

Article

Graminoid Invasion in an Insular Endemism Hotspot and Its Protected Areas

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Abstract: Invasive plant species are increasingly altering species composition and the functioning of ecosystems from a local to a global scale. The grass species *Pennisetum setaceum* has recently raised concerns as an invader on different archipelagos worldwide. Among these affected archipelagos are the Canary Islands, which are a hotspot of endemism. Consequently, conservation managers and stakeholders are interested in the potential spreading of this species in the archipelago. We identify the current extent of the suitable habitat for *P. setaceum* on the island of La Palma to assess how it affects island ecosystems, protected areas (PAs), and endemic plant species richness. We recorded in situ occurrences of *P. setaceum* from 2010 to 2018 and compiled additional ones from databases at a 500 m × 500 m resolution. To assess the current suitable habitat and possible distribution patterns of *P. setaceum* on the island, we built an ensemble model. We projected habitat suitability for island ecosystems and PAs and identified risks for total as well as endemic plant species richness. The suitable habitat for *P. setaceum* is calculated to cover 34.7% of the surface of La Palma. In open ecosystems at low to mid elevations, where native ecosystems are already under pressure by land use and human activities, the spread of the invader will likely lead to additional threats to endemic plant species. Forest ecosystems (e.g., broadleaved evergreen and coniferous forests) are not likely to be affected by the spread of *P. setaceum* because of its heliophilous nature. Our projection of suitable habitat of *P. setaceum* within ecosystems and PAs on La Palma supports conservationists and policymakers in prioritizing management and control measures and acts as an example for the potential threat of this graminoid invader on other islands.

Keywords: alien; biodiversity; African fountain grass; non-native; *Pennisetum setaceum*; species distribution modeling; invasibility; exotic; invasive; endemism

1. Introduction

On many islands, humans have substantially altered species composition and functioning of ecosystems. A major driver of these changes is invasive species [1]. Wealthy islands with large human populations, such as the Canary Islands, host higher numbers of invasive species compared to less wealthy islands with a low GDP (gross domestic product) as recent large-scale analyses reveal [2,3]. Biological invasions on islands have even led to the reversal of fundamental biogeographic patterns, such as the species-isolation relationship [4]. Thus, understanding the patterns of distribution and spread of invasive species is particularly relevant for islands.

Islands are generally species-poor, mostly due to their isolation and in some cases also due to their young age [5]. However, they can harbor high numbers of endemic plant species [6] and thus contribute far above average to global biodiversity. Therefore, islands are of priority interest for conservation, especially in the context of rapid species and biodiversity loss [7]. Although islands only cover approximately 5% of the global terrestrial surface, they host around 17% of all plant species [8]. The Canary Islands are no exception, and they are known for their richness in endemic plant species [6,9].

Unfortunately, island biota is known to exhibit extraordinarily high extinction rates [10,11]. Island floras are already under pressure by changes in climate because of their isolation, small distribution area, and small populations [12]. This vulnerability is exacerbated by the introduction of alien and invasive species, which become the main driver of these losses [13,14]. On the Canary Islands, many endemic plant species are currently considered highly endangered as a result of invasive species [15–18]. The survival of endangered endemics will largely depend on adequately controlling invasive species based on scientifically sound knowledge of their distribution, population dynamics, and ecology.

Precise information on distributions of introduced plant species is scarce. A timely and sound monitoring of invaders with high temporal and spatial resolutions is often lacking, also because of the immense workload and financial resources that are required for such an assessment [19]. However, the development of conservation projects requires spatial information about invasive species to assure the responsible use of ever-scarce financial resources and the effectiveness of the applied measures.

Species distribution models (SDMs) are an established and powerful tool to assess the potential occurrences of species [20,21]. They are mostly applied to identify the potential range of native species with long-term established populations. However, an increasing number of studies use SDMs to predict the distribution of invasive species, e.g., [22–24]. SDMs correlate known species occurrence records with environmental variables, making it possible to 1) provide information about suitable environments, and to 2) map the potential species' distributions.

General concerns about the modeling of invasive species' distributions have been voiced because of the potential nonequilibrium distributions of these species [25,26]. Furthermore, it is likely that the precision of modeling is strongly influenced by the phase of invasion with more stochastic model outputs in early stages [27]. However, West et al. have validated SDMs of invasive species with field data and confirmed the realistic modeling of processes. In addition, modeling invasive species can be informative when estimates about the potential distribution of an invader are urgently needed for conservation management [28].

Pennisetum setaceum (Forssk.) Chiov. (Poaceae) is included in the List of Invasive Alien Species of Union concern that is part of the 2020 Biodiversity Strategy of the European Union [29] which implements the Biodiversity Targets of the Convention on Biological Diversity (CBD). Target 5 of the EU Biodiversity Strategy aims at controlling, eradicating, or containing invasive species that have been identified to threaten biodiversity in the EU [29]. *P. setaceum* is a known invader in Hawaii, New Caledonia, Australia, and South Africa [30] and, in consequence, efforts to control the further spread of the species should be given high priority.

In recent years, *P. setaceum* has been identified as a rapidly spreading invasive plant in the Canary Islands as well as on La Palma (Palomares-Martínez, personal observation) [31,32], yet its potential threat remains unclear. La Palma hosts various areas with differing protection status, including the Caldera de Taburiente National Park. The entire island is also a World Biosphere Reserve of the

UNESCO (United Nations Educational and Cultural Organization). La Palma is a highly suited target island because it offers a large range of habitats and a diverse set of endemic species [33] where we intend to fill the knowledge gap on the invasion of *P. setaceum*. Specifically, we aim at (a) modeling its potential occurrence, (b) analyzing its distribution patterns, and (c) evaluating its habitat suitability with regard to ecosystems, endemic plant species richness, and location of protected areas on La Palma.

2. Materials and Methods

La Palma is an oceanic island located in the Atlantic Ocean off the coast of northwest Africa and belongs to the Canary Islands (Spain, Figure 1). It contains high elevations and, therefore, exhibits strong environmental gradients, e.g., in temperature and precipitation [34]. The highest peak, Roque de los Muchachos (2426 m a.s.l.), is located in the northern part of the island. Precipitation is mainly driven by trade winds coming from the northeast causing humid conditions in the windward part of the island [34]. Several vegetation zones are structuring the island. The dry and hot zone is located below the dew point at elevations up to 800 m a.s.l. and is dominated by coastal and succulent vegetation [35]. The zone within the clouds is characterized by broadleaved evergreen vegetation composed of laurel and tree heath forests [36,37]. Laurel forests are mainly restricted to the northeastern slopes of La Palma where precipitation is high [34]. Canary pine forests range between altitudes of 800 to 2000 m a.s.l. [35]. Higher elevations above 2000 m are mainly covered by subalpine mountainous shrub species [35]. In total, 176 archipelago endemic plant species and 40 single island endemics (SIE) can be encountered on La Palma [36]. The Canary Islands have been inhabited for millennia by aborigine peoples and later by Europeans [38], who introduced hundreds of non-native plants [39]. Currently, La Palma has a population of approximately 80,000 people and is visited by more than 250,000 tourists per year [40]. In modern times of prospering tourism, frequent air traffic and cruise ship embarkments are major pathways for plant introductions [41].

Pennisetum setaceum (Figure 2) originates from northern Africa and the Middle East but is now present on most continents and many oceanic islands in the Pacific and Atlantic Ocean [30,42]. The invader is suspected to have arrived in La Palma during the construction of the new airport in the 1970s [43,44]. It shows several traits that are common among invaders, like drought-tolerance [45,46]. Furthermore, it is a C4 apomictic bunchgrass [47] and polyploid ($2n = 27$), which increases the plasticity of the species [48]. Polyploidy maintains genetic diversity within the species by the use of duplicated loci from apomictic seeds, even when the diversity among individuals is low [48]. This might explain its success as an invader despite low genetic diversity. *Pennisetum setaceum* is dependent on recruitment from seeds, as it has no vegetative propagation [47]. Seeds stay viable for up to 10 years (Acevedo Rodríguez, personal observation) and germinate without light [49].

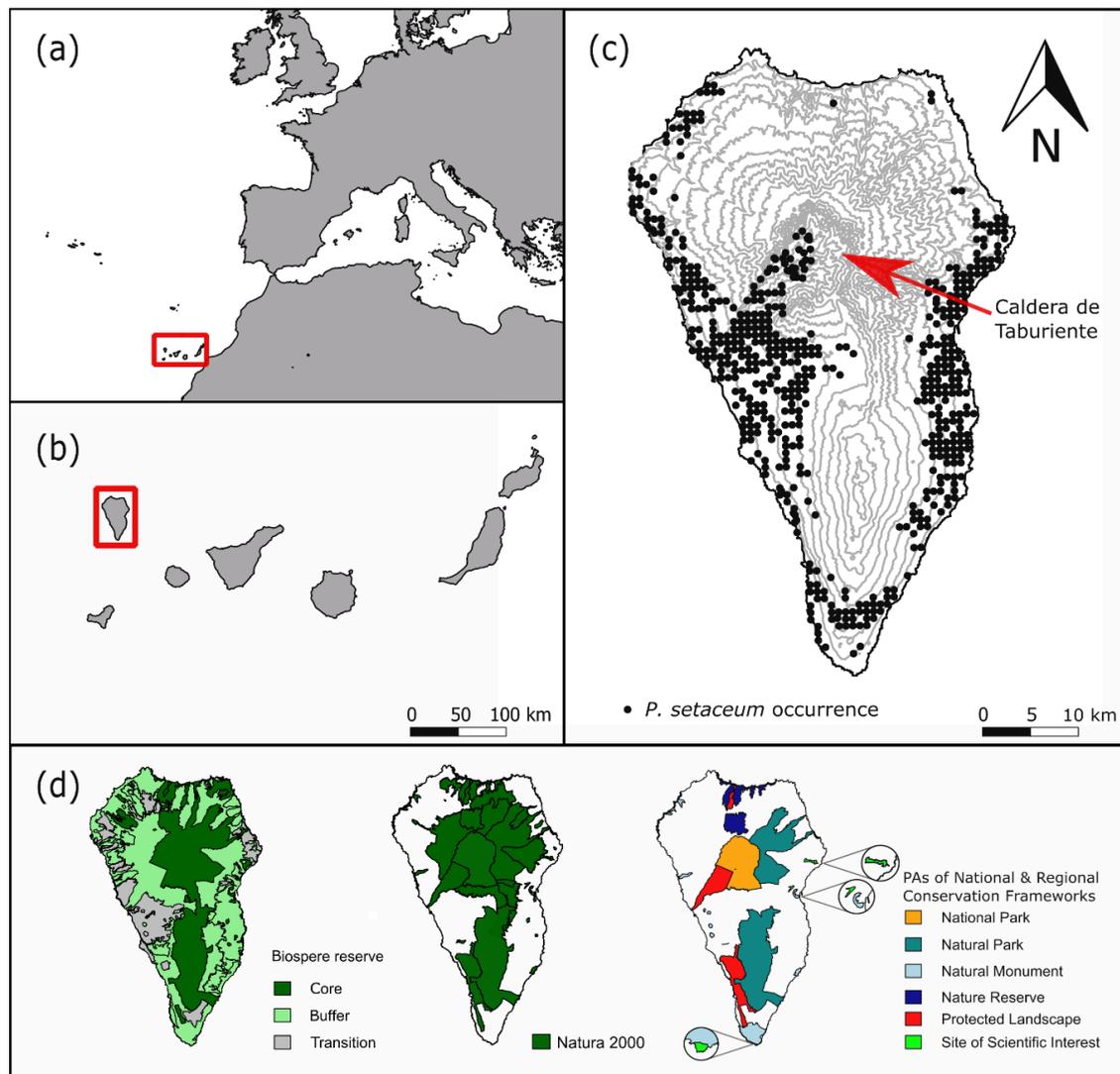


Figure 1. Location of the Canary Islands (a) and the position of La Palma within the archipelago (b). Distribution of *Pennisetum setaceum* occurrence points after correction for autocorrelation ($n_{\text{thinned}} = 561$) that was used for species distribution modeling (c). Biosphere reserve (left, d), Natura2000 sites (middle, d), and nationally and regionally designated protected areas (right, d).



Figure 2. The Crimson fountain grass *Pennisetum setaceum* as an invader on La Palma.

2.1. Compilation of Data Sets

A dataset with occurrence data of *P. setaceum* on La Palma ($n_{\text{total}} = 786$) was compiled from four sources:

1. Occurrence data from the National Park Directorate of La Palma for *P. setaceum* within the National Park “La Caldera de Taburiente” from 2016, $n = 55$.
2. Fieldwork based occurrence data collected on a yearly basis from 2010 to 2018, $n = 19$.
3. Entries in the GBIF (Global Biodiversity Information Facility) database [50] for *P. setaceum* (only geo-referenced data; basis of record: observation, human observation) from 2012 till 2017, $n = 21$.
4. Occurrence data from the Atlantis database [51]. From this raster data, we created centroids within each pixel of *P. setaceum* occurrence with the highest precision level and a resolution of 500×500 m to extract occurrence points, $n = 691$.

We corrected for spatial correlation by spatially thinning the occurrence points in R Studio Version 3.5.3 [52] with the package spThin [53]. Based on a PCR of all occurrence points we selected a thinning parameter of 3.5 to avoid spatial clumping ($n_{\text{thinned}} = 561$, Figure 1c).

To model the distribution of *P. setaceum* on La Palma, we selected a set of environmental variables that account for climatic, topographic, and anthropogenic aspects (Table 1, Figure A1). We used data on elevation, slope, and aspect (its components northness and eastness have been used for modeling) as topographic information. For climate, we used mean annual temperature, mean annual precipitation, and solar radiation. For model building, the anthropogenic variables ‘nearest road’ and ‘nearest settlement’ were chosen. The variable geological age was used as a proxy for bedrock nature, which is of importance for the vegetation on a young volcanic island like La Palma. We accounted for collinearity (Pearson correlation coefficient threshold of $|r| = 0.7$ (sensu) [54]) of the variables selected

for modeling and removed mean annual temperature and nearest settlement from the analysis as these variables highly correlated with elevation. We decided to consider elevation in the modeling process and to drop the other variables because first, temperature interpolations are based on elevation linked with just a few weather stations on the island and second, elevation is more important for SDMs than the environmental variable ‘nearest settlement’.

Table 1. Environmental variables used for species distribution modeling of suitable habitat of *P. setaceum* on La Palma, including also the calculations of variables and the source.

Category	Variable	Calculation of Variables	Sources
Topography	Elevation	Rasterized at a resolution of 0.5×0.5 km deriving from a digital elevation model (DEM) of 2×2 m.	Original Data: Cabildo Insular de La Palma, [33]
	Slope	Calculations were based on a DEM of 2×2 m. Resolution was rescaled to 0.5×0.5 km.	Original Data: Cabildo Insular de La Palma, Calculations [33]
	Aspect (northness, eastness)	Calculations were based on a DEM of 2×2 m. Resolution was rescaled to 0.5×0.5 km. Northness was calculated as $\cos(\text{aspect})$ and eastness as $\sin(\text{aspect})$.	Original Data: Cabildo Insular de La Palma, Calculations [33]
Parent material	Geological age	Resolution was rescaled to 0.5×0.5 km.	Cabildo Insular de La Palma, [33]
Climate data	Mean annual precipitation	Interpolation (Linear regression kriging), using data collected from meteorological stations for the Canary Islands ($n = 214$). Time span from 1969 to 1998. Resolution was rescaled to 0.5×0.5 km.	Original Data: Cabildo Insular de La Palma, Calculations [33]
	Solar radiation	Calculation from DEM 100×100 m using a standard diffuse atmosphere and based on latitude, elevation, slope, and aspect. Resolution was rescaled to 0.5×0.5 km.	Original Data: Cabildo Insular de La Palma, Calculations [33]
Infrastructure	Nearest road	Resolution was rescaled to 0.5×0.5 km.	[33]
Land cover	Vegetation types (coniferous forest, broadleaved evergreen forest, scrubland, cultivated land, barren land)	Rasterized at a resolution of 0.5×0.5 km	Original Data: Cabildo Insular de La Palma [33]

2.2. Ensemble Modeling

An ensemble model to project the suitable habitat of *P. setaceum* on La Palma was created with the package biomod2 [55]. The spatial analysis was carried out at a resolution of 500×500 m.

Ensemble methods improve the accuracy of predictive models by synthesizing the results of single models into a single score [56]. For model building, we used presence-only data and thus used three sets of 561 randomly chosen pseudo-absences with 10 replications. An ensemble model was built based on a generalized linear model (GLM), gradient boosting machine (GBM), random forest (RF), and maximum entropy model (MaxEnt). One hundred evaluation runs were made using a 70/30 data plot approach advocated by Araújo et al. [57]. The ensemble model was built using AUC (area under the relative operating characteristic curve) as an evaluation metric. In total 3902 models with $AUC > 0.7$ were included in the ensemble model building. Ensemble predictions were calculated using the mean of the single models. The ensemble model prediction had a good predictive ability with $AUC = 0.9$ and TSS (true skill statistic) = 0.7. The AUC cutoff (threshold minimizing the absolute difference between sensitivity and specificity) of the mean was used as a threshold to transform the projection of suitable habitat for *P. setaceum* derived from the ensemble model into a binary presence–absence map (sensu) [58]. Further calculations were based on this binary map.

2.3. Projecting Habitat Suitability onto Ecosystems, PAs, and Endemic Plant Species Richness

Modeling results were processed for further assessment and compared with the distribution of ecosystems, species richness, and PAs on La Palma. All data were tested for normal distribution with the Shapiro–Wilk test. To compare differences in mean annual temperature and the distance to the

nearest settlement of suitable and unsuitable habitat for *P. setaceum*, a Mann–Whitney U test was used considering a non-normal distribution of the data.

For post-modeling analysis, the environmental variables ‘mean annual temperature’ and ‘nearest settlement’ were included but had been excluded beforehand from the model building. For the environmental variables ‘mean annual temperature’, ‘annual precipitation’, ‘elevation’, ‘nearest road,’ and ‘nearest settlement,’ we extracted minimum and maximum values to depict the range these variables cover on La Palma. We calculated the percentages of these environmental gradients which we identified as suitable habitat for *P. setaceum*.

We derived raster maps of total plant species richness and SIE richness from Irl et al. [33]. Therein the presence/absence data of native vascular and endemic perennial plant species from 890 plots on La Palma were interpolated into richness maps. The resolution was upscaled to our model resolution of 500×500 m. We compared SIE richness and total plant species richness of projected suitable and unsuitable habitat for *P. setaceum*.

To evaluate modeling results in combination with designated areas of different protection status we considered the locations of the core, buffer, and transition zone of the biosphere reserve [59], Natura 2000 sites defined by the EU Habitat Directive [60], and nationally/ regionally designated protected areas, which include the national park, protected landscapes, natural parks, natural monuments, sites of scientific interest, and nature reserves [61]. The vector data was rasterized and scaled to 500×500 m. We calculated the projected suitable habitat for *P. setaceum* within designated areas of each protection status (cover in % and km^2).

3. Results

Under current climatic conditions, 34.7% of the land surface of La Palma is identified to be suitable habitat for *P. setaceum*. This suitable habitat for *P. setaceum* is located mainly along the coasts and enters via the Barranco de las Angustias into the Caldera de Taburiente National Park on the leeward side of La Palma (Figures 3 and A2).

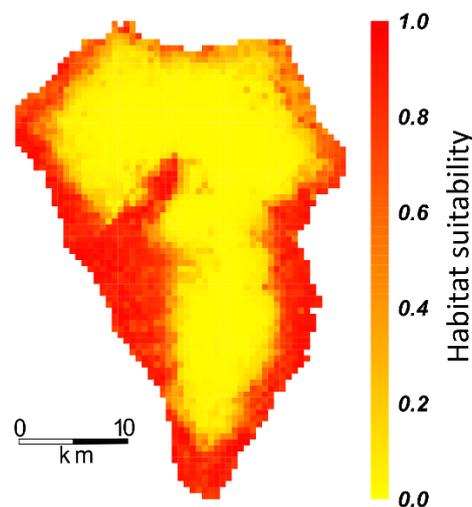


Figure 3. Projected suitable habitat conditions of *P. setaceum* on La Palma based on the ensemble model of generalized linear model (GLM), gradient boosting machine (GBM), random forest (RF), and maximum entropy model (MaxEnt). Habitat suitability ranges from 1 (high probability of occurrence, red) to 0 (low probability of occurrence, yellow).

For the single model algorithms GLM, GBM, RF, and MaxEnt, on which the ensemble model is built, we calculated the mean variable importance. In all models, elevation had the highest variable importance, followed by distance to the nearest road and mean annual precipitation (Table 2).

Table 2. Variable importance for the single model algorithms (GLM, MaxEnt, RF, and GBM) of the ensemble modeling approach. The three most important variables for each model are written in bold. Variables are ranked from highest (1.) to lowest (9.) importance.

Variable	GLM	MaxEnt	RF	GBM
1. Elevation	0.963	0.573	0.480	0.676
2. Precipitation	0.043	0.245	0.155	0.162
3. Nearest road	0.180	0.225	0.073	0.071
4. Solar radiation	0.153	0.104	0.080	0.061
5. Slope	0.012	0.137	0.034	0.017
6. Vegetation	0.022	0.051	0.027	0.006
7. Northness	0.000	0.070	0.021	0.008
8. Eastness	0.000	0.090	0.013	0.002
9. Geological age	0.000	0.063	0.023	0.007

Projected occurrences of *P. setaceum* were detected more frequently in proximity to human settlements at a mean distance of 1118 m. In contrast, projected species absence pixels had a mean distance of 2168 m to human settlements (Mann–Whitney U test, $p_{\text{settlement}} < 0.0001$, Figure 4a). The invasive grass species typically occurred at mean annual temperatures of 17.3 °C. In contrast, projected species absence pixels had a temperature of 14.9 °C (Mann–Whitney U test, $p_{\text{temp}} < 0.001$, Figure 4b). Mean annual temperature of suitable habitat of the invasive grass species ranged between 11.9 °C and 19.7 °C (Figure 5). Areas of projected suitable habitat for *P. setaceum* ranged between an elevation of 41 m and 800 m, with some exceptional occurrences at 1214 m. These high elevational projected occurrences were located without exception in the Caldera de Taburiente. For projected species presence, the precipitation varied between 212 mm/year and 901 mm/year. The distance of areas suitable for the invasive grass species to the nearest road ranged between 3 m and 2445 m. The projected suitable habitat for *P. setaceum* covers the entire gradient of the variables ‘nearest road’ and ‘nearest settlement’. We projected unsuitable habitat for *P. setaceum* on La Palma to be found in areas with low temperature, high precipitation, and high elevation.

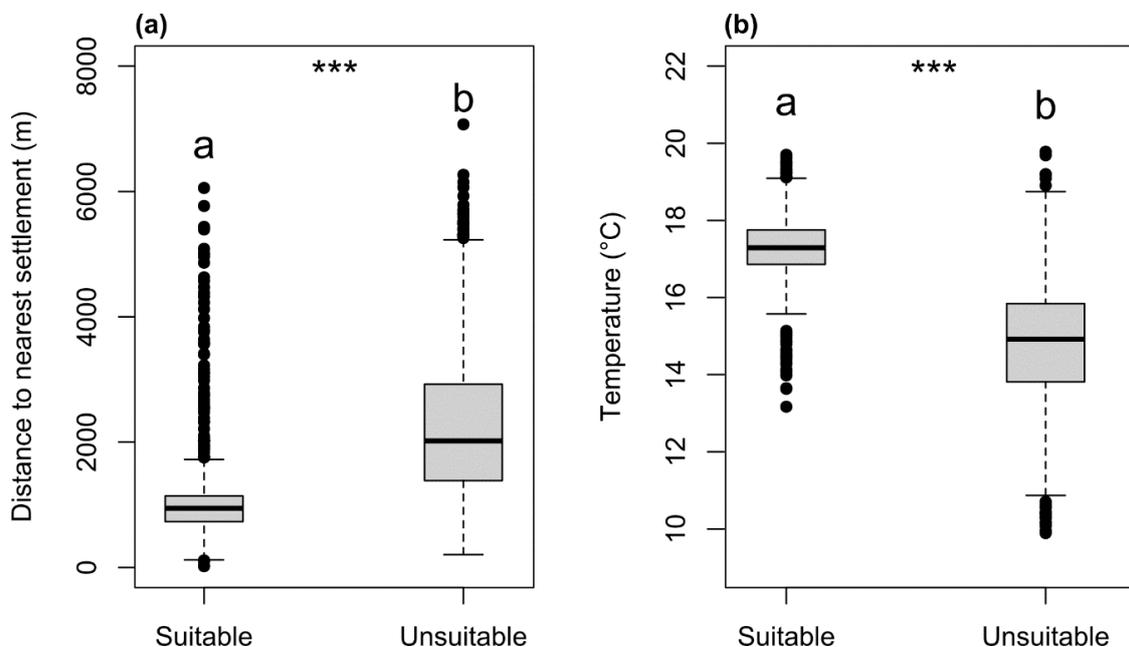


Figure 4. (a) Pixels that were modeled as suitable habitat for *P. setaceum* show smaller distances to the nearest settlement compared to pixels without *P. setaceum*. (b) Average mean annual temperatures of pixels with *P. setaceum* presence are considerably higher compared to pixels where the species is absent. Highly significant results are indicated by three asterisks.

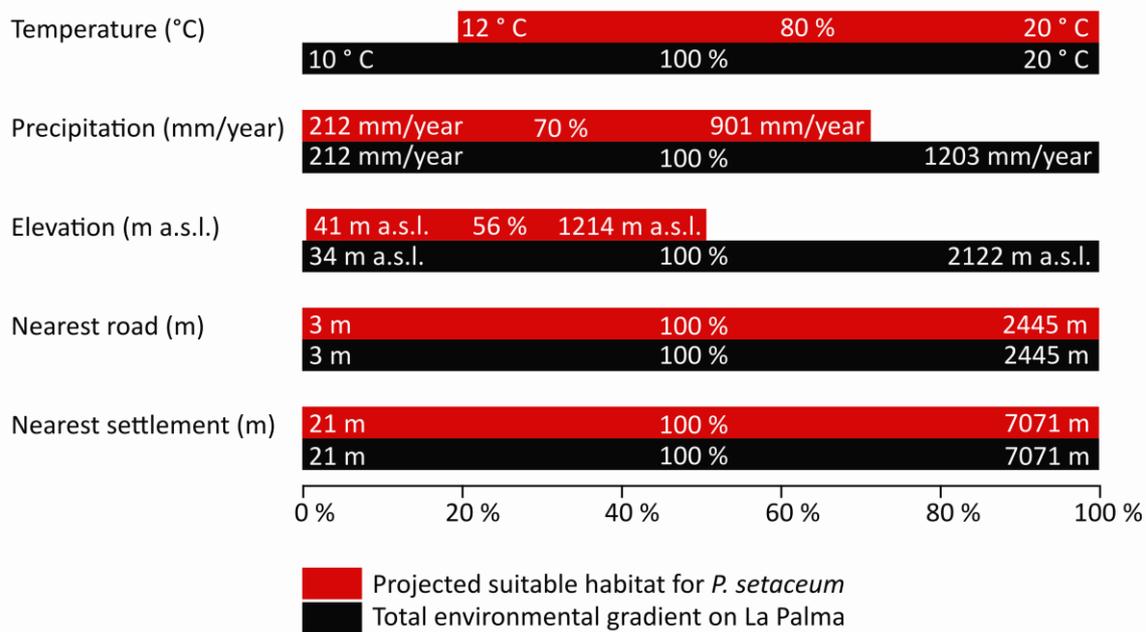


Figure 5. Total environmental gradients of mean annual temperature, annual precipitation, elevation, nearest road, and nearest settlement on La Palma (black bar). Red bars show the range of the environmental gradients projected to represent a suitable habitat for *P. setaceum* on La Palma. Note that the gradients elevation, nearest settlement, and nearest road do not start at zero due to calculations made on the bases of mean values for pixels the size of 500 × 500 m.

Total species richness of SIE was significantly lower in areas of suitable habitat for *P. setaceum* compared to areas classified as unsuitable (Mann–Whitney U test, $p_{SIE} < 0.001$, Figure 6a). However, total species richness was higher in areas suitable for *P. setaceum* compared to areas classified as unsuitable for the grass species (Mann–Whitney U test, $p_{richness} < 0.001$, Figure 6b). *Pinus canariensis* forests cover large areas on La Palma and are poor in plant species diversity. We projected only a small area of this forest type to be suitable habitat for *P. setaceum*. Thus, when comparing total plant species richness between suitable and unsuitable habitat for *P. setaceum*, the *P. canariensis* forest might account for differences. When we excluded this ecosystem from our analysis no differences in species richness between suitable and unsuitable habitat for *P. setaceum* were found (Mann–Whitney U test, $p_{richness-no-pinus} = 0.391$, Figure 6c). Additionally, we projected coniferous and broadleaved evergreen forests to be suitable habitat for *P. setaceum* only at very low percentages while scrubland, cultivated land, and bare soil were more strongly affected (Table 3).

Table 3. Projected suitable habitat for *P. setaceum* within the coniferous forest, broadleaved evergreen forest, shrubland, cultivated land, and bare soil of La Palma as total cover of ecosystem, total suitable habitat for *P. setaceum*, and percentage cover of suitable habitat for *P. setaceum*.

Ecosystem	Total Cover in km ²	Suitable Habitat for <i>P. setaceum</i>
Coniferous forest	224 km ²	20 km ² (9%)
Broadleaved evergreen forest	99 km ²	1 km ² (1%)
Scrubland	78 km ²	51 km ² (65%)
Cultivated land	214 km ²	130 km ² (61%)
Bare soil	34 km ²	22 km ² (65%)

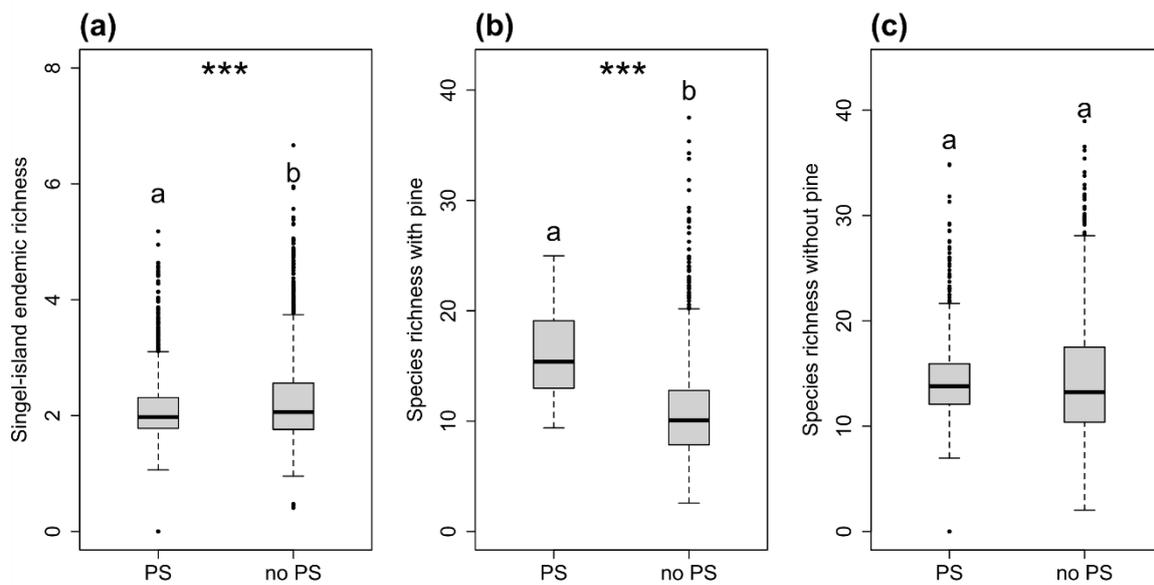


Figure 6. (a) Single island endemic plant species richness in projected suitable and unsuitable habitat for *P. setaceum*. (b) Total species richness in areas suitable and unsuitable for *P. setaceum*. (c) Species richness compared to suitable habitat excluding the *Pinus canariensis* forest. Highly significant results are indicated by three asterisks.

While within the core of the La Palma Biosphere Reserve only 6.2% of the area was potential habitat for *P. setaceum*, the coverage reached 33.2% in the buffer zone and 67.1% in the transition zone of the biosphere reserve (Figure 7). Within Natura 2000 protected areas, a projected suitable habitat for *P. setaceum* of 8.6% was calculated. For the Caldera de Taburiente National Park, the natural parks, and nature reserves, low coverages of *P. setaceum* below 17% were detected. For other protected areas such as protected landscapes or natural monuments, the potential coverage with *P. setaceum* was far higher, reaching 63.0% and 93.1%, respectively.

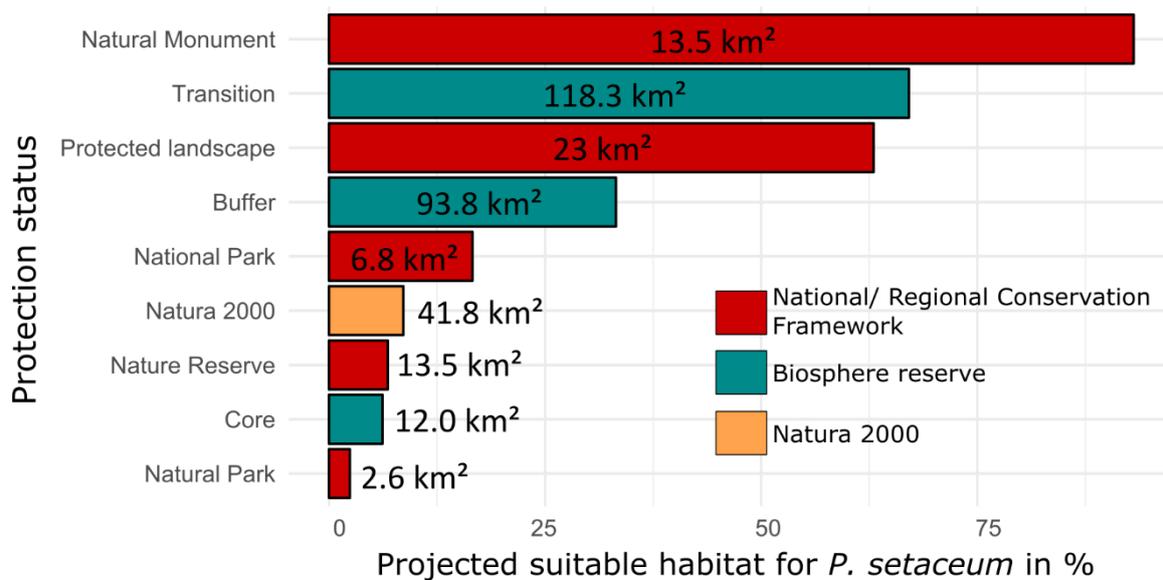


Figure 7. Projected suitable habitat for *P. setaceum* in protected areas on La Palma in coverage percent and area in km².

4. Discussion

Our study is the first published assessment of the distribution and potential threat of the graminoid invader *P. setaceum* on La Palma. We find that about one-third of the surface of La Palma is potentially suitable for *P. setaceum*. The projected suitable habitat covers wide environmental gradients on the island, except for areas at very high elevations (or low temperatures) and with high amounts of precipitation. This raises major concerns for large parts of the vegetation of this island. Invasion by *P. setaceum* may considerably affect local ecosystems and native biodiversity. This threat demands priority control measures, especially in arid areas at low elevations and areas with high conservation value.

The importance of anthropogenic variables, e.g., the distance to the nearest road or settlement for the distribution of *P. setaceum*, indicates that this plant benefits from human infrastructure and activity. This is in accordance with findings from South Africa where roads strongly promote its dispersal [45,46,62,63] and relates to the dispersal of seeds by wind and car drag. Additionally, this graminoid invader is adapted to aridity typical for disturbed, sun-exposed sites in the vicinity of roads and settlements [63]. Furthermore, *P. setaceum* is favored by horticulturalists as an ornamental plant which adds to its success on anthropogenically influenced sites [64,65]. Recently, an exceptional occurrence of *P. setaceum* has been located in the northern coastal parts of La Palma (personal observation, Palomares-Martínez). However, the surroundings are anthropogenic habitats with occurrences of exotics of the genera *Furcraea* and *Opuntia*, which emphasizes the importance of disturbed areas for the dispersal of *P. setaceum*.

Elevation was the most important variable explaining the distribution of *P. setaceum* on La Palma in all model algorithms (GLM, GBM, RF, and MaxEnt) combined for the ensemble model. Our model shows a higher elevation of projected suitable habitat for *P. setaceum* within the Caldera de Taburiente compared to the rest of the island. As elevation is a proxy for temperature, microclimatic differences in temperature, caused by the protection from cool oceanic winds within the Caldera, can help to explain these findings. Furthermore, strong tropical storms from the southwest might be a factor to elucidate the high occurrences of *P. setaceum* within the Caldera de Taburiente. After storms, leaves of *Persea americana* and *Musa sp.*, both agricultural plants occurring in the vicinity of the coast, have been recorded up to 2423 m a.s.l. (Acevedo Rodríguez, personal observation). Recently, occurrences of the invasive grass have been found at altitudes of 1500 m in the “Barranco Risco Liso”, located within the Caldera de Taburiente.

The elevational distribution pattern of *P. setaceum* hints at environmental factors playing a role in the distribution of this grass species that have not been considered in the modeling of this invasive species in this study. In the sheltered environment of the Caldera, thermal updraft might explain the differing elevational pattern of projected suitable habitat. The dispersal of *P. setaceum* is exclusively dependent on apomictic seeds and thus assessing the wind dispersal potential of the diaspores in combination with local wind patterns could help explaining these patterns [48,66]. Precise spatial information on predominant wind direction and topographically induced turbulence is not available for La Palma. Future provision of such maps can enhance model quality of anemochorous invasive plants.

Touristic activity within the National Park might explain the extend of the projected suitable habitat for *P. setaceum* within the Caldera de Taburiente. Tourism and recreational activities can influence the spread of non-native species [41]. Unpaved paths used by hikers are dispersal pathways for species such as *P. setaceum* [67].

For conservation efforts, the impact of invaders on natives and particularly on endemic species is of importance [68]. Remarkably, the number of endemic plant species on La Palma is significantly lower in areas identified as suitable habitat for *P. setaceum* compared to unsuitable areas. We can draw from this that there is little concern for this invasive grass species to outcompete or displace endemic plants on La Palma due to lower SIE richness in these areas. The latter is in accordance with general distribution patterns of endemic and invasive plant species on high-elevation islands [33,69]. While high elevations host the highest number of endemic species [69] and the aggregation of rare endemics most vulnerable to extinction aggregate there as well [59], non-native species richness peaks

at elevations around 500 m [69]. Mean elevation of projected suitable habitat for *P. setaceum* was 543 m and matches this pattern quite precisely. *P. setaceum* is a C4 plant and thus well adapted to arid and semi-arid habitats [70], which explains the low coverage by suitable habitat for *P. setaceum* of broadleaved evergreen forest on La Palma. These broadleaved evergreen forests are mainly laurel forest communities (monteverde), located in the northeastern part of La Palma where some SIE and high numbers of Macaronesian plant endemics can be encountered [59]. The main occurrences of laurel forest coincide with high precipitation and humid localities exposed to trade winds. There are transition zones between laurel forest and the *Erica-Morella*-Forest (fayal-breza) but also distinct ecotones of the pine forest driving diversity patterns linked with particular ecosystems [71].

Even though total species richness seemed to differ between projected suitable and unsuitable habitats for *P. setaceum*, we could show that this pattern was distorted by the *P. canariensis* forest on La Palma. The closed canopy of the forest prevents *P. setaceum* invasion and this forest type additionally contains lower species numbers compared to other ecosystems on the Canary Islands [72]. *P. setaceum* derives from arid areas of the Middle East and northern Africa where lush evergreen forest is scarce which can explain this pattern [42]. Additionally, *P. canariensis* forests historically have a high fire frequency of dominant pine species being fire-tolerant and having the ability to resprout after fire [73]. *Pennisetum setaceum* seeds lying on the soil surface can be killed by forest fires [47] and on the short run frequent forest fires seem to help to stop invasions of this graminoid. However, seeds buried deeper in the soil can survive these forest fires [47] and the native flora and fauna can be affected negatively by this hazard. Additionally, disturbances of natural systems (deforestation, human-caused low fire frequencies) might aid the graminoid invader in establishing within or in proximity to forest ecosystems and should be accounted for when developing conservation measures concerning *P. setaceum*.

A common disturbance on islands is the browsing of introduced herbivores. However, *P. setaceum* seems not to be negatively affected by browsing, although the graminoid mainly occurs at low elevations where introduced rabbit density is high [18]. Very likely, this results from the sharp blades of the plant using silica phytoliths as a mechanical defense against herbivory [74].

Another relevant aspect of conservation is the impact of invaders on protected areas aiming to promote and conserve endemic and native biodiversity. La Palma hosts different protected areas with different levels of protection status, as well as a UNESCO Biosphere Reserve, which covers the entire island. The specific aim of biosphere reserves is the conservation of ecosystems, species, and genetic variation [75]. We found the biosphere core area, where most rare and potentially endangered endemics are found [59], to be influenced very little by *P. setaceum* and, therefore, we currently do not see great concern for plant diversity within this area. The projected suitable habitat for *P. setaceum* in the transition area of the biosphere reserve, natural monuments, and protected landscapes reached covers of more than 60%. However, our study constitutes a snapshot in time, while biological invasions are dynamic processes that change with time and interact with their environment. A future spread of *P. setaceum* as a result of niche shifts via adaptation [26] and/or climate change [12] cannot be ruled out.

Evidence-based conservation allows conservationists and policymakers to focus conservation efforts and resources on problematic species that cause unwanted ecological changes or economic losses. Proceeding this way prevents misspending conservation funds on restoration measures, i.e., the eradication and control of invasive species that do not pose threats to biodiversity and human wellbeing [76]. Our identification of suitable habitat for *P. setaceum* on La Palma is a basis for conservationists and policy makers to prioritize conservation actions and to utilize conservation funds efficiently to maintain and protect plant species diversity on La Palma.

We suggest that immediate control measures (e.g., manual and chemical species removal efforts) should take place to prevent a further spread of *P. setaceum* into PAs and endanger unique endemic species. A specific focus should be put on potential vectors and invasion pathways, e.g., along roads and hiking paths. Furthermore, the control should be carried out from the border of its current distribution to avoid further spreading. Prioritized control in areas of high conservation value is recommended because monetary and labor resources are limited. Engagement of citizens, public administrations,

and volunteers by means of environmental education would be useful to raise awareness and facilitate monitoring and controlling both in PAs and private land. Prohibiting the commercial use of *P. setaceum* lowers propagule pressure and is thus another instrument to control further spreading of the graminoid. Furthermore, we recommend implementing a monitoring system for this species in order to enable quick response times in terms of management and control of *P. setaceum*, if further spreading into areas of great biodiversity and ecological value is observed.

Our study on the distribution of *P. setaceum* as well as environmental and anthropogenic influence factors on the spread of this global invader constitutes a model case study for further islands and regions where this species has been identified as (potentially) problematic.

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Appendix A

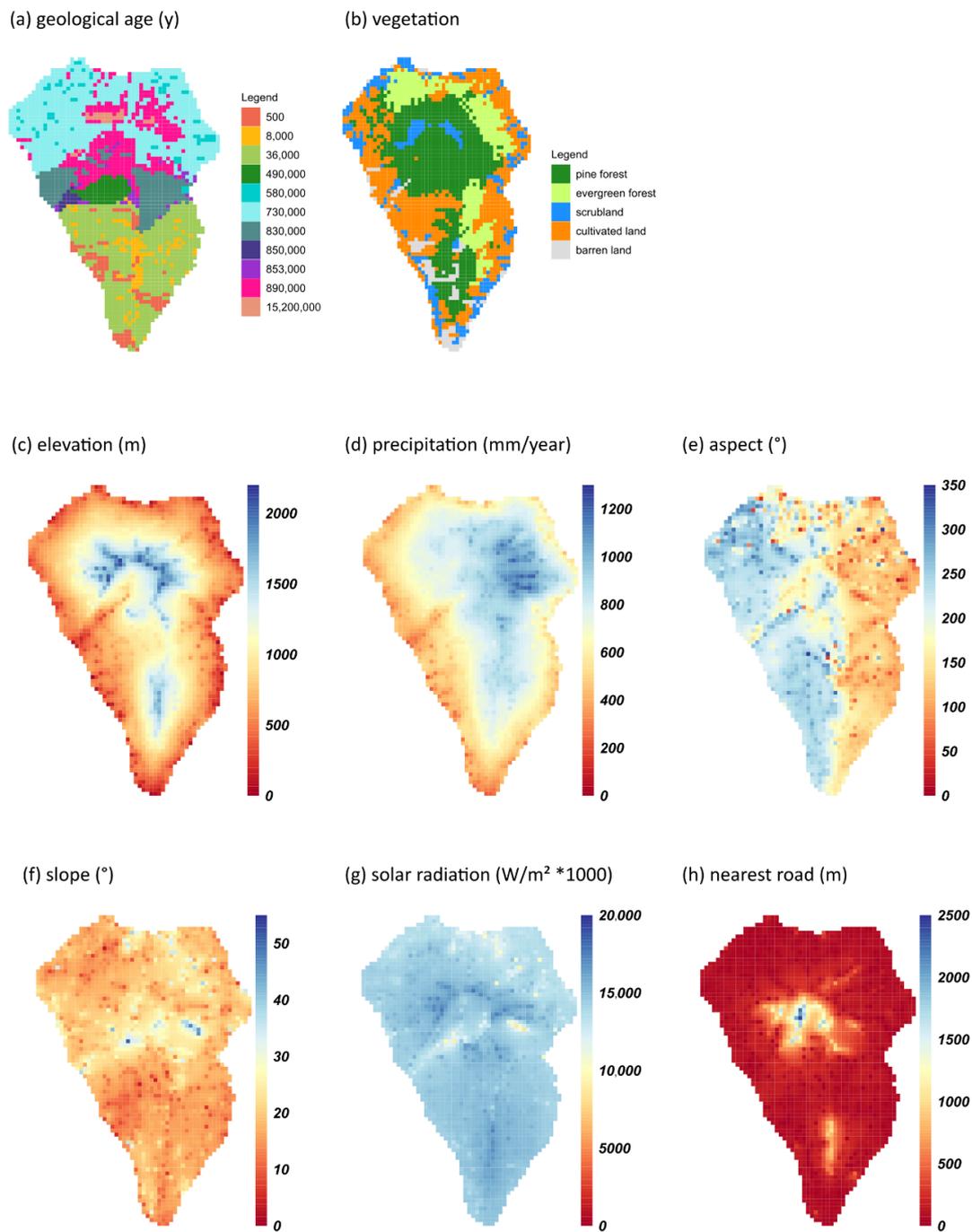


Figure A1. Environmental variables used for building the ensemble model for *P. setaceum* on La Palma: geological age (a), vegetation (b), elevation (c), mean annual precipitation (d), aspect (e), slope (f), solar radiation (g), and the distance to the nearest road (h).

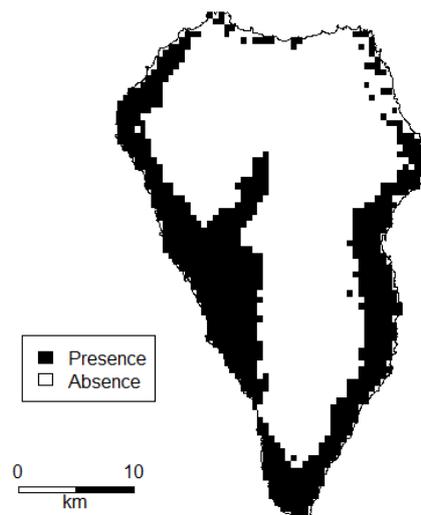


Figure A2. Projected suitable habitat of *P. setaceum* on La Palma as a result of the ensemble model based on a GLM, GBM, GF, and MaxEnt model. Conversion of the modeled habitat suitability into a presence/absence-based map on 0/1 was done using the AUC (area under the relative operating characteristic curve) cutoff of the weighted mean with a threshold value of 509.5, scaled to 0.5095 in Figure 2.

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