



Integrating global and regional niches with nested hierarchical SDMs reveals niche features and invasion-phase shifts under climate change in oceanic-island grass invaders

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Received: 25 November 2025 / Revised: 13 May 2026 / Accepted: 17 May 2026 /
Published online: 29 May 2026
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Abstract

On oceanic islands, biological invasions challenge species distribution models (SDMs) because estimated niches depend on spatial scale and invasion phase. Islands further complicate SDMs because their limited extent truncates the local environmental space, steep elevational gradients create strong microclimatic heterogeneity, and invasion data are often sparse and spatially biased. We present a Nested Hierarchical SDM (NHSDM) framework that explicitly links global and regional niches to improve model transferability and management relevance. We model three invasive C4 grasses, *Cenchrus setaceus*, *Melinis repens* subsp. *repens*, and *Setaria parviflora*, combining worldwide occurrences with a high-resolution regional workflow for the Canary Islands. NHSDMs comprise global and regional ensembles, plus two integrative products: (i) a covariate-augmented regional model that includes the global prediction, and (ii) a multiplicative consensus. To diagnose scale effects, we introduce two metrics: the Variable Importance Deviation Index (VIDI), which quantifies shifts in predictor importance, and the Gradient Response Deviation Index (GRDI), which summarises differences in the shapes of predictor–response curves. We project suitability under current climate and late-century scenarios (SSP3-7.0, SSP5-8.5; 2071–2100) and estimate spatial overlap among species. NHSDMs reveal species-specific scale dependence: *C. setaceus* shows broad warm-xeric suitability and a relatively low VIDI (consistent responses across scales), while *M. repens* and *S. parviflora* display mesic-montane affinities with higher VIDI and GRDI, indicating stronger scale-driven shifts, particularly for precipitation seasonality. Despite modest environmental niche overlaps, spatial co-occurrence is projected to increase, especially under SSP5-8.5, suggesting emerging multi-species impact hotspots where coordinated control may be most cost-effective. By translating future suitability into management-oriented risk metrics, our approach supports spatial prioritisation of surveillance and control; its main value lies in guiding decisions that reduce impacts on insular biodiversity and protected habitats.

Communicated by Akihiro Nakamura.

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Keywords Species distribution models · Invasive species · Grasses · Climate change · Niche dynamics · Archipelagos

Introduction

Alien species, defined as taxa occurring outside their native range due to human-mediated transport, are not inherently harmful. However, a subset of them becomes invasive, spreading and causing significant impacts on biodiversity, ecological stability, and ecosystem services across biomes (Pyšek et al. 2012; Simberloff et al. 2013; Garbowski et al. 2024). Accelerating global trade, tourism, and climate change are promoting biological invasions through pathways that outpace natural long-distance dispersal, while the annual number of first detections continues to rise steeply (Early et al. 2016).

Oceanic islands, which cover only 5% of the Earth's land surface, host nearly 10% of vascular plant species, thereby disproportionately contributing to global biodiversity (Whittaker and Fernández-Palacios 2007). Their isolation and high levels of endemism make them particularly vulnerable to biological invasions (Whittaker and Fernández-Palacios 2007; Fernández-Palacios et al. 2021). Invasive alien species can drastically alter community structure and ecosystem processes, posing a major threat to these biodiversity hotspots (Kueffer et al. 2010; Walentowitz et al. 2023).

Species distribution models (SDMs) provide a quantitative framework for assessing invasion risk, yet their transferability is challenged by niche non-equilibrium, biased occurrence data, and background selection (Petitpierre et al. 2012; Atwater et al. 2018). Transferability is particularly problematic when models are calibrated in one environmental–geographic domain and projected across space and time (Yates et al. 2018). This can amplify non-equilibrium effects, niche shifts, and scale mismatches, especially on islands where local environmental space is constrained (Chevalier et al. 2022). These limitations are not exclusive to invasions, but they are often exacerbated in invasion forecasting because invaded ranges may be far from equilibrium and sampling is strongly biased toward accessible areas (Gallien et al. 2012; Menuz et al. 2015; Moudry et al. 2024). Although these challenges remain important, recent methodological approaches have been developed to mitigate their effects. For instance, spatially nested hierarchical SDMs combine coarse global extents with fine regional data to alleviate niche truncation (Benavides-Ríos et al. 2024; Mateo et al. 2024), and methods such as USE It improve pseudoabsence selection through environmentally stratified sampling (Da Re et al. 2023). Despite these methodological advances, SDMs may still be affected by common sources of error, including overfitting, spatial autocorrelation, and inappropriate thresholding, which can inflate apparent predictive performance (Sillero and Barbosa 2021; Booth 2025). Under nonequilibrium invasion scenarios, the absolute probabilities produced by SDMs should be interpreted cautiously because species may not yet occupy all environmentally suitable areas. For this reason, relative rankings of suitability can be more informative than raw probability values when identifying areas with greater potential for future spread (Zarzo-Arias et al. 2022).

Modeling alien species is challenging and requires careful decision-making. Some authors have emphasised that including both native and invaded ranges is good practice (Loo et al. 2007; Broennimann and Guisan 2008), as this approach avoids niche truncation, captures potential niche shifts, and reduces projection uncertainty. In addition, invaders are

often globally distributed, providing a rich background of invaded ranges that helps contextualise the local invasion process. Furthermore, invasive populations undergo rapid evolutionary changes and niche shifts that enhance persistence in new environments (Colautti and Barrett 2013; Udo 2016; Udo et al. 2018; Santana et al. 2024). However, niche shifts are rare among terrestrial invaders, reinforcing the usefulness of incorporating both ranges (Petitpi-erre et al. 2012). On the contrary, some authors argue that only the invaded range should be used, as it may better reflect the realised niche under novel conditions and possible ecological shifts (Sillero and Barbosa 2021; Santana et al. 2024). The choice of occurrence data and pseudoabsences is also crucial, as it can significantly affect model performance; worldwide random pseudoabsences generally perform best (VanDerWal et al. 2009; Barbet-Massin et al. 2012; Capinha et al. 2011). Overall, while native-range occurrences tend to predict native ranges well and invaded-range occurrences predict invaded ranges best, combining both provides the best overall balance in projections (Capinha and Anastácio 2011).

Beyond methodological choices, future projections add further complexity. Projected warming and aridification under SSP3-7.0 and SSP5-8.5 are expected (Khalyani et al. 2016), and drought-driven fire regimes that favor flammable grasses are likely to intensify (Salesa et al. 2024). However, invasion outcomes are modulated by the human footprint, propagule availability, and the spatial arrangement of microclimates across steep elevational gradients (Irl et al. 2021). Because models may underestimate potential distributions and invasion risks when the full environmental envelope is not represented (Zarzo-Arias et al. 2023; Goicolea et al. 2024), hierarchical species distribution models (HSDM) that integrate local, regional, and global scales have been proposed as an effective strategy to mitigate such biases and improve predictive accuracy and management decisions (Fornoso-Freire et al. 2023; Mateo et al. 2024).

Local administrations increasingly recognise alien species as a priority issue. Surveillance in areas with frequent first detections can identify invasion hotspots and guide priority actions (Sofaer et al. 2024). Monitoring and complementary citizen science platforms (e.g., GBIF, iNaturalist) enable the creation of high-quality occurrence datasets that improve model predictions (Dimson et al. 2023; González-Moreno et al. 2024), although these data are often spatially and temporally biased (Meeus et al. 2021; Bracho et al. 2024). Community-based initiatives further complement scientific monitoring, aiding early detection and rapid response (Dimson et al. 2023; González-Moreno et al. 2024). Integrating citizen science data with bias-correction tools improves the realism of SDMs and helps prioritise surveillance (Bracho et al. 2024; García-Rodríguez et al. 2024).

Invasive perennial C₄ grasses exert profound ecological impacts due to their rapid growth, efficient dispersal strategies, and effects on native communities (Walentowitz et al. 2019). By altering fire regimes, nutrient cycles, and hydrological processes, they induce cascading changes that reshape ecosystem composition and dynamics (Berio Fortini et al. 2021; Morente-López et al. 2023; Walentowitz et al. 2023; Guarino et al. 2024). Their success is associated with human disturbances such as agriculture and urbanisation, which create favorable niches and facilitate their spread (Barros et al. 2022; Pfadenhauer et al. 2024; Rojas-Sandoval et al. 2024). Their generalist character and tolerance to extreme conditions give them an advantage over native species (Diez et al. 2012).

On oceanic islands, invasive grasses pose a particularly severe threat (Gillespie et al. 2008; Russell et al. 2017). The Canary Islands, with high biodiversity and more than 1,000 alien plants, provide a natural laboratory for invasion studies. Fortunately, only about 100

are naturalised, and fewer than 20 dominate natural vegetation, most belong to Poaceae (Morente-López et al. 2023). Invasions originate mainly from the Neotropics and the Mediterranean basin, reflecting biogeographic connectivity and human pathways (Morente-López et al. 2023). Three grasses spearhead this ‘grassification’ in the Canaries: *Cenchrus setaceus* (Forssk.) Morrone (detected in 1943; Rodríguez-Delgado and García-Gallo 2009), *Melinis repens* (Willd.) Zizka subsp. *repens* (detected in 1976; Afonso López and Wildpret 1976), and *Setaria parviflora* (Poir.) Kerguelén (detected in 1971; Hansen 1971). They spread rapidly along roadsides, lava flows, and shrublands on Tenerife, Gran Canaria, and La Palma. For *C. setaceus*, local SDMs based on Canary Island records confirm high habitat suitability in La Palma (Walentowitz et al. 2019) and Tenerife (Da Re et al. 2020). Native to arid Africa and the Middle East, *C. setaceus* shows high ecological plasticity and invasiveness across multiple archipelagos (Poulin et al. 2005; Da Re et al. 2020). It invades not only disturbed sites but also protected natural areas, including Mediterranean islands (Caldarella et al. 2010; Minissale et al. 2023; Musarella et al. 2025). *M. repens*, native to Africa and Asia, colonises road margins and disturbed habitats in southern Europe, sometimes overlapping with *C. setaceus* (Hidalgo-Triana et al. 2022). *S. parviflora*, introduced from South America to Europe in the nineteenth century (Godron 1853), shows increased growth and fertility under climate change (Chuine et al. 2012).

From a management perspective, our aim is to anticipate where suitability is likely to increase within the Canary Islands, which species are likely to co occur and thus potentially compound impacts, and whether each species appears to be at an earlier or more advanced invasion stage. We infer invasion stage indirectly from the degree of agreement between global and regional models. Higher agreement in predictor importance and response curve shape suggests a more advanced stage of invasion, whereas lower agreement is consistent with non equilibrium and or niche truncation at the regional scale. To address this, we use NHSDMs together with two cross scale diagnostic metrics: the Variable Importance Deviation Index (VIDI), which quantifies shifts in predictor importance between scales, and the Gradient Response Deviation Index (GRDI), which measures differences in the shape of species responses to environmental gradients. Together, these tools allow us to translate global information into high resolution risk maps for island surveillance and control prioritisation. Based on these considerations, we hypothesise that the three invasive grasses examined here exploit different environmental conditions within the Canary Islands. Specifically, we expect that *Cenchrus setaceus* will have the broadest niche and be associated with comparatively warmer, drier portions of environmental space. In contrast, *Melinis repens* is expected to occupy intermediate conditions and be more concentrated in disturbance-prone environments, partly overlapping with *C. setaceus*. Finally, *Setaria parviflora* is predicted to occupy a narrower, currently truncated niche in the archipelago, with suitability shifting more strongly across climatic gradients. We expect these contrasts to be reflected in differences in niche position and breadth across environmental and geographic space (i.e., lower interspecific overlap and distinct niche distributions across scales). Our second hypothesis is that differences between global and regional models reflect distinct invasion phases among the analysed species. We expect *C. setaceus* to be in an advanced invasion phase, followed by *M. repens*, whereas *S. parviflora* is in an early stage. Accordingly, we predict a gradient of global–regional agreement: *C. setaceus* should show high coherence between global and regional models (similar variable importance and consistent response curves), *M. repens* should show intermediate coherence, and *S. parviflora* should exhibit the strongest decou-

pling (low agreement in variable importance and more divergent responses to environmental gradients), consistent with non-equilibrium and/or niche truncation at the regional scale.

Materials and methods

Study area

Our study focuses on the Canary Islands archipelago (Fig. 1), a group of seven volcanic islands located approximately 96 km off the northwest coast of Africa, between 13°20'–18°10'W and 27°37'–29°25'N. Biogeographically, the Canaries are part of the Macaronesian ecoregion, which also includes the Azores, Madeira, the Selvagens, and the Cape Verde Islands (Fernández-Palacios et al. 2024). The archipelago exhibits remarkable geological, climatic, and bioclimatic diversity, primarily shaped by elevation, ranging from sea level to 3,715 m at Teide Peak, and by differential exposure to the prevailing trade winds. This variability plays a key role in the distribution of vegetation belts, including succulent scrub, thermophilous forest, evergreen laurel forest, pine forest, and summit vegetation, along the elevational gradient (Del Arco and Rodríguez-Delgado 2018; García-Alvarado et al. 2024). These steep gradients are particularly pronounced when moving from the drier, easternmost islands (Fuerteventura and Lanzarote) to the central islands (Tenerife and Gran Canaria) and the westernmost islands (La Gomera, La Palma, and El Hierro). These islands also differ significantly in age, annual precipitation, and temperature regimes.

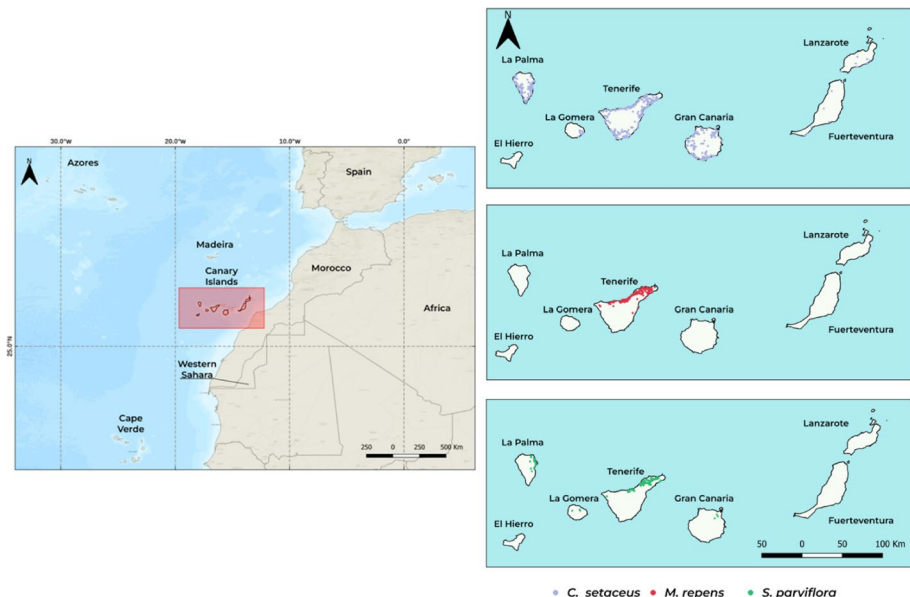


Fig. 1 The study area on the left, and the density of species records, are shown over the Canary archipelago

Environmental variables

Predictor selection was conducted a priori to balance ecological relevance, low collinearity, and comparability across scales. We retained BIO1 (mean annual temperature), BIO12 (annual precipitation), and BIO15 (precipitation seasonality) because they summarise major temperature and water availability gradients expected to constrain plant distributions and because equivalent layers were available from both CHELSA v1.2 (Karger et al. 2017) and CanaryClim (Patiño et al. 2023) for the same baseline period (1979 to 2013). This ensured that the same predictor set could be used consistently in the global and regional models. BIO1 from CanaryClim was converted to °C to harmonise units across datasets. Collinearity was then evaluated separately for each scale using Pearson correlation coefficients computed from values extracted from *N* randomly sampled raster cells with the *terra* package, and only variables with pairwise correlations below $|r| = 0.7$ were retained.

To generate projections under new climate scenarios, we used projections from the IPSL-CM6A-LR global circulation model (GCM), as it is one of the most widely used and evaluated models within the CMIP6 framework (Eyring et al. 2016; Boucher et al. 2020). This model has been shown to provide reliable simulations of atmospheric and oceanic dynamics at both global and regional scales (Dufresne et al. 2013; Boucher et al. 2020), and it is frequently employed in ecological and biogeographical studies (Thuiller et al. 2019). The IPSL model is particularly suitable for our study region because it captures key climate processes relevant to the Mediterranean and Macaronesian areas, such as seasonality of temperature and variability of precipitation (Lionello and Scarascia 2018). Using this model in two scenarios (SSP3–7.0 and SSP5–8.5), we evaluated distribution responses under an intermediate and a high emission scenario, thus providing a robust framework to evaluate potential future range shifts (O'Neill et al. 2016). We selected SSP3–7.0 and SSP5–8.5 as contrasting scenarios to bracket plausible late-century conditions for risk-averse island management. Restricting the analysis to these two SSPs also improves the interpretability of cross-scale comparisons.

Occurrence data

We compiled global occurrence records from the Global Biodiversity Information Facility (GBIF, 2025a–c) and split them into two datasets. The first dataset, used for our global models, included records from both the species' native range and other invaded ranges, excluding records from the Canary Islands. The second dataset focused exclusively on the Canary Islands and was supplemented with our own field-collected records for the regional analysis. Both data sets were pre-processed using the 'FormatingData' function from the *sabinaNSDM* R package (Mateo et al. 2024). This function was employed to clean and spatially thin the occurrence records, ensuring consistency with the spatial resolution of the global (~1 km at the equator) and regional (100 m) environmental covariates. We generated 10,000 background points (for the MaxEnt model) and pseudo-absence points (for the remaining modeling algorithms) using a stratified sampling strategy. This approach was based on a principal component analysis (PCA) of all environmental covariates. The first two principal components were divided into quartiles and combined to produce a stratification variable with 16 categories (strata). Background and pseudo-absence points were then randomly allocated in proportion to the area represented by each stratum. This procedure

ensured that the background and pseudo-absence data represented the main combinations of available climatic conditions while preserving their proportional availability across the study area. This is particularly relevant for oceanic islands, where environmental gradients are steep and some climatic conditions, such as high-mountain environments, occupy much smaller areas than coastal or lowland sectors. Importantly, sampling was conducted using the geographic raster representation of the PCA-derived strata; therefore, no inverse transformation from PCA space to geographic coordinates was required.

For *Cenchrus setaceus*, the number of global occurrences was reduced from 33,108 to 8,557, and the regional occurrences from 1,178 to 544. For *Melinis repens*, the global data set decreased from 34,022 to 15,278 occurrences, and the regional data set decreased from 612 to 353. For *Setaria parviflora*, the global dataset decreased from 33,841 to 17,502 occurrences, and the regional dataset decreased from 319 to 203.

Modelling framework and post-processing models

Our modelling approach is based on nested hierarchical species distribution models (NHSDM). This approach combines algorithms trained on global data to capture broad climatic niches with those trained on local data and predictors to produce fine-resolution predictions. Spatially nested models allow us to combine global and regional projections, avoiding constraints from limited local data or small geographical extents, thereby accounting for all available data and preventing niche truncation (Thuiller 2004; Goicolea et al. 2024). For this purpose, we used the R package *sabinaNSDM* (Mateo et al. 2024), which provides a framework for preparing presence and background/pseudo-absence data, calibrating and evaluating models, selecting covariates, and projecting models across global and local scales. To this end, it leverages the functionalities of the *biomod2* R package (Thuiller et al. 2009) to efficiently manage and evaluate multiple individual models, thereby increasing the robustness and predictive accuracy of species projections. A diverse set of established modelling algorithms was used to fit the species-environment relationships: GAMs (Generalized Additive Models), GBMs (Generalized Boosted Models), GLMs (Generalized Linear Models), MAXNET (Maximum Entropy Models), and RF (Random Forests). The final ensemble model was constructed by calculating a median habitat suitability across raster pixels from the predictions of the best-performing individual models, based on the AUC (area under the ROC, receiver operating characteristic curve), but also taking into account the balance with the non-standardised True Skill Statistic (TSS; Allouche et al. 2006; Elith et al. 2006). We selected only models with AUC > 0.7 from 10-fold cross-validation to build the final model for each approach. See Appendix S1 for more information on model selection. For each modelling approach, we first generated an ensemble prediction from the best-performing individual algorithms. We then derived four NHSDM outputs: a global model trained with global data, a regional model trained with local data, a covariate augmented regional model in which the global prediction was incorporated as an additional predictor when its correlation with the regional predictors was below the predefined collinearity threshold, and a multiple prediction integrating the different NHSDM outputs.

To obtain the final consensus model, we used the cell by cell suitability values from the four NHSDM outputs as input for a Principal Component Analysis. Because all four layers were expressed on the same suitability scale, no standardisation was applied. We used the first principal component as a summary of the spatial pattern shared among the four predic-

tions, and its loadings as a data driven weighting scheme to combine them into the final consensus map. This PCA based step was used to summarise the common signal among correlated NHSDM outputs, rather than to imply superiority over conventional weighted model averaging approaches (Barbosa 2015; Araújo et al. 2005; Baquero et al. 2021). This procedure was implemented using the ‘fuzzyConsensus’ function from the R package *fuzzySim* (Barbosa 2015).

Each model was binarised into presence–absence maps using thresholds that maximise the sum of specificity and sensitivity (maxTSS) and the AUC curve (maxAUC). Subsequently, we warped these binary rasters using the nearest neighbour method from geographic coordinates (EPSG:4326) to projected coordinates (EPSG:32628) to obtain occupancy areas for each species and climate period considered. See Supporting Information and Appendix S2 for detailed information.

Differences in niche and invasion phase

We analysed species niche divergence under different ecological conditions using PCA-env and Schoener’s D (Schoener 1970; Warren et al. 2008), following the ordination framework of Broennimann et al. (2012) implemented in the *ecospat* R package (Di Cola et al. 2017). This approach accounts for sampling bias by incorporating the available environmental space (E-space) and applying kernel smoothing to the occurrence densities. The niche overlap values of the niche (0 = complete dissimilarity, 1 = complete overlap) were interpreted following Rödder and Engler (2011): null to very low (0–0.2), low (0.2–0.4), moderate (0.4–0.6), high (0.6–0.8), and very high (0.8–1.0). We further tested niche equivalency (indistinguishable niches) and similarity (niche conservatism) by (1) estimating occurrence and environmental densities along PCA-env axes for each species pair and (2) quantifying overlap across the multivariate gradient (Broennimann et al. 2012). Specifically, ‘ecospat.grid.clim.dyn’ was used to estimate species occurrence densities in the gridded PCA environmental space, and ‘ecospat.niche.overlap’ was used to quantify pairwise climatic niche overlap through Schoener’s D and Hellinger’s I.

Additionally, we used two spatial metrics to compare the climatic niches in the Canary Islands geographical space. Hence, we compared species in terms of the overlapped pixels obtained from binarised habitat suitability predictions, using thresholds that maximised the sum of specificity and sensitivity (maxTSS) and the area under the ROC curve (maxROC).

To compare our global and regional models, we developed two distinct metrics: the Variable Importance Deviation Index (VIDI) and the Gradient Response Deviation Index (GRDI). This dual approach allowed us to assess differences in both the relative importance of environmental predictors and the specific shape of the species’ response curves (Berio-Fortini et al. 2024):

$$VIDI = \sum_{j=1}^p (I_{g,j} - I_{r,j})^2$$

where p is the total number of predictors, and $I_{g,j}$ and $I_{r,j}$ are the relative importance values of predictor j in the global and regional models, respectively. The VIDI is a unitless metric that quantifies the overall discrepancy in predictor importance between scales. Values close

to zero indicate similar importance rankings across scales, whereas larger values reflect greater divergence in which environmental variables structure the species' distribution. We recognise that the VIDI provides a useful, but incomplete, measure of niche differences. It tells us which variables matter most, but not how the species responds to those variables. For instance, a predictor such as precipitation could be equally important in both models, but the optimal conditions (e.g., wet vs. dry) could differ significantly.

To address this limitation and assess differences in the fundamental relationship between species and environmental gradients, we developed a slightly modified version of the GRDI from Berio-Fortini et al. (2024). This index indicates niche conservatism or divergence between the global and regional models. For each environmental predictor, we fitted separate Generalized Additive Models (GAMs) to the global and regional datasets, after restricting the global data to the range of values observed at the regional scale. Each predictor (BIO1, BIO12, and BIO15) was modelled independently as the explanatory variable, with model suitability as the response variable and a Gaussian error distribution.

For each scale and predictor, four alternative smoothing structures (knots=3, knots=6, cubic regression splines, and tensor smooths) were compared using the Akaike Information Criterion (AIC), and models were ranked by ΔAIC , with models with $\Delta\text{AIC} \geq 2$ relative to the best-supported model considered to have substantially less support (Burnham and Anderson 2002). The best-supported model for each scale was retained for subsequent analyses.

Predicted suitability values from the selected global and regional GAMs were evaluated along a common sequence of evenly spaced values for each predictor, yielding two response vectors. To isolate differences in response-curve shape rather than magnitude, predictions were standardized by centering and scaling them across evaluation points. For each predictor j , the Gradient Response Deviation Index (GRDI) was calculated as:

$$GRDI_j = \sum_{i=1}^n (z_{g,i} - z_{r,i})^2$$

where n is the number of evaluation points along the predictor gradient, $z_{g,i}$ is the standardised suitability predicted by the global model at evaluation point i , and $z_{r,i}$ is the corresponding standardised suitability predicted by the regional model. The subscript j identifies the predictor for which the index is calculated, whereas g and r denote the global and regional models, respectively. Larger GRDI values indicate greater divergence in response-curve shape between scales.

To complement this distance-based metric, we also quantified agreement between the standardised global and regional response curves using Lin's Concordance Correlation Coefficient (CCC):

$$CCC = \frac{2\rho s_g s_r}{s_g^2 + s_r^2 + (\mu_g - \mu_r)^2}$$

where ρ is the Pearson correlation coefficient between the two predicted response vectors, μ_g and μ_r are their means, and s_g and s_r are their standard deviations. The CCC combines

measures of correlation (precision) and deviation from the 1:1 line (accuracy) to provide an overall measure of agreement between global and regional response curves (Lin 1989).

Results

Nested Hierarchical SDM (NHSDM)

The predictions of habitat suitability reveal significant differences between *Cenchrus setaceus* and the other two species, *Melinis repens* and *Setaria parviflora*. *C. setaceus* shows the highest suitability in the coastal and lowland sectors of the westernmost islands (Fig. 2A), with remarkable shifts in suitability under both climate projections (SSP3-7.0 and SSP5-8.5) upward. A similar trend occurs in the easternmost islands, albeit to a lesser extent. In particular, a loss of habitat suitability is also predicted in the lowlands of Gran Canaria and Tenerife. On the contrary, the suitability predictions for *M. repens* and *S. parviflora* show a strong spatial correspondence across the archipelago (Fig. 2B and C). The high suitability values for these species are mainly found in the northern and northeast sectors of La Palma, Tenerife, and Gran Canaria. On La Gomera, suitability is moderate in the north, while El Hierro appears to be the least suitable island for these species within the westernmost group. These patterns persist across the SSP3-7.0 and SSP5-8.5 scenarios, showing minimal gains or upward shifts, largely confined to the northern sectors. High suitability values show strong persistence, and the eastern sector of the archipelago remains unsuitable for these species.

Comparing projected areas at global and regional scales reveals that global projections for *C. setaceus* and *M. repens* consistently show greater potential coverage than regional projections, a trend that holds across all climate scenarios and threshold measures (Fig. 3). Under these binary predictions, *C. setaceus* occupies a larger area than *M. repens*. On the contrary, regional models predict a larger occupancy area for *S. parviflora* than global models, particularly under the SSP3-7.0 scenario. Despite this, the models indicate that *S. parviflora* would ultimately occupy the smallest potential range within the archipelago.

Niche inferences in invaded environmental and geographical spaces

The metrics in the environmental space (Table 1), specifically Schoener's D and I, reveal low niche overlaps between *C. setaceus* and the other two species, *M. repens* and *S. parviflora*, across all three climatic scenarios. On the contrary, there is a high degree of overlap of niches between *M. repens* and *S. parviflora*. This is further supported by the environmental PCA, where the contours and most frequent values of *M. repens* and *S. parviflora* overlap strongly along the first two axes (Fig. 4). In terms of niche width, both *M. repens* and *S. parviflora* have niches constrained to a limited portion of environmental space, while *C. setaceus* can occupy a wider range of environmental conditions. Future climate projections indicate that the environmental overlap among the three species will decrease. This is reflected in the kernel density plots, which show a shift towards positive values on Axis 2 for *C. setaceus* and reduced overlap between the species' contours.

Despite these findings in the environmental space, there is a significant mismatch in the geographical space (Table 2). Pixel counts from thresholded predictions indicate a high

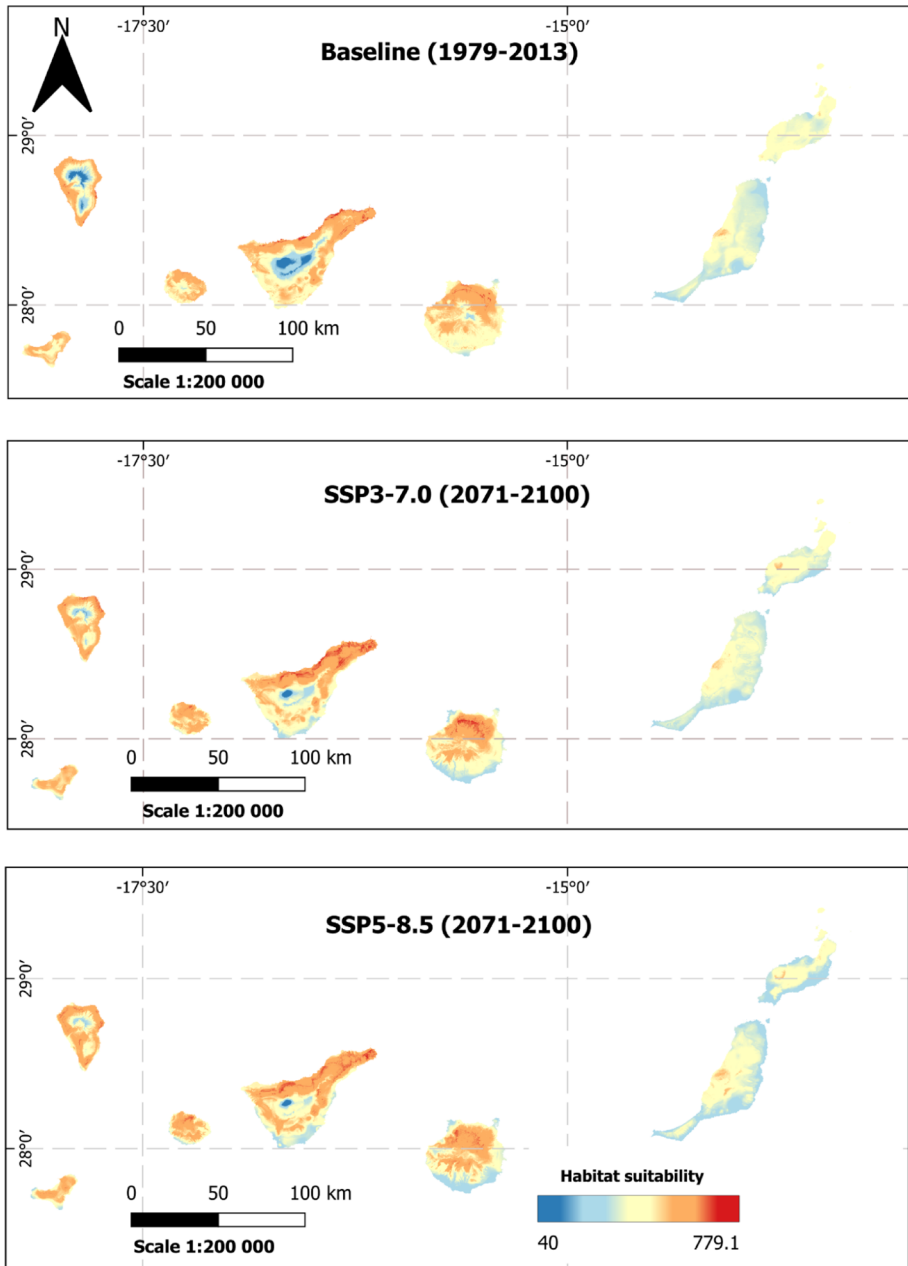


Fig. 2 **A** Ensemble SDM for *Cenchrus setaceus*, scaled from 40 to 779.1 for each climate period considered. **B** Ensemble SDM for *Melinis repens*, scaled from 12 to 872 for each climate period considered. **C** Ensemble SDM for *Setaria parviflora*, scaled from 10 to 820 for each climate period considered

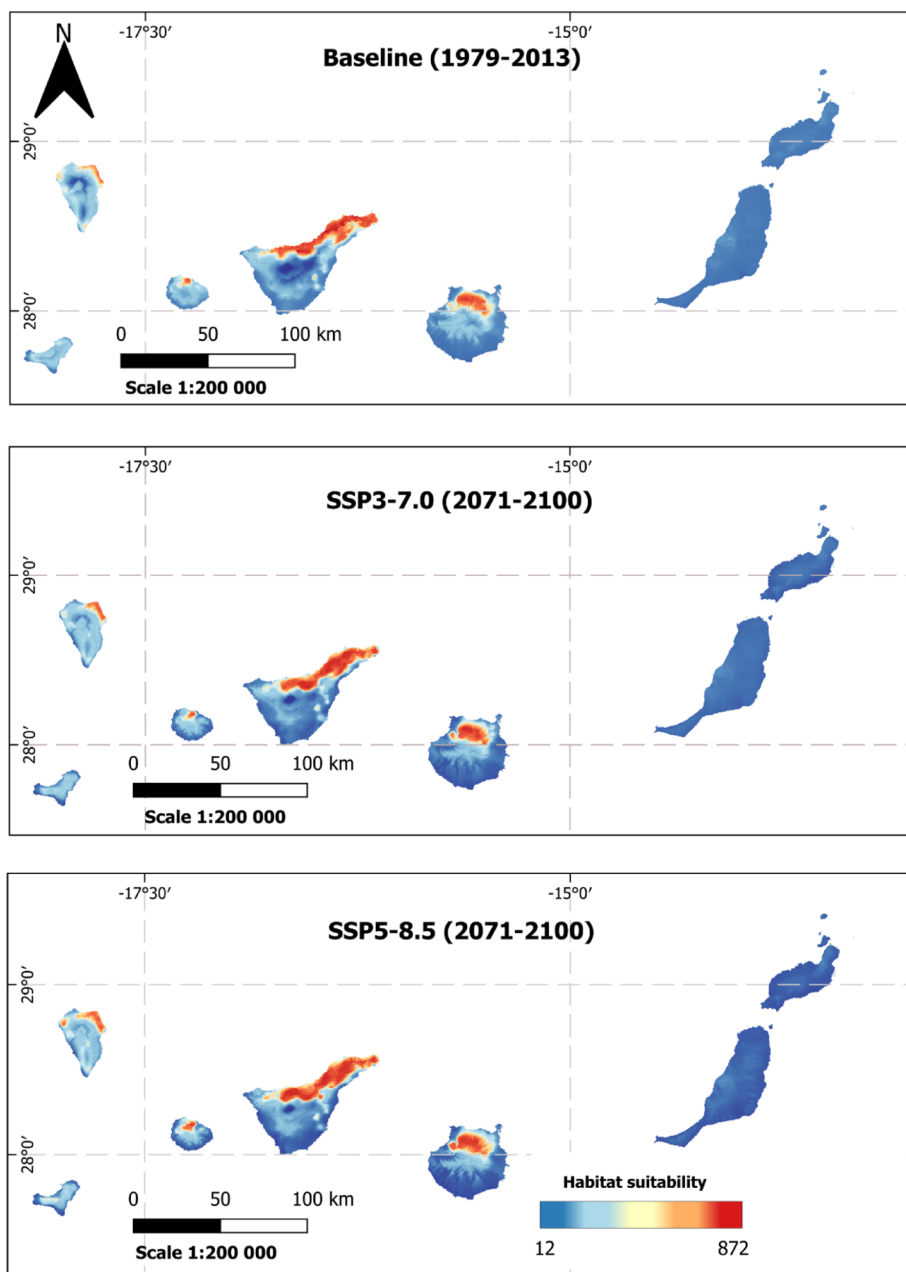
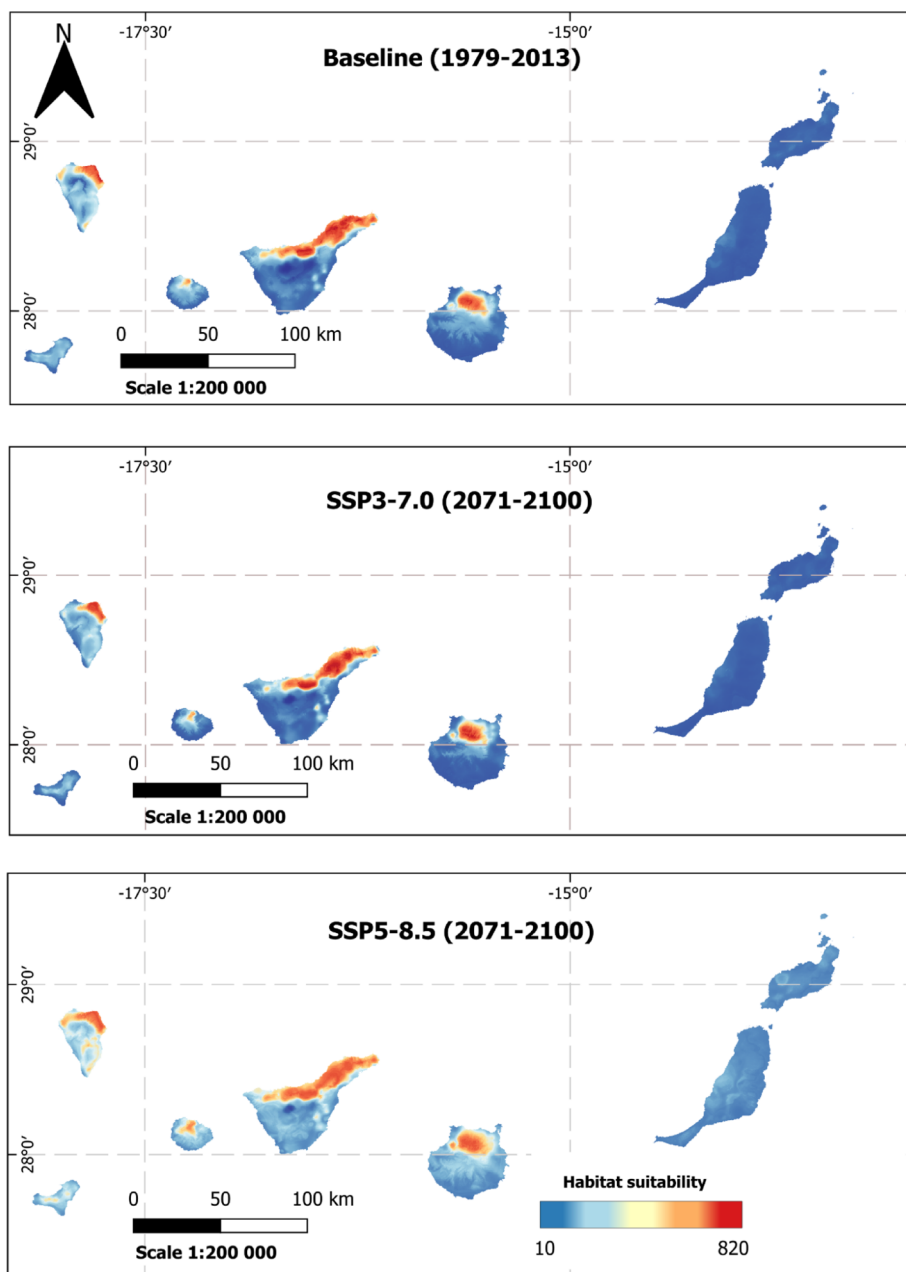


Figure 2 (continued)

and increasing spatial overlap among all three species across future climate projections. This is particularly significant for the spatial co-occurrence between *C. setaceus* and *M. repens*, which is unexpected given their low environmental niche overlap. This discrepancy

**Figure 2** (continued)

between environmental and geographical spaces highlights the complex dynamics of species distribution under climate change.

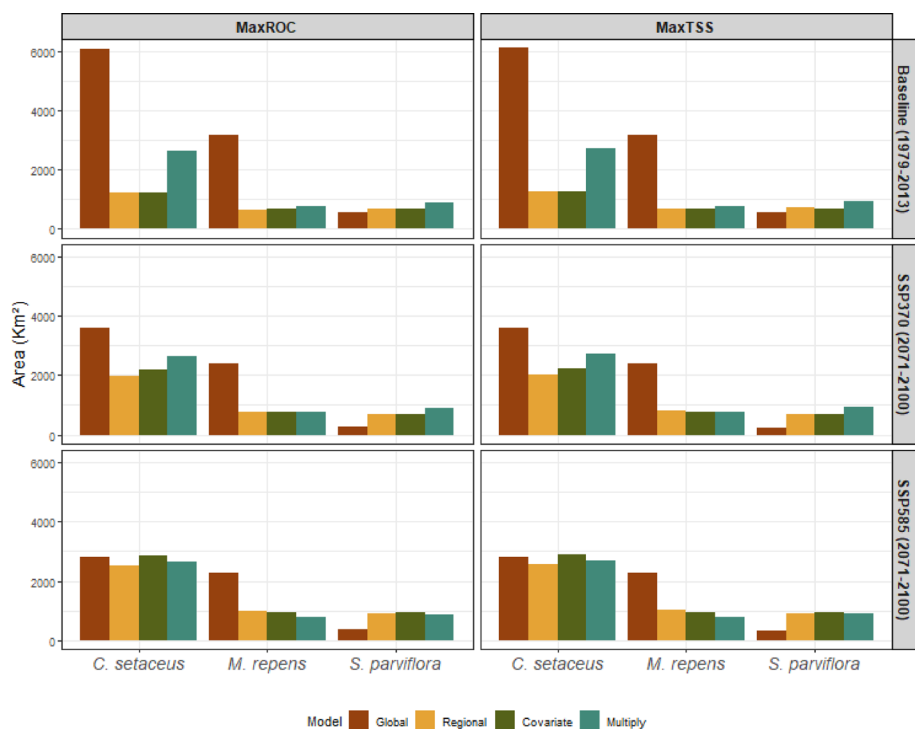


Fig. 3 Projected occupancy area (Km²) for the three species (*Cenchrus setaceus*, *Melinis repens*, and *Setaria parviflora*), differentiated by model type (global, regional, covariate nested and multiply nested), different climate projections, and two threshold-based binarizations (MaxRoc, MaxTSS)

Table 1 Comparison of the importance of the variable (expressed as percentage; %) for species across global and regional models. The bold values indicate the lower VIDI

Species Model	Variable Importance (BIO1)		Variable Importance (BIO12)		Variable Importance (BIO15)		Variable Importance Deviation Index (VIDI)
	Global	Regional	Global	Regional	Global	Regional	
<i>C. setaceus</i>	90.3	53.4	12.4	52.2	6.6	29.4	3,454
<i>M. repens</i>	80.3	9.4	21.6	20.8	11.8	88.2	10,872
<i>S. parviflora</i>	59.6	12.4	23.4	18.4	7.9	83.8	8,018
<i>C. setaceus</i>	90.3	53.4	12.4	52.2	6.6	29.4	3,454

Assessing differences in variable importance, gradient responses, and projected areas

SDMs reveal significant differences in variable importance among the three species. On the global scale, BIO1 is always the most important variable for all species, whereas on the regional scale, this pattern holds except for *C. setaceus*. Accordingly, *C. setaceus* has the lowest VIDI scores, indicating greater consistency in the contribution of the three environmental variables (BIO1, BIO12, and BIO15) across the different model scales. For this species, BIO1 is consistently the most influential predictor, followed by BIO12 and BIO15,

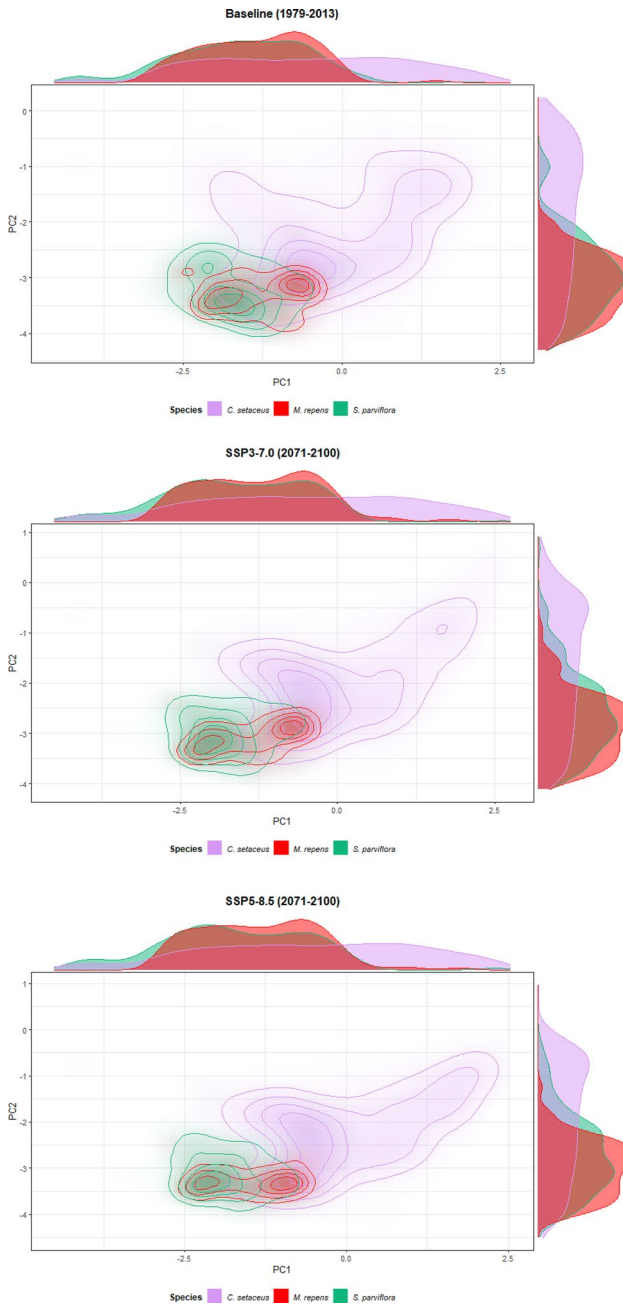


Fig. 4 Overlap of species' climatic niches in environmental space. The shaded areas represent the density of climatic conditions occupied by each species in the PCA environmental space. The contour lines are isodensity lines; that is, they connect cells with similar estimated occurrence density and summarize different levels of species density within the occupied environmental space. Marginal plots reflect the density distributions in the environmental space (summarised in the first two components) of each species

Table 2 Niche inferences in the invaded range (regional models). The maxROC and maxTSS threshold values for each species and regional ensemble were as follows (scaled from 0 to 1000): *C. setaceus* (429.5 and 427); *M. repens* (465.5 and 433); *S. parviflora* (493.5 and 489)

Species Inferences		Metrics in the environmental space (Niche overlap)		Metrics in the geographical space (overlapped pixels)	
		Schoener's D	Hellingers' I	maxROC	maxTSS
Baseline (1979–2013)					
<i>C. setaceus</i>	<i>M. repens</i>	0.2276	0.4479	35,432	35,949
<i>C. setaceus</i>	<i>S. parviflora</i>	0.257	0.468	27,560	28,997
<i>M. repens</i>	<i>S. parviflora</i>	0.591	0.8029	51,495	53,550
SSP 3–70 (2071–2100)					
<i>C. setaceus</i>	<i>M. repens</i>	0.15	0.34	63,851	67,649
<i>C. setaceus</i>	<i>S. parviflora</i>	0.17	0.35	53,263	54,310
<i>M. repens</i>	<i>S. parviflora</i>	0.60	0.82	59,144	60,161
SSP 5–85 (2071–2100)					
<i>C. setaceus</i>	<i>M. repens</i>	0.15	0.33	87,555	92,119
<i>C. setaceus</i>	<i>S. parviflora</i>	0.18	0.36	72,290	73,348
<i>M. repens</i>	<i>S. parviflora</i>	0.56	0.76	76,952	78,319

Table 3 Predictor-specific deviations in species responses to environmental gradients between global and regional distribution models. Gradient Response Deviation Index (GRDI); CCC (Lin's Concordance Correlation Index). The bold values indicate the best concordance between global and regional predictions. BIO1 = mean annual temperature, BIO12 = mean annual precipitation, BIO15 = seasonal precipitation

Species	BIO1		BIO12		BIO15	
	GRDI	CCC	GRDI	CCC	GRDI	CCC
<i>C. setaceus</i>	615.1	0.692	3,612	-0.808	3,287	-0.645
<i>M. repens</i>	1,030.9	0.484	3,011.8	-0.507	1,605.4	0.2
<i>S. parviflora</i>	1,224.4	0.387	771.6	0.614	896.4	0.551

although with varying degrees of weight. In contrast, *M. repens* and *S. parviflora* show much higher VID scores, reflecting a less consistent and more uneven distribution of variable importance between the two modelling scales (regional and global). Although BIO12 has a similar contribution for both species at both scales, there is a stark difference in the primary predictors. On the global scale, BIO1 is the most important variable, while on the regional scale, BIO15 becomes the most influential predictor, highlighting a scale-dependent shift in the key climatic drivers for these two species (Table 3 and Fig. 5).

GRDI reveals a different trend in species-specific responses to environmental conditions. *Setaria parviflora* demonstrates the most coherent and consistent response across both modelling scales, with positive concordance for all three variables (BIO1, BIO12, and BIO15). This is further supported by its lower GRDI values for BIO12 and BIO15, indicating minimal divergence between its regional- and global-scale responses. *Cenchrus setaceus* shows strong concordance in its response to BIO1, coinciding with the most important variable on both scales as well. However, its responses to BIO12 and BIO15 are highly divergent, with regional- and global-scale responses nearly reversed and more constrained. In contrast, for *M. repens*, there is a positive concordance in its responses to BIO1 and BIO15, although the concordance for BIO15 is very low. Furthermore, its response to BIO12 shows negative concordance, indicating a significant reversal in its niche response between the two scales.

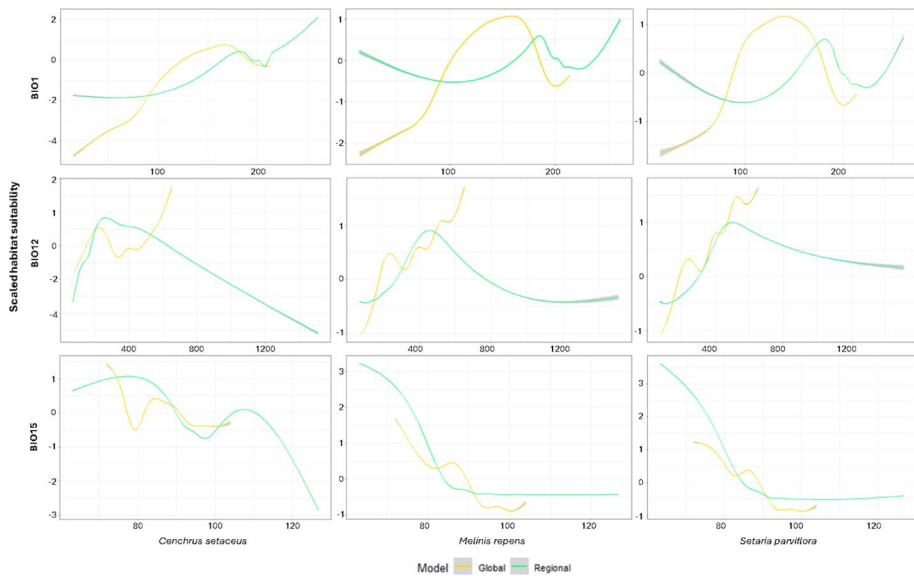


Fig. 5 Comparison of the species curves (smoothers) between global (gold) and regional (green) GAMs applied for the three species studied. Responses were scaled by standard deviation and centered by mean values along each curve to minimise distance. BIO1=mean annual temperature, BIO12=mean annual precipitation, BIO15=seasonal precipitation

Discussion

Invasive plants are a major global driver of biodiversity loss, and climate change is expected to further amplify their impacts by expanding the environmental space suitable for invasion, particularly in water-limited island systems. Against this backdrop, we present a scale-sensitive framework for assessing the invasive characteristics of grass species by integrating spatial predictions with explicit niche diagnostics. The central contribution of this study is to translate future suitability projections into management-relevant priorities for minimising biodiversity impacts of invasive grasses in the Canary Islands. The approach nests global species distribution models (SDMs) trained on occurrences from native and invaded ranges within high-resolution regional SDMs for the Canary Islands and adds two integrative products (a covariate-augmented regional model and a multiplicative consensus) to refine potential distributions. Beyond traditional suitability maps, we quantify niche status in the invaded range using two cross-scale metrics: the Variable Importance Deviation Index (VIDI), and the Gradient Response Deviation Index (GRDI). Together, these elements reveal species-specific invasion dynamics: *Cenchrus setaceus* shows broad warm-xeric suitability and comparatively low cross-scale divergence, consistent with a more advanced invasion phase, whereas *Melinis repens* and *Setaria parviflora* display mesic-montane affinities and higher precipitation-related divergence, indicating stronger scale dependence and earlier invasion phases. By reconciling patterns across environmental and geographical projections and standardising response-curve comparisons, the framework yields management-ready insights, pinpointing prospective co-occurrence hotspots under late-century climate scenarios and clarifying which climatic filters most constrain each species. This integrated

perspective addresses non-equilibrium and niche-truncation issues that often limit island invasion forecasts, providing a transparent basis for prioritising surveillance and interventions for invasive grasses under ongoing climate change.

Suitability models and niche metrics

The three grasses are distributed along a warm-dry to cool-humid gradient, with *C. setaceus* exploiting markedly different conditions from *M. repens* and *S. parviflora*, in partial agreement with our main hypothesis of niche divergence within the archipelago. SDMs reinforce this idea, showing that *C. setaceus* is highly suitable for the warmest areas of the western islands, consistent with previous results in other systems (Walentowitz et al. 2019; Musarella et al. 2025), although it has a very broad ecological valence (Jacobi and Warshauer 1992). This translates into a broader niche as well, regardless of the assessed climatic projection. Additionally, it is important to emphasise the species' extraordinary competitiveness against native species, its high tolerance to drought, and its ability to invade habitats with pronounced seasonal precipitation (Khalyani et al. 2016; Potter et al. 2023; Patiño et al. 2024). In contrast, *M. repens* and *S. parviflora* track mesic-montane conditions, with the highest suitability in the north and north-east of the Canaries, closely matching trade-wind humidity, laurel-forest belts, and cloud-affected pine zones. Together, these patterns indicate that the suitability of *C. setaceus* is expanding or consolidating, while remaining comparatively constrained for the other moisture-dependent species (Franklin et al. 2023).

M. repens and *S. parviflora* show highly correlated suitability values in both geographical and environmental spaces. In both species, high suitability values are more closely associated with wetter sectors, where humidity, in a broad sense, appears to determine their distribution. This is directly related to the narrow niche width of both species. In contrast, *C. setaceus* shows broad environmental tolerance and is strongly associated with thermal gradients. According to the literature, *M. repens* has requirements similar to those of *C. setaceus*, both of which occur in the same habitats (Hidalgo-Triana et al. 2022). Therefore, its current distribution in the Canary Islands may be underestimated, consistent with an early stage of invasion. However, *S. parviflora* is associated with wetter conditions than *C. setaceus*, so suitability in environmental space likely aligns with its potential distribution, although that potential distribution may expand under climate change (Chuine et al. 2012). Such differences highlight how invasion success is shaped not only by propagule pressure and dispersal, as emphasised in theoretical models (Irl et al. 2021), but also by the interaction between species' ecological requirements and the dominant environmental filter along the gradient.

Taken together, the signatures indicate a mismatch between multidimensional and spatial approaches. Hence, *C. setaceus* overlaps more with *S. parviflora* in environmental space, whereas in geographical space it overlaps with *M. repens*. This has been noted previously, with *M. repens* described as a coloniser and an extraordinary competitor against native flora, both independently and in areas of contact with *C. setaceus* (Hidalgo-Triana et al. 2022; Yelenik et al. 2024).

VIDI, GRDI, and projected areas

Shifts in predictor contributions across modelling scales are widely reported (e.g., Nyström et al. 2013; Chauvier et al. 2022). Consistent with this, BIO1 (mean annual temperature) typically emerges as the primary global driver (Berio-Fortini et al. 2024). At coarse resolutions, BIO1 effectively captures latitudinal and elevational patterns, whereas topography-linked variables are diluted (Franklin et al. 2012). At finer resolutions, irregularities in precipitation amount and seasonality can dominate, particularly at mid-elevations, where event irregularity matters (Karger et al. 2023). This effect is even more pronounced in insular environments, where topographic complexity and steep gradients shape elevational patterns of plants and vegetation belts (e.g., Garzón-Machado et al. 2013; Barajas-Barbosa et al. 2025), as well as differences within and between islands (Frazier et al. 2016).

At the mapping stage, the threshold method is critical for binarising predictions and estimating invasive range size, but it often leads to underestimation (Guisan et al. 2013; Hellegers et al. 2025). However, the choice of threshold is not crucial for island-level invasion risk because derived blacklist patterns are consistent across thresholds, as shown for the Pacific Islands (Holle et al. 2025). This aligns with the coherence observed in our projected area patterns across species and scenarios, revealing similar trends in predicted coverage and low sensitivity to threshold choice. Additionally, for *C. setaceus* and *M. repens*, there is an underlying pattern in which the global and nested models project much larger areas of suitable habitat than the regional model. This has been linked to nonsaturation during the invasion process, potentially leading to further spread (Berio-Fortini and Kaiser 2023). Although this phenomenon is projected to decrease in future climate projections for *C. setaceus*, it remains the species with the largest projected area, with notable upward shifts, as previously reported in Tenerife (Da Re et al. 2020). Trait-based approaches have shown that under warmer, drier future climates, species with conservative strategies and the ability to exploit habitats with limited water availability will succeed (Cao-Pinna et al. 2024).

In the case of *S. parviflora*, we detect contradictory signals regarding its invasion phase: partial saturation and a stage distinct from those of the other species. Furthermore, signals of niche conservatism are apparent, as shown by the high concordance in the responses of BIO12 and BIO15 between the global and regional models. Similar patterns have emerged from studies of the niche dynamics of gorse (*Ulex europaeus* L.) in New Zealand, a region characterised by high climate matching with its native range (Christina et al. 2019). However, differences in suitability between the global and regional models in *S. parviflora*, as reflected in contrasting loadings in the multi-model PCA, are more consistent with ongoing colonisation and adaptation (Eckert et al. 2020) than with niche equilibrium. This interpretation is further reinforced by the lower projected suitable area in the global model compared to the regional and nested models.

Furthermore, precipitation seasonality remains the most important variable at the regional scale, with suitability decreasing as monthly precipitation variability increases. Downward- or left-skewed curves in scaled habitat suitability versus precipitation seasonality are mainly associated with invasive species limited to temperate, humid environments in the area of introduction, as indicated in Hawaii for *Melinis minutiflora* P.Beauv., *Morella faya* (Aiton) Wilbur, and *Ulex europaeus* (Berio-Fortini et al. 2024). *S. parviflora* requires humid environments, regular rainfall, and disturbed habitats. Its distribution in the southern, driest parts of the islands is attributable to cultivation in urban gardens. This ecological

profile explains its non-cultivated distribution, which includes the wet north-eastern sector of La Palma and the northern part of Tenerife. At the same time, it can prevent an increase in suitability in drier regions of the archipelago, and it is directly related to the species' narrow niche breadth.

Management implications in climate change and key limitations

Operationally, our projections support (1) containment/impact mitigation for *C. setaceus* in warm lowlands and upslope-shift fronts, and (2) early detection and rapid response for *M. repens* and *S. parviflora* in humid northern belts where suitability persists or expands. Because co-occurrence is projected to increase, integrated management targeting shared corridors (e.g., road networks and disturbed interfaces) may improve efficiency. Although this work presents a novel and transferable framework for distinguishing niche approaches among three invaded grasses, we infer only the species' ecological niches and potential distributions. In fact, we partially neglect human-driven factors (infrastructure, land-use change, abandoned farmland, etc.) intimately linked to the establishment and spread of grasses and other invaders (Da Re et al. 2024; Rojas-Sandoval et al. 2024), and well documented in the Canaries (e.g., Arévalo et al. 2005; Otto et al. 2014; Bacaro et al. 2015). Recent syntheses emphasise that disturbance proxies are critical predictors in habitat-suitability models for terrestrial invaders and caution that purely climatic suitability may understate realised spread where propagule pressure and anthropogenic filters dominate (Kueffer et al. 2010; Williams et al. 2024). However, our inferences are based solely on climatic drivers because high-resolution products for human-derived factors in the Canaries and their projections are lacking.

As a caveat, our models are partly subject to variable sampling effort and taxonomic bias inherent in public repositories such as GBIF (Soto et al. 2025), although we also included curated field records. In this regard, disturbed low-elevation areas are more likely to be surveyed, potentially inflating records of target species in more degraded, warm environments (Akasaka et al. 2015; McLean et al. 2017). Previous studies indicate that differences in data quality and the use of more complete surveys within the invaded range can determine the final quality of models (Young et al. 2024). Dispersal simulations and barriers can be incorporated into nested modelling approaches to more accurately assess potential species expansion (Lázaro-Lobo et al. 2025).

Complementary approaches can consider the relationship between species with native and invaded ranges, where niche expansion has been reported as common (Jay-García et al. 2025; under review). Designs contrasting native and invaded niches remain valuable, given the ongoing debate over true niche expansion versus apparent shifts driven by transfer/background effects. Using nested models alongside native–invaded contrasts is the cautious approach (Broennimann et al. 2012; Franklin et al. 2023; Guisan 2025). Therefore, potential niche instability is particularly relevant for oceanic islands, whose disharmonic biota and interaction-poor networks can sometimes ease establishment and spread (Petitpierre et al. 2012; Atwater and Barney 2021; Fernández-Palacios et al. 2023; Liu et al. 2025).

In our case, multi-species actions should outperform single-species interventions under warming (Tisshaw and Menges 2018; Williams et al. 2024). This corridor focus aligns with island invasion syntheses and recent field evidence in Macaronesia (Bacaro et al. 2015; Steinbauer et al. 2017; Da Re et al. 2020). The picture of these species in Macaronesia is

very different. Despite its use as an ornamental species in the Azores, *C. setaceus* is established only in Madeira, where it was first detected in 2018 (Jardim and de Menezes 2021), and is already showing early-stage invasive characteristics (Verloove et al. 2024). For *S. parviflora*, the species is naturalised in both the Azores (Elias et al. 2021) and Madeira (Jardim and de Menezes 2008). Taken together, these findings place the Macaronesian archipelagos on the early warning list, with these species showing clear potential to colonise and establish regionally.

Conclusions

Invasive species are a global environmental problem and a leading driver of biodiversity loss. Climate change, another major driver of biodiversity loss, can further exacerbate these impacts by promoting the expansion of alien species, which are often favoured under changing environmental conditions. The results of this study indicate that *M. repens* and *S. parviflora* occupy broadly similar ecological niches, whereas *C. setaceus* shows no niche overlap with either species. However, *C. setaceus* partially overlaps with *M. repens* in its geographic distribution. In terms of the invasion phase, *M. repens* and *S. parviflora* appear to be in earlier phases of establishment than *C. setaceus*, which is more advanced along the invasion trajectory. The two former species are associated with relatively narrow, humidity-dependent niches, whereas *C. setaceus* exhibits a broader ecological niche, in which temperature is the dominant environmental driver. Under future climate-change scenarios, all three species are projected to substantially expand their potential geographic ranges. Although our analyses focus on the Canary Archipelago, these findings illustrate general mechanisms by which niche breadth, invasion phase, and climate interact to shape the spread of alien plants in water-limited island and coastal ecosystems worldwide. Expanding niche-based analyses of alien species to include a wider set of environmental and anthropogenic drivers will allow more accurate delineation of potential distributions and more robust identification of invasion phases. Such information is essential for prioritising surveillance and management actions for invasive species and for safeguarding the integrity of natural and semi-natural ecosystems in oceanic islands and other vulnerable regions under global change. By linking global information with island-scale projections, our approach delivers management-ready maps that highlight where suitability and co-occurrence are most likely to increase. These outputs can be directly used to prioritise surveillance, allocate control resources, and plan multi-species interventions under SSP3-7.0 and SSP5-8.5.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-026-03379-9>.

Acknowledgements This work was supported by project PROID2021010099, “Un tridente de gramíneas invasoras (Pennisetum–Melinis–Setaria) en un contexto de cambio global: ¿colonización del territorio o reparto del nicho?”. We thank the Cabildo Insular de Tenerife (Servicio de Biodiversidad) and GESPLAN S.L. for supporting this project and assisting with the required permits.

Author contributions Conceptualisation: J.R.A.; data curation: R.D.C.P, J.J.G.A.; funding acquisition: J.R.A.; investigation: R.D.C.P, J.J.G.A.; methodology: R.D.C.P, J.J.G.A.; project administration: J.R.A.; supervision: J.R.A.; visualisation: R.D.C.P, J.J.G.A.; writing – original draft: R.D.C.P, J.J.G.A.; writing – review and editing: R.D.C.P, J.J.G.A., C.G.M., J.R.A.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature.

Data availability The R code used can be viewed at <https://github.com/Juanjolizard/Invasive-grasses-Paper/tree/main/scripts>. The worldwide occurrence data can be accessed at GBIF.org under <https://doi.org/10.15468/dl.gac3cr>, <https://doi.org/10.15468/dl.xnvdkb>, and <https://doi.org/10.15468/dl.kpzns8>. The occurrence data for the Canary Islands can be shared upon request from the corresponding author.

Declarations

Competing interests The authors declare no competing interests.

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