740 m asl, personal observation of DDR and ZNP in April 2019). *P. setaceum* established firstly along the roadside, and then it spread deeper into the surrounding landscapes, confirming that roads remain a crucial dispersion pathway for this species and could promote its spread into protected areas (Foxcroft et al. 2019; Walentowitz et al. 2019). However, its ability to compete and outstand native plant communities could be questioned in areas characterized by a high degree of biotic resistence and where the native community has sufficient propagule pressure for new colonization (Schuster et al. 2018).

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

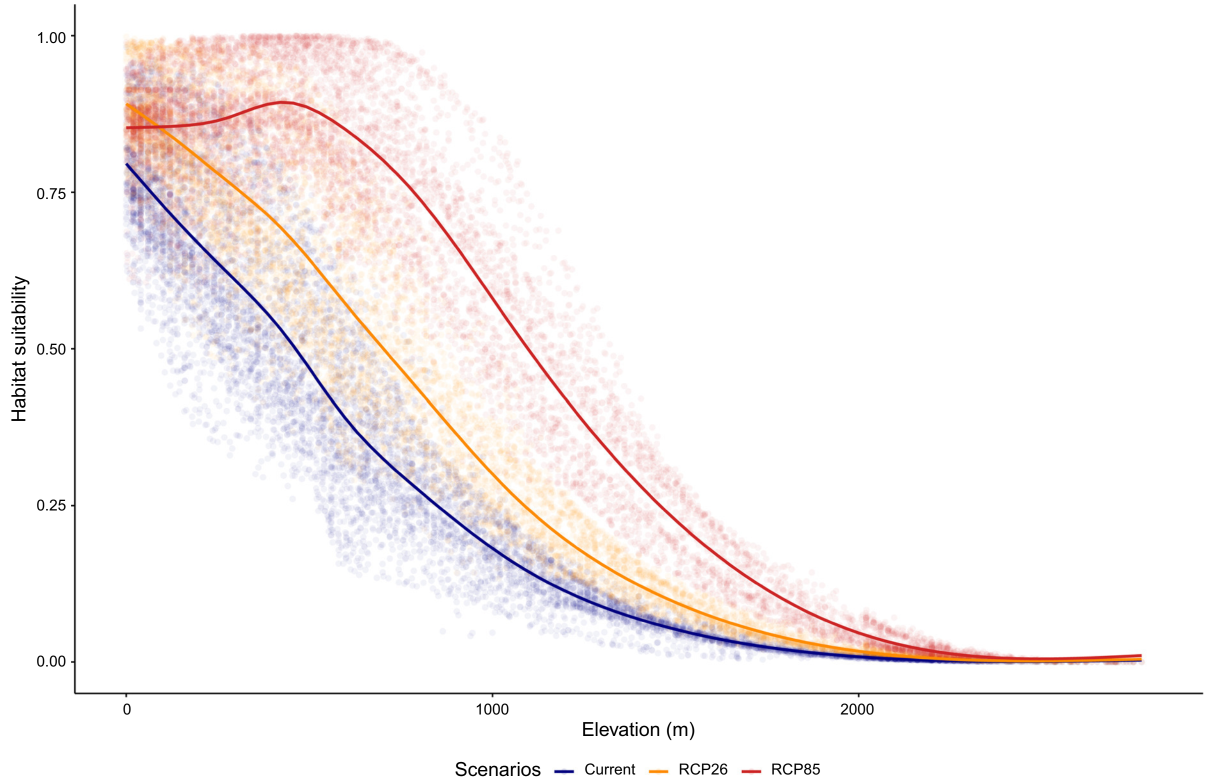

Fig. 3 Relationships between *P. setaceum* HSM predictions and elevation: blue dots and line, current climatic conditions; orange dots and line, RCP2.6 climatic conditions; red dots and line, RCP8.5 climatic conditions

Limiting factors, functional traits, and competitive advantages

Generally, rainfall and temperature patterns are among the most important limiting factors determining plant distribution and abundance (Stephenson 1990), affecting reproduction and other life-history traits. Temperature is a strong limiting factor for the species, which usually prefers areas with temperature higher than 10 °C (Fig. 4). Under the current conditions, these areas are located under 1000 m asl, but they are expected to rise under both the climate change scenarios analysed (RCP2.6 and RCP8.5). The geographic distribution of the species in both scenarios showed an elevation shift, particularly pronounced in the RCP8.5 scenario. The species could move to higher elevation probably benefitting from the effect of orographic precipitations, and it could migrate in the north-western part of the island, where the trade winds enhance water availability (Figs. 2, 3). The ecophysiological traits of *P. setaceum* support its large size, extensive canopy, shorter leaf senescence period, and the capacity to buffer seasonal and local water shortages (González-Rodríguez et al. 2010). Indeed, they confer considerable competitive advantages to the invader, and this can partially explain its invasion success in the Canary archipelago, considering local environmental and climatic conditions. On the other hand, seedlings' growth could be a limiting factor of *P. setaceum* invasion success: despite their relatively broad germination requirements, seedling cannot cope with low soil moisture or drought conditions (Adkins et al. 2011; Goergen and Daehler 2002), and it has been suggested that they do not tolerate more than one month of drought (Rahlao et al. 2010). Interestingly, once the seedlings are established, the amount of water does not seem to affect their performance, even under higher temperature regimes. When favourable conditions occur, *P. setaceum* can quickly thrive (already under sub-optimal ecological conditions) and overcome native coexisting species through rapid exploitation of available resources (such as water and nutrients), thanks to its broad ecological tolerance and high phenotypic plasticity (Williams and Black

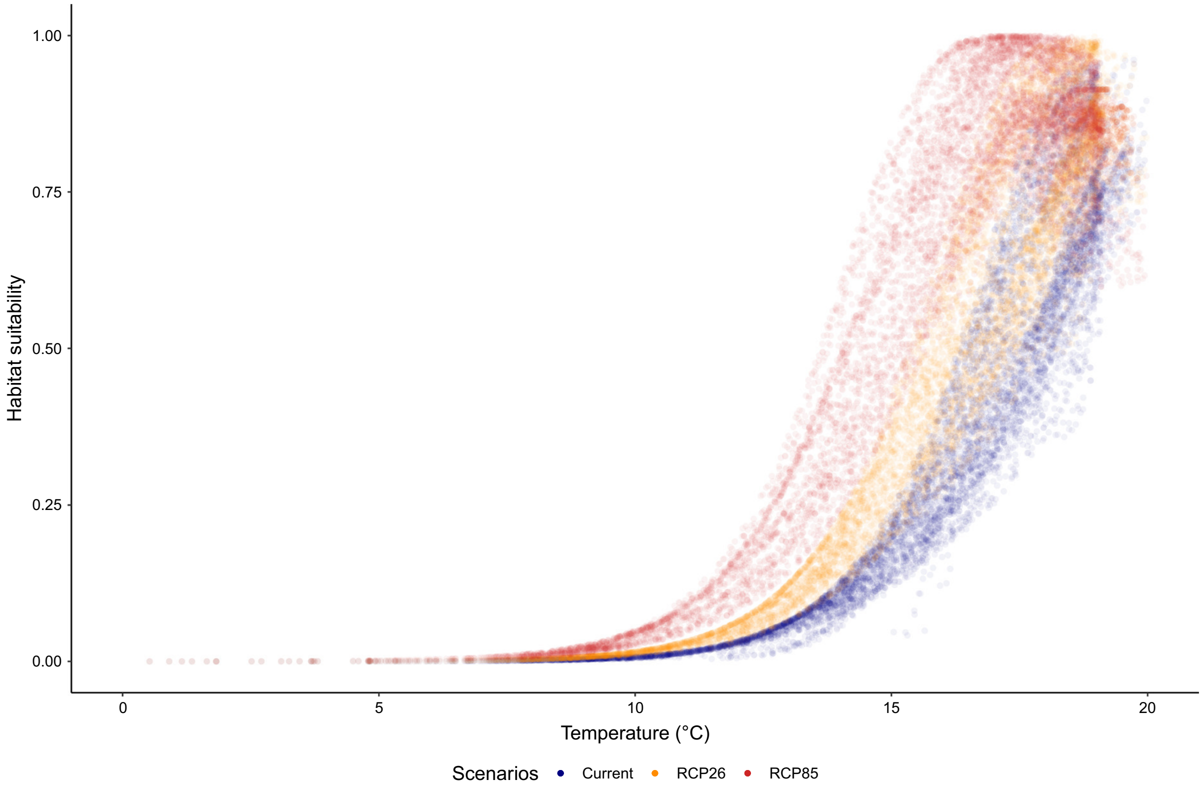

Fig. 4 Relationships between *P. setaceum* HSM predictions and temperatures: blue dots, current climatic conditions; orange dots, RCP2.6 climatic conditions; red dots, RCP8.5 climatic conditions

1993; Poulin et al. 2007; Rahlao et al. 2010). Furthermore, under drought or limited resources availability, the alteration of biomass allocation patterns in favour of roots seems to be a conservative strategy (Williams et al. 1995; Rahlao et al. 2010). This may explain why *P. setaceum* is an excellent invader of habitats characterized by fluctuating resources, frequently disturbed or with an irregular rainfall pattern, in agreement with Davis' theory of community invasibility (Davis et al. 2000). Compared to native species, the higher nitrogen and water use efficiency (González-Rodríguez et al. 2010) allow *P. setaceum* to compete effectively in warmer, drier areas, conferring it a considerable competitive advantage (Tordoni et al. 2020). Recently, Rodríguez-Caballero et al. (2017, 2018) have shown how *P. setaceum* could establish symbiosis with different mycorrhizal fungi and act as a transformer (Pyšek et al. 2004) modifying the soil bacterial community related to N cycle. As a consequence, it also tends to increase the risk of intense wildfires (to which it is well adapted), thus posing a further threat to resident native communities (Tunison 1992).

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

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

Conclusions

Our model predictions highlight that the distribution of *P. setaceum* in Tenerife will be strongly affected by climate change and particularly by the predicted increase in aridity on the island. Our model (particularly RCP8.5) foresees that the species would move to higher elevation and to the north-western part of the island, likely to benefit both from orographic precipitations and enhanced water availability promoted by trade winds. Moreover, under the current socio-economic perspectives, the RCP2.6 scenario is becoming year after year less feasible (Davis and Socolow 2014), making the RCP8.5 one even more likely. The species may consequently have negative impacts on entire ecosystems, due to its strong competitive capacities and being a driver of other invasive species. Particularly, the predicted invasion of areas at higher elevation poses the question of its ability to penetrate the pine forests (especially the more xeric ones in the southern part of the island). Its establishment could drastically affect the dynamics of this unique ecosystem (e.g. natural regeneration, fire regime), if proper conservation plans will not be developed to support ecosystem health and diversity. However, even though our predictions are coherent with the auto-ecology of the species, climate change predictions are extremely simplified and should be therefore interpreted with care. More powerful outcomes may be obtained downscaling climatic data from global models such as Global Circulation Model (GCM), but to our knowledge spatially interpolated fine scale GCM projections for the Canary Islands are still lacking. Moreover, it has been showed that whereas global scale products are generally applicable at broad geographical scale, modelling climate surface on islands needs 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* niche model outputs presented. Such cartographic products provide an immediate tool for understanding potential changes in species distributions, and they can be used to disseminate and increase the awareness of biological invasion outside the academia. Considering the dramatic effects that an uncontrolled increase of *P. setaceum* may have on Tenerife, understanding its future potential habitat distribution is therefore crucial from a conservational perspective. Immediate control measures (e.g. manual and chemical species removal efforts) should be carried out from the border of *P. setaceum* current distribution, focusing especially along invasion pathways (Walentowitz et al. 2019). Furthermore, prohibiting the commercial use of *P. setaceum* propagules could be another tool to control the species further spread. In fact, Potgieter et al. (2019) showed that ornamental plants are still perceived as having aesthetic benefits when confined to private gardens; however, shifts in perceptions may occur when they become widespread in the wild, leading to economic and environmental costs. Finally, specific Citizen Science projects have been shown to be effective to raise the awareness about biological invasions and to engage both public administrations and citizens in monitoring and controlling invasive species and therefore could be a valuable tool to help controlling the species invasion and its deleterious effect on Canary Islands (e.g. Sladonja and Poljuha 2018).

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