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ORIGINAL PAPER



Assessing the impacts of land use and climate change on the distribution patterns of *Ulex europaeus* L. (Fabaceae) in the Canary Islands

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Abstract Biological invasions are one of the major threats to biodiversity, but their impact is particularly detrimental on oceanic islands like the Canary Archipelago. The common gorse (*Ulex europaeus* L. (Fabaceae)) is a highly invasive shrub with established populations in Tenerife, the sole island of the archipelago where it is present. Understanding the habitat preferences of *U. europaeus* is essential for predicting its current and potential future distribution across Tenerife and other Canary Islands, guiding effective local management practices. In 2019 and 2020, we surveyed different populations of *U. europaeus* in Tenerife, retrieving information on its

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Department of Geography, University of Las Palmas de Gran Canaria, Las Palmas de Gran Canaria, Spain e-mail: agustin.naranjo@ulpgc.es abundance, presence of other invasive species and most frequent natural and anthropogenic characteristics of the landscape. We used this information to build explanatory and predictive models to identify the key natural and anthropogenic drivers of U. europaeus abundance in Tenerife and estimate the potential distribution of the species across the whole archipelago under current and future climatic conditions. Our findings showed that U. europaeus thrives in humid areas impacted by human activities where other invasive species persist. Both current and future climatic conditions do not support the presence of the species in the more arid islands of the archipelago (i.e., Fuerteventura and Lanzarote), rather highlight that the windwards, and thus more humid, areas of the other islands might support the species also

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M. González INRAE, Bordeaux Sciences Agro, UMR 1391 ISPA, 33882 Villenave-d'Ornon, France under future warmer climatic scenarios. These findings deepen our understanding of *U. europaeus* local dynamics and are crucial to inform targeted management strategies to mitigate its impact across the Canary Archipelago and, ultimately, oceanic islands.

Keywords Biological invasions · Climate change · Common gorse · Machine learning Oceanic islands

Introduction

Biological invasions are one of the main drivers of habitat degradation and species loss (Bellard et al. 2016; IPBES 2023). This threat is particularly pronounced on oceanic islands (Donlan and Wilcox 2008; Kueffer et al. 2010), where their inherent remoteness fostered the evolutionary isolation of native communities, leaving them particularly susceptible to invasive alien species—IAS (Hulme 2009; Silva and Smith 2004; Pauchard et al. 2009; Moser et al. 2018). Human activities, including globalisation and land cover/land use change, have emerged as the major forces driving the proliferation of IAS that often lead to a taxonomic and functional homogenisation of insular biotas (Levine and d'Antonio 2003; Westphal et al. 2008; Pysek et al. 2010; Tordoni et al. 2019; Caro et al. 2022). Unfortunately, the Canary Islands (Spain) are no exception to this trend (Atkinson and Cameron 1993; Arévalo et al. 2005; 2010; Bacaro et al. 2015). Conserving biodiversity on oceanic islands is crucial due to their unique ecosystems and isolation, which often results in high levels of endemism representing hotspots for evolution (Whittaker and Fernández-Palacios 2007). Without conservation efforts and IAS management practices, the delicate balance of these insular ecosystems could be disrupted, leading to irreversible loss of species and ecological functions (Kier et al. 2009).

Ulex europaeus L. (Fabaceae), commonly known as the common gorse, is one of the most invasive shrubs in the world, having been associated with displacing native species and the homogenisation of ecosystems in areas where it has been established (León Cordero et al. 2016; Galappaththi et al. 2023). The impact of *U. europaeus* on the native flora of the Canary archipelago was evident with studies revealing its dispersal along the northern regions of Tenerife, the only island of the archipelago where the species is currently naturalised (García-Gallo et al. 1989, 2008). The species was presumably introduced multiple times on the island: though the first observation dates back to the nineteenth century (Buch 1825), most of the introductions likely happened during the 1960s, coinciding with the importation of trees from the Iberian Peninsula for reforestation purposes (Sanz et al. 2004; Morente-López et al. 2023), primarily *Pinus radiata* or *Eucalyptus* spp. (see Marrero 2016 concerning Gran Canaria).

Human-induced land use change is considered one of the main drivers of the expansion of U. europaeus, a pioneer and shade intolerant species, given its propensity to colonise abandoned agricultural regions (Elorza et al. 2004; Muthulingam and Marambe 2022). The Canary Islands government estimates that about 60% of agricultural land in the archipelago has been left fallow in recent decades (Gobierno de Canarias 2023), making it susceptible to colonisation by opportunistic invaders (Benning et al. 2002; Mosher et al. 2009; Essl et al. 2020; Roberts and Florentine 2021). In the case of Tenerife Island, there are no documented uses of the species for agriculture (Sanz et al. 2004), though its application for compost, fodder and hedge plant has been reported in the rural areas of the island (Álvarez Escobar 2011; oral communications collected by M.A. Padrón-Mederos). If human-driven land use change can favour the expansion of U. europaeus in the Canary Islands, global warming might likely limit it. Despite its ability to tolerate warm periods, U. europaeus typically thrives in cooler and rainy areas (Roberts and Florentine 2021), indicating potential challenges for the species in adapting to future climate conditions. Over the past seven decades, the Canary Archipelago has observed an upward shift in temperature values, with an increase of approximately 0.6 °C in mean temperature, with minimum night temperatures alarmingly increased by almost 1.5 °C (Martín et al. 2012).

The impacts of land use change and global warming and their interaction can yield different and sometimes contrasting outcomes for this species, complicating the design of effective management strategies. Numerous studies have explored the primary factors influencing the distribution of *U. europaeus* over large geographical scales (Hernández-Lambraño et al. 2017; Christina et al. 2020; Roberts and Florentine 2021; Ángel-Vallejo et al. 2024), however, effective management practices necessitate a finer-scale understanding of the species' ecology. Therefore, it is crucial to evaluate the predominant anthropogenic and natural drivers of U. europaeus in Tenerife Island and subsequently, to anticipate dispersion trajectories, assessing which areas of Tenerife, as well as other islands within the Canary Archipelago, may be susceptible to invasion. In addition, we can speculate that patterns of co-occurrence with other IAS can reflect similar introduction pathways or shared ecological properties (Kuebbing and Nuñez 2015), and may involve physical modifications in the soil which, in turn, might promote future invasions (Vujanović et al. 2022). In literature, the interaction among IAS has been detected to be mostly negative or neutral (Kuebbing and Nuñez 2015; Lortie et al. 2021), and resulted in further complicate management and restoration activities due to the interacting effects of cooccurring invaders (Zenni et al. 2020).

In this study, we surveyed different populations of *U. europaeus* located on Tenerife Island, collecting information about the abundance of the species, the land use, and the presence of other invasive species. We aimed to answer the following questions employing machine learning and classic statistical approaches:

- 1. What are the main natural and human-related factors influencing the abundance of *Ulex europaeus* on Tenerife Island?
- 2. Are other invasive plant species associated with the abundance of *U. europaeus*?
- 3. What is the potential habitat distribution of the species in Tenerife and the other islands of the Canary Archipelago under the current and future climatic scenarios?

We attempted to answer these questions to deepen our understanding of *U. europaeus* local dynamics, which are crucial to inform targeted management strategies to mitigate its impact across the Canary Archipelago and, ultimately, oceanic islands.

Methods

Species ecology

Ulex europaeus is an invasive, evergreen and highly plastic shrub listed as one of the most invasive species

in the world (Altamirano et al. 2016; Broadfield and McHenry 2019). This species has been introduced in different parts of the world since the nineteenth century (Australia, New Zealand, South America, California, and South Africa, among other regions) and is now distributed from equatorial to temperate regions (POWO 2023).

Ulex europaeus has a low-temperature tolerance limit and cannot withstand severe and prolonged freezing temperatures (Atlan and Udo 2019; Christina et al. 2020). Therefore, it is typically found in areas where monthly temperatures average above zero, though it has colonised coastal areas at higher latitudes in Europe and in the Americas (Clements et al. 2001; Angel-Vallejo et al. 2024). Concerning precipitation, the species prefers regions with moderate to high annual rainfall (e.g. between 500 to 1500 mm/ year; Broadfield and McHenry 2019), as adequate moisture availability during the growing season is crucial for its survival and growth. Despite its preference for moderate to high rainfall, U. europaeus is well-adapted to tolerate dry and drought conditions during the summer months. It can withstand periods of water scarcity due to its deep root system and water-conserving adaptations like spiny leaves and taproot (Christina et al. 2023).

In Tenerife, flowers and seeds of U. europaeus can be found throughout the year (although more abundant in January-February), and seed germination is strongly stimulated by fire, as occurred with the wildfire of 2007 on the north side of the island (Christina et al. 2023). In its non-native range, U. europaeus spread is fostered not just by fires, but also by the high species reproductive fitness, a long vegetative period, prolonged seed longevity and rapid growth and the absence of native competitor (Kariyawasam and Ratnayake 2019). The dispersion of U. europaeus alters soil and landscape dynamics in areas of major invasion, inhibiting the growth of agricultural and native species, creating shelter for pest species and reducing the richness of competing species at a site, all of which contribute to the economic and environmental degradation of the land (Altamirano et al. 2016; Udo et al. 2018). In addition, U. europaeus reduces soil fertility through the depletion of nutrients (Bateman and Vitousek 2018) or promotes vegetation flammability becoming a management fire control problem in these invaded areas (Atland and Limbada, 2019). Because of that, the invasion by U. europaeus has changed the native habitat on the island of Tenerife and is preventing the regeneration of native plant communities on abandoned fields (personal communication of J Arévalo Sierra and A Naranjo-Cigala).

Sampling design

The Biodiversity Database of the Canary Islands (BDCI; Gobierno de Canarias 2024) is the official taxonomic record for the archipelago, containing information on the list and known distribution of plants, fungi, animals, and other living organisms in the Canary Islands and their waters (https://www. biodiversidadcanarias.es/biota/). The BDCI records the species occurrences using a 500 m spatial resolution grid covering the entire Archipelago. According to the BDCI (accessed in 2019, before the fieldwork activities), U. europaeus had two main populations on Tenerife Island. The first is located near the Macizo de Anaga, northeast of the island, and covers approximately 4.25 km². The second one, located in the northwest part of the island, covers approximately 66.5 km² (Fig. 1).

Starting from these known locations, during January–March 2020 and 2021, we surveyed each grid cell where the BDCI reported a *U. europaeus* occurrence. Furthermore, we systematically examined the eight adjacent cells surrounding each grid cell with a confirmed occurrence. If the species

was detected in any of these neighbouring cells, the sampling scope was expanded to include additional neighbouring cells. Following the methodology adopted in several vegetation surveys conducted on the island (Panareda and Nuet 1981; Panareda 2000; Naranjo-Cigala et al. 2009; 2016; 2017; Arévalo et al. 2010), we recorded the relative abundance of the species (see the abundance class definition in Table SM1.1), as well as the dominant geomorphological characteristics (plateau, hill, bottom of ravines, lava flow, or badland - from Spanish malpaís -), and main human land uses, indicating whether the area was an abandoned field, bordering a trail, or terraced (Table SM1.2). The level of anthropisation (low, medium or high) was recorded following a semiguantitative scale described in Arévalo et al. (2005) to determine the level of anthropisation (Table SM1.2). Furthermore, accessibility information was documented, detailing whether the site was reachable via trails or roads and specifying the level of ease of access (<100 m from a trail or road), low difficulty (<500 m), or high difficulty (>500 m). Finally, the presence of other invasive species was noted, according to the chorological status adopted in the BDCI (Gobierno de Canarias 2024), except in several cases where the chorological status is uncertain (e.g. Pteridum aquilinum).

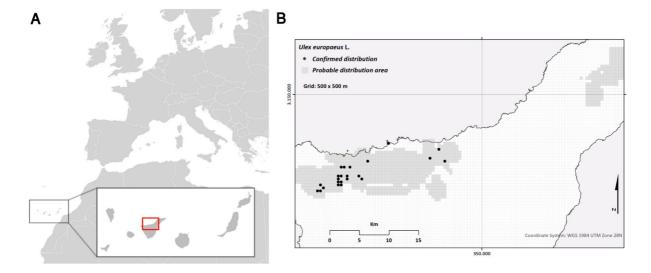


Fig. 1 a Location of the Canary Archipelago with respect to Europe and portion of Tenerife Island surveyed (in red); b Location of the populations of *Ulex europaeus* in Tenerife Island according to the BDCI (accessed in 2019, before the fieldwork)

Data analysis

This section provides a concise overview of the methodologies employed to address the diverse questions posed in the introduction. This includes outlining the specific approaches and techniques utilised to investigate the relationships of the species with anthropogenic features, assessing the role of the species within the vegetation community, and delving into itscurrent and future habitat range dynamics.

What are the main natural and human-related factors influencing the abundance of U. europaeus on Tenerife Island?

We used a Random Forest (RF) model to investigate how the different natural and anthropogenic factors present in the surveyed areas of Tenerife Island influence the species' abundance. Random Forest is a machine learning method widely used for classification and regression tasks (Breiman 2001; Liaw and Wiener 2002). It combines multiple decision trees, each trained on random subsets of the data and features (i.e., predictor variables) through a process called bootstrap aggregation, whose individual predictions are combined through a majority vote (classification) or averaging (regression). Random Forest has been widely applied in ecological studies (e.g., Evans, et al. 2010; Guisan et al. 2017; Rodríguez-Alarcón et al. 2024) and is known for its flexibility and robustness.

We investigated the effect of the natural and anthropogenic variables collected during the fieldwork (dominant geomorphological features, human land uses, road density and accessibility; n=23, Table SM1.2) on the categorised abundance of U. europaeus. We performed a variable selection procedure using the Boruta algorithm (Kursa and Rudnicki 2010) to build a parsimonious model including non-correlated variables. Boruta is a feature selection method used in machine learning to identify the most relevant variables for predictive modelling. It operates by comparing the importance of each predictor variable against randomised versions of itself, measuring its significance to random noise. Variables deemed significantly more important than their random counterparts are considered relevant and retained for further analysis, while those deemed less important are discarded. Finally, the hyperparameters of the RF model were tuned using a grid search in the parameter space and a tenfold cross-validation procedure with 3 repetitions using the R package 'caret' (Kuhn 2008). The observations were partitioned with 80% used for training the model and 20% for testing. The classification accuracy of the model was assessed on the test dataset using sensitivity and specificity metrics derived from a confusion matrix, which compares predicted and actual class labels (for more details about the data partitioning and hyperparameter tuning see SM2).

As with other machine learning algorithms, one of the notable drawbacks of RF is its perceived lack of explicability, often rendering it like a black box. Recent developments introduce explainable artificial intelligence (xAI), a set of methods designed to enhance the interpretability of machine learning predictions (Ryo et al. 2021; Pichler and Hartig 2023). In particular, we used the variable importance and Shapley's values (Lundberg and Lee 2017) to interpret the relative importance of the different variables contributing to the abundance of U. europaeus. Variable importance refers to the measure of the contribution of each predictive t variable (feature) in the predictive performance of the model. Random forest uses an ensemble of decision trees, and variable importance is determined by assessing how much each variable decreases the accuracy of the model when it is randomly permuted while keeping other variables constant. The greater the decrease in accuracy, the more important the variable is considered. Shapley's value is a concept from cooperative game theory that, in the machine learning context, assigns a fair and unique contribution value to each variable based on its marginal impact across all possible combinations of variables.

Are other invasive plant species associated with the abundance of U. europaeus?

We conducted a co-occurrence analysis to examine the associations between *U. europaeus* and other IAS observed in the field. This analysis aimed to determine whether strong co-occurrence patterns with *U. europaeus* indicate that these species share similar ecological features. Specifically, we calculated pairwise co-occurrence patterns from the community dataset using the R package 'cooccur' (Griffith et al. 2016). This algorithm uses the probabilistic model developed by Veech (2013) to evaluate if the observed co-occurrence patterns deviate from the one expected by chance. Positive values indicate a high probability that two taxa co-occur and vice versa. Co-occurrence values around 0 indicate random patterns. Co-occurrence matrices were calculated both considering all abundance classes together than for each class, independently.

What is the potential distribution of U. europaeus in Tenerife and the other islands of the Canary Archipelago under the current and future climatic scenarios?

Correlative species distribution models (SDMs) are valuable tools used in ecology and conservation biology to predict the spatial distribution of species across a specific geographic area (Elith and Leathwick 2009; Guisan and Thuiller 2005; Guisan et al. 2017; Da Re et al. 2023). These models integrate environmental variables, such as temperature, precipitation, and land cover, with known species occurrence or abundance observations to estimate the areas where a species is likely to occur. SDMs have been extensively used in biodiversity conservation and invasive species monitoring (e.g., Da Re et al. 2019; 2020; Romero et al. 2021), as they can provide estimates of the potential spread of invasive species in new environments, providing an effective tool to develop proactive strategies to prevent further spread and control their impact on native ecosystems.

We used an RF model to investigate how different abiotic variables contribute to the abundance of the species on Tenerife Island. We selected eight abiotic variables based on the known ecology of the species, namely BIO5: Maximum Temperature of Warmest Month, BIO6: Minimum Temperature of Coldest Month, BIO8: Mean Temperature of Wettest Quarter, BIO9: Mean Temperature of Driest Quarter, BIO13: Precipitation of Wettest Month, BIO14: Precipitation of Driest Month, BIO16: Precipitation of Wettest Quarter, BIO17: Precipitation of Driest Quarter (Table SM1.3), from the CanaryClim dataset. CanarvClim v1.0 (Patiño et al. 2023) is a climate dataset created by downscaling the global climate model of CHELSA v1.2 (Karger et al. 2017) to 100 m spatial resolution, ensuring a finer representation of the mesoclimate of the Archipelago. The dataset spans two time periods: the near-present (1979-2013) and the late-century (2071–2100), the latest including future climate scenarios based on various warming shared socio-economic pathways (SSPs) within the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (https://www.ipcc.ch/report/ar6/wg1/#TS).

Also in this case we performed a variable selection procedure using the Boruta algorithm, the data partitioning and the hyperparameter tuning using the same settings already described in section "What are the main natural and human-related factors influencing the abundance of *Ulex. europaeus* on Tenerife Island?". Likewise, the classification accuracy of the model was evaluated using a confusion matrix and calculating sensitivity and specificity metrics for each abundance class. We interpreted the relative importance of the different abiotic variables contributing to explaining the abundance of *U. europaeus* computing the variable importance and Shapley's values.

To project the potential dispersion of the species under different climatic scenarios, we extrapolated the model predictions, originally trained on Tenerife Island, to encompass the other islands within the archipelago under current and future climatic conditions. We used three different future scenarios characterised by varying levels of sustainability. SSP126 represents a high sustainability pathway with strong climate action and significant mitigation efforts, resulting in lower greenhouse gas emissions and a relatively modest increase in global temperatures. SSP370 reflects a medium sustainability pathway with some climate mitigation efforts but still relatively high emissions, leading to more pronounced temperature increases compared to SSP126. SSP585 denotes a low sustainability pathway and is considered the "business-as-usual" scenario, characterised by minimal climate action and high emissions, resulting in the most severe temperature increases among the scenarios.

We assessed the climatic dissimilarity of the study area in future scenarios compared to current conditions using the multivariate environmental similarity surfaces (MESS) index (Elith et al. 2010) to mitigate extrapolation concerns (see Chapt. 17 in Guisan et al. 2017). The MESS index gauges the similarity of environmental conditions at each pixel to those observed in the training data. A positive MESS value signifies that conditions at that pixel fall within the range of those observed in the training data, indicating reliable extrapolation. Conversely, a negative MESS value suggests that conditions at that pixel lie outside the range of the training data, potentially signifying unreliable extrapolation and advising caution in interpreting model predictions in those regions.

Results

Out of the total 8519 grid cells covering Tenerife Island, 1095 quadrats were examined and 301 showed the presence of *U. europaeus* with varying degrees of abundance/cover: Class0 (absence) with 794 observations, Class1 (1 to 10 specimens) with 50 observations, Class2 (10–49 specimens) with 45 observations, Class3 (50–99 specimens) with 49 observations, Class4 (100–199 specimens) with 40 observations and Class5 (>200 specimens) with 117 observations (Tab SM1.1).

Our survey allowed identify three main populations of the species in Tenerife Island: the fieldwork confirmed the presence of the species in the Macizo de Anaga (northeast part of the island), and better defined the two populations located in the northwest (Fig. 2). During the sampling, 45 additional plant-invasive species were recorded (Table SM3.1).

Natural and human-related factors influencing the abundance of *U. europaeus* on Tenerife Island

The variable selection performed with the Boruta algorithm discarded the percentage cover of flat areas as an informative variable. Following the hyperparameter tuning, the minimum node size was set equal to 9 and the mtry equal to 2, resulting in an overall model classification accuracy of 0.9297 (95% CI 0.9129, 0.9441; Table S3.4). Both the variable importance and the global mean Shapley values highlight the access to roads and different levels of anthropic pressure as the most important variables driving the abundance of *U. europaeus* on Tenerife (Fig. 3a, b); this pattern is also relevant across different abundance classes (Fig. 3c).

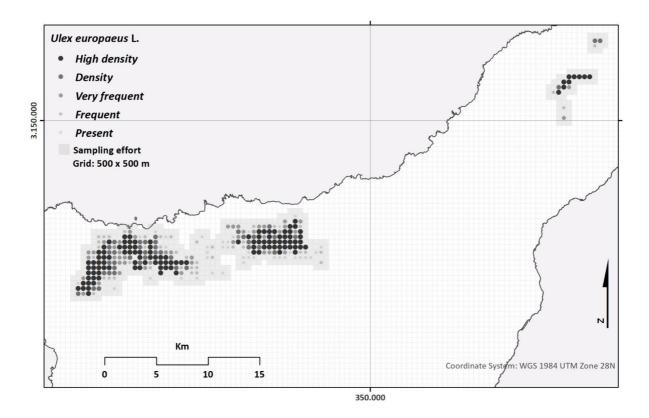


Fig. 2 Relative abundance of *Ulex europaeus* resulting from the fieldwork conducted in 2020–2021

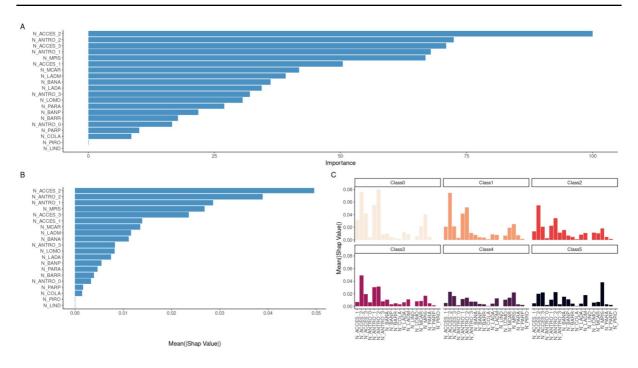


Fig. 3 Results of the Random Forest model assessing the natural and human-related factors influencing the abundance of *U. europaeus* on Tenerife Island: **a** Variable importance, **b** Global average Shapley value, **c** Shapley's values broken down for the

Other invasive plant species associated with the abundance of *U. europaeus* on Tenerife Island

Co-occurrence patterns were estimated in 16.3% of species pair combinations (the others were removed since expected co-occurrence was < 1). Of this, we detected higher levels of positive ecological associations, especially for classes 3 and 5 (Fig. 4; Table S3.2). Most of these associations occurred with Ageratina adenophora (Spreng.) R.M.King and H.Rob. (Asteraceae) (Aga), *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) (Pa), *Chasmanthe floribunda* (Salisb.) N.E.Br. (Iridaceae); and *Opuntia* sp. (Cactaceae) (Osp). Notably, when considering all classes pooled (Fig. 4f), all the associations with the other IAS in Tenerife Island were never different from random expectations.

Current and future distribution of *U. europaeus* in the Canary Islands

The Boruta algorithm, used for variable selection, retained all the selected abiotic variables. Subsequent

different abundance categories. Class1 (1 to 10 specimens); Class2 (10–49 specimens); Class3 (50–99 specimens); Class4 (100–199 specimens); and Class5 (> 200 specimens)

hyperparameter tuning established a minimum node size of 6 and a mtry value of 2, yielding an overall model classification accuracy of 0.68 (95% CI 0.61, 0.74; Table S3.4). Among these variables, those related to temperature, specifically BIO6, BIO5, and BIO8, emerged as the most influential in shaping *U. europaeus* abundance (Fig. 5a). Notably, BIO8 also showed the highest Shapley values (Fig. 5b), although the contribution of each abiotic variable varied across different abundance classes (Fig. 5c). In Tenerife, the model prediction indicates some new potential areas of establishment of the species on the windward side of the island.

The MESS index consistently identified areas of extrapolation across various climatic scenarios, predominantly occurring in the driest islands of the archipelago, such as Fuerteventura and Lanzarote, as well as in the drier regions of the other islands (Fig. S3.5). Regarding the predicted abundance class of *U. europaeus* across the Canary Islands, an East–West aridity gradient was observed, which remained consistent irrespective of the climatic scenario under consideration (Fig. 6a; Fig. S3.6–S3.7).

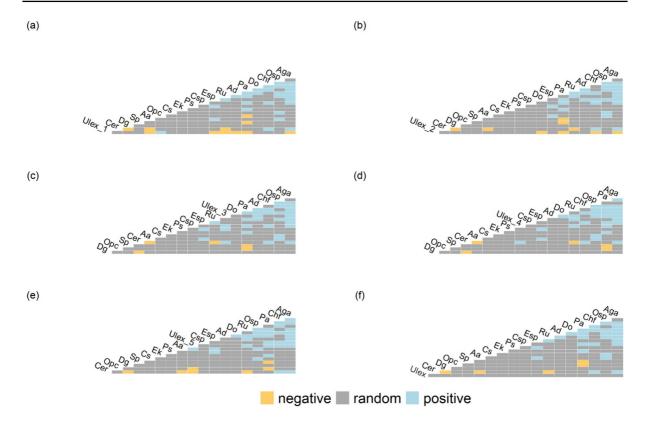


Fig. 4 Co-occurrence matrix of the invasive species in Tenerife Island (n = 47). Each panel display the co-occurrence matrix associated with a specific class of *U. europaeus* abundance **a** Class1, **b** Class2, **c** Class3, **d** Class4, **e** Class5, and using all *U. europaeus* abundances classes (**f**). Orange squares represent negative associations between species pairs, blue squares represent positive associations between species pairs, and grey squares represent random associations between species pairs. Class1 (1 to 10 specimens); Class2 (10–49 specimens); Class3 (50–99 specimens); Class4 (100–199 specimens); and Class5 (> 200 specimens). *Ageratina adenophora* (Asteraceae): Aga; *Agave americana* L. (Asparagaceae):

The easternmost and driest islands, Fuerteventura and Lanzarote, were deemed unsuitable for the species. Conversely, areas predicted to be more suitable to the presence and abundance of *U. europaeus* were situated on the windward sides of the other islands, characterised by cooler and more humid conditions. The proportion of grid cells occupied by the species, indicating the ratio of cells with predicted abundance class above or equal to one to the total number of grid cells, shows a decreasing trend for El Hierro, La Gomera, and Gran Canaria islands towards warmer climatic scenarios compared to the

Aa; Arundo donax L. (Poaceae): Ad; Centranthus ruber (L.) DC. (Caprifoliaceae): Cer; Chasmanthe floribunda: Chf; Cortaderia spp. (Poaceae): Csp; Cytisus scoparius (L.) Link (Fabaceae): Cs; Daphne gnidium L. (Thymelaeaceae): Dg; Delairea odorata Lem. (Asteraceae): Do; Eucalyptus ssp. (Myrtaceae): Esp; Erigeron karvinskianus DC. (Asteraceae): Ek; Opuntia sp.: Osp; Oxalis pes-caprae L. (Oxalidaceae): Opc; Pennisetum setaceum (Forssk.) Chiov. (also known as Cenchrus setaceus (Forssk.) Morrone): Ps; Pteridium aquilinum: Pa; Rubus ulmifolius Schott (Rosaceae): Ru; Sporobolus sp (Poaceae): Sp

current climatic conditions (Fig. 6b). Conversely, the trend is less pronounced for Tenerife and La Palma islands: on Tenerife, the proportion of occupied cells is anticipated to decline under SSP126 and SSP370 compared to current climatic conditions, with a subsequent rise under SSP585. Conversely, on La Palma, the proportion of occupied cells is projected to increase slightly under SSP126 but decrease under SSP370 and SSP585 scenarios. Notably, La Palma consistently exhibits the highest predicted proportion of occupied grid cells across all climatic scenarios.

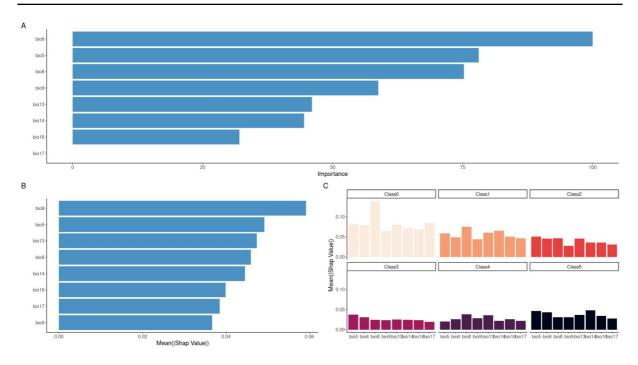
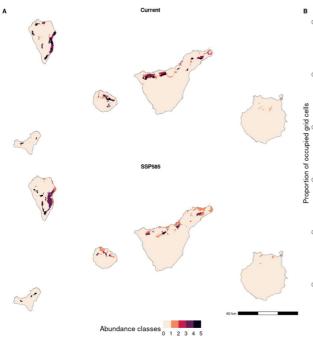


Fig. 5 Results of the Random Forest model assessing the environmental factors influencing the abundance of *U. europaeus* on Tenerife Island: **a** Variable importance, **b** Global average Shapley value, **c** Shapley values broken down for the



different abundance categories. Class1 (1 to 10 specimens); Class2 (10–49 specimens); Class3 (50–99 specimens); Class4 (100–199 specimens); and Class5 (> 200 specimens)

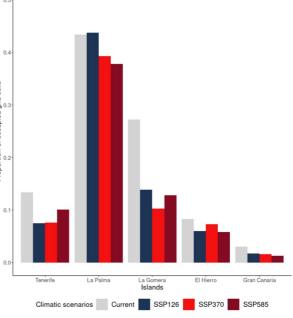


Fig. 6 a Predicted abundance of *Ulex europaeus* in the Canary Islands under current climate conditions and the SSP585 scenario. Currently, the species is only present on Tenerife Island. Lanzarote and Fuerteventura were not displayed because they

were unsuitable for the four climatic scenarios investigated; all the scenarios are available in Fig. SM3.6-3.7; **b** Proportion of occupied grid cells in each island across different climatic scenarios

Discussion

Previous surveys on other species such as Acacia farnesiana (L.) Willd. (Fabaceae)(also known as Vachellia farnesiana (L.) Wight & Arn.) (Naranjo-Cigala et al. 2016) and Nicotiana glauca Graham (Solanaceae) (Naranjo-Cigala et al. 2017) have provided valuable insights into their distribution and their impact on native communities in the Canary Islands. These studies, based on bibliographic references, herbarium information, fieldwork, and cartographic data, served as a foundation and support for designing the methodology of this study. The results of this study have updated the knowledge on the current distribution of U. europaeus on Tenerife Island (García-Gallo et al. 1989), confirming the presence of the species in the northeast part of the island and better estimating the extent of the two populations located in the northwest part of the island. These results are particularly relevant in light of establishing early detection strategies for this species in other places in Tenerife (and by extension the entire Canary Islands), within the early-warning control programs developed by local authorities (e.g. Red Canaria de Alerta Temprana de Especies Exóticas Invasoras, RedEXOS).

The two largest populations of *U. europaeus* in the northwest area of the island coincide with the locations reported for the first records of this species (Buch 1825). This could suggest a very ancient introduction of this species in the northwest of the island and could indicate different introduction events for the population located in the northeast, but molecular analyses are necessary to confirm this hypothesis, similar to that carried out by Hornoy et al. (2013).

Natural and anthropic drivers of *U. europaeus* abundance in Tenerife

The RF model used to investigate how the different natural and anthropogenic factors contribute to the abundance of *U. europaeus* in Tenerife Island suggested the significant influence of human-related variables, specifically anthropogenic pressure and access to roads. This aligns with previous research emphasising the substantial impact of human activities on native communities and invasive species distributions (Jones et al. 2016; McKinney 2006; Bacaro et al. 2015; Da Re et al. 2020). Anthropogenic pressure, including land development and urbanisation, has been shown to alter habitat suitability and facilitate the spread of invasive species (Ricotta et al. 2019; Simberloff 2009; Tordoni et al. 2021). Similarly, road networks serve as corridors for invasive species dispersal, facilitating their colonisation of new areas (Arévalo et al. 2005; 2010; McKinney 2008; Bacaro et al. 2015).

IAS co-occurrence patterns of *U. europaeus* depend on its abundance

The co-occurrence analysis showed that co-occurrence patterns between U. europaeus and other invasive species strongly depend on their level of abundance. We found significant positive associations, especially for lower levels of abundance which become predominantly positive for higher abundance class (Table S3.2). Interestingly, when all classes were pooled together we did not detect any significant association with the other IAS in Tenerife. This apparent discrepancy might be explained by extreme heterogeneity in the observations. Indeed, individual classes may be diluted due to the broader range of contexts and interactions included in the analysis or by the fact that U. europaeus may have strong associations with certain species due to specific environmental conditions or ecological interactions that are unique to those classes. When pooling classes, the specific conditions that favour these associations might be averaged out, leading to a lack of significant association across the entire dataset.

Notably, we observed an increase in positive associations with the abundance of U. europaeus, and this pattern is related to the average number of IAS in the cell (Fig. S3.3). This is in agreement with the so-called "invasion meltdown" hypothesis (Simberloff and Von Holle 1999; Daly et al. 2023), stating that already invaded areas may facilitate the proliferation of other IAS through change in the biotic and abiotic components in the community (Uboni et al. 2019; Calizza et al. 2021). For instance, it is known that Ageratina adenophora (Aga) invasion may affect soil nutrient dynamics, particularly phosphorus, potentially altering ecosystem functions and structure (Wu et al. 2020). Furthermore, this pattern suggests potential ecological similarities or shared environmental preferences among IAS species in Tenerife Island, which may contribute to their co-occurrence and proliferation within invaded ecosystems. Other studies have already shown that invasive species often exhibit overlapping habitat preferences and ecological traits, facilitating their coexistence and expansion (Catford et al. 2011; Simberloff et al. 2013). Given their frequent association with human-induced disturbances, such as abandoned fields, road margins, and areas subjected to soil removal or intensive trampling, these invasive species exhibit a propensity to thrive in anthropogenically altered environments (McKinney 2006; Pyšek et al. 2012; Bacaro et al. 2015).

U. europaeus thrives in cooler environments in the Canary Islands

Under the current climatic scenario, the outputs of the habitat suitability model indicate that the easternmost and driest islands, Fuerteventura and Lanzarote, are unsuitable for the species. This aligns with expectations, as this species typically thrives and is more abundant in cool and humid environments (Atlan and Udo 2019; Christina et al. 2020). On the other islands, the areas predicted to be more suitable for U. europaeus presence and abundance are predominantly located on the windward sides, which are known for their relatively cooler and more humid conditions (Chazarra et al. 2011). Notably, this spatial pattern remained consistent across different climatic scenarios, suggesting that the observed distribution pattern of U. europaeus is robust and not significantly influenced by future climate projections. However, the total proportion of cells occupied by the species does reduce under future and warmer scenarios and can be related to the decrease of germination and establishment capacity of its seeds, thereby restricting their dispersal process and hindering colonisation or persistence in new areas (Udo et al. 2017; Atlan and Udo 2019). These findings are in agreement with the results of other studies employing SDM approaches over larger spatial extents (Hernández-Lambraño et al. 2017; Christina et al. 2020; Roberts and Florentine 2021; Ángel-Vallejo et al. 2024). In a similar study, Da Re et al. (2020) examined the habitat suitability dynamics of Pennisetum setaceum, another invasive plant species in Tenerife, yielding similar findings. Despite utilising less sophisticated climate change scenarios, their results also indicated increased suitability under climate change for more humid and cooler areas of the island.

It is worth noting that the highest predicted abundance values were observed in Tenerife, which served as the training island for our model, whilst for the other islands the model predominantly predicts the average values of the observed abundance distribution. This discrepancy may reflect the higher certainty associated with predictions in Tenerife due to its status as the training dataset, while the predictions for other islands are more generalised. Furthermore, the apparent absence of significant invasion on the other islands, despite predicted suitability, raises questions about the factors influencing the dispersion of the species.

While SDMs have been effectively used to assess the potential spread of various invasive plant species-such as Pennisetum setaceum on Tenerife (Da Re et al. 2020), Cytisus scoparius in New Zealand, and Hakea sericea in South Africa (Wiser and Leduc 2011; Midgley et al. 2016)-it is important to recognize that these models rely on several key assumptions that can limit their accuracy and define their usage boundaries (Guisan et al. 2017). One of the main assumptions is that the species is in (or near) equilibrium with its environment, meaning it has already colonized all suitable locations while being absent from unsuitable ones (Hattab et al. 2017). This assumption was also made in our study. Additionally, we acknowledge that using only three climate scenarios and five models (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-LR, MRI-ESM2-0, UKESM1-0-LL) may have limited our ability to fully capture the range of possible future conditions and their impacts on the species. However, our decision to use CanaryClim was driven by data availability; it is the only dataset that offers high spatial resolution climate change scenarios specifically for the Canary Archipelago, making it the most suitable option for our research.

Management practices

Effective management approaches should prioritise mitigating anthropogenic impacts, such as reducing habitat fragmentation and implementing measures to minimise the spread of invasive species via road networks (Simberloff and Von Holle 1999). Integrating landscape-scale planning and habitat restoration efforts can further enhance the resilience of native ecosystems to invasive species by restoring and maintaining ecological connectivity (Hobbs et al. 2009). Currently, in the Canary Islands, there needs to be more specific programs aimed at rehabilitating abandoned agricultural areas, primarily due to challenges in identifying landowners and addressing variations in soil categories and management practices. Although some areas have witnessed successful restoration efforts, such as the recovery of approximately 20,000 hectares of *native forest* stands on the island since 1996 (Pardo et al. 2012), it is noteworthy that not all restored areas feature native species, with exotic species like *Eucalyptus camaldulensis*, *E. globulus* or *Pinus radiata* being employed, and in certain instances, samples from continental Spain were transported to the Canary Islands for restoration purposes (Marrero 2016).

Furthermore, U. europaeus is a fire-prone species that significantly modifies the frequency and intensity of fire across the landscape by increasing the amount of necromass and biomass, primarily dead branches and spines, thereby intensifying and promoting fire (Altamirano et al. 2016). Fires also facilitate the germination and dispersion of U. europaeus, and while high-intensity fires can harm the native plant community, U. europaeus is highly adapted to such conditions (Roberts and Florentine 2021). Cleaning areas after a fire has become another important factor favouring the dispersion and germination of U. europaeus. Therefore, postfire management efforts should focus on restoration and mechanical eradication of the species to prevent its dominance in the area, as observed in previous incidents. Recent management practice field experiments, combining chemical treatments, mechanical removal, and the plantation of native species, have shown improved results in restoring native plant communities (González-Montelongo et al., 2024).

Additionally, considering the recognised presence of the species along secondary roads and trails, the introduction of biosecurity hygiene practices, such as boot brushing, could be a low-impact management strategy that people can adopt to help prevent the introduction and dispersal of IAS, as already adopted in some areas of the United States of America and Australia (Gill et al. 2020; Dolman and Marion 2022; HDLNR 2022).

The results of our research contribute to a deeper understanding of the ecological dynamics of *U. europaeus* in isolated oceanic islands, offering valuable information on its potential dispersion patterns in response to climate change. These findings not only enhance our knowledge of the species but also provide essential support for conservation efforts by helping to formulate informed strategies tailored to the unique ecological challenges posed by *U. europaeus* in the Canary Islands.

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Data availability The data and the R scripts used to perform the analysis are available on request to the corresponding author.

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