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Characterisation and modelling of the native and invaded niche of castor bean (*Ricinus communis*): the Iberian Peninsula as a case study

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Abstract. *Ricinus communis* (Euphorbiaceae), commonly known as castor bean, is a species of great economic and cultural importance. Native to the northeast region of Africa, its earliest uses by humans date back to the Late Pleistocene. Castor bean

is currently distributed in temperate and tropical zones in both hemispheres and has become an invasive species in several areas of the world. However, there are still no detailed studies to confirm whether it exclusively occupies environments similar to its native range or whether it has expanded its climatic niche. The main objective of this study is to characterize and model the climatic ecological niche of castor bean in its native region (northeast Africa) and in an invaded area (Iberian Peninsula). We will determine the differences between the two niches to assess whether this species is expanding its niche and identify the potentially habitable regions for castor bean. To characterize and model the castor bean niche, we use occurrence data in both areas and 19 bioclimatic variables. Our results show that castor bean occupies areas with climates absent in its native range, indicating a wide ecological plasticity that could have facilitated its naturalization in the Iberian Peninsula and other areas worldwide.

Highlights.

- *Ricinus communis* shows very low climatic niche overlap between its native range and the Iberian Peninsula confirming a major climatic niche expansion.
- Its ability to tolerate a broad range of environmental conditions explains its strong invasive capacity.
- In the Iberian Peninsula, the castor bean occupies a wider range of biomes than in its native range, demonstrating its ability to colonize more diverse environments as an invasive species.
- The low overlap between the native and invaded predictive distribution models reinforces the conclusion that castor bean now thrives in climates that native populations seemingly cannot occupy.

- Our results and historical records indicate that castor bean has been established in the Iberian Peninsula for centuries, suggesting a long and stable naturalization process.

Keywords. Invasive species, niche conservatism, niche modelling, ecological plasticity, niche expansion, species distribution model, bioclimatic variables.

Introduction

The introduction of non-native species by humans has been primarily for economic and social purposes. The intensification of global trade, the alteration of ecosystems and the development of society have accelerated and escalated this process, often ending in biological invasion (Theoharides and Dukes 2007; Vilà et al. 2008). Introduced species are usually strong agricultural or ornamental varieties, with resistance to diseases, droughts, floods, or extreme temperatures (Theoharides and Dukes 2007; González 2012). The naturalisation and posterior invasion success of these species are mainly related to geographical origin, native range extension and dispersal ability (Theoharides and Dukes 2007; Sasidharan and Venkatesan 2019). Although two environments may be far apart geographically, their climatic conditions may be very similar (Godoy et al. 2008). Species could occupy new territories with similar climatic conditions to the native range, given the appropriate transport circumstances, and if they overcome existing biotic and abiotic filters to become established (Theoharides and Dukes 2007; Godoy et al. 2008). The conjunction of environmental conditions that characterise and allow populations to maintain themselves in space is known as the fundamental niche (Guisan et al. 2014). Some biological invasions are the result of the establishment of species in

regions that are geographically distant, but within their fundamental niche (Aravind et al. 2022). If the species maintains its own ecological requirements over time and space, there is niche conservatism (Broennimann et al. 2007), otherwise there is niche shift. Niche shift in a species is therefore defined as changes in its physical and environmental requirements over time and geographic space due to ecological and/or evolutionary changes (Broennimann et al. 2007; Pack et al. 2022). Both niche shift and niche conservatism may have important implications for understanding the effects of climate change, biological invasions and speciation (Broennimann et al. 2007).

Most invasive species tend to be niche-conserving (Petitpierre et al. 2012; Guisan et al. 2014; Aravind et al. 2022), which may increase the risk of invasion in regions with similar niches (Petitpierre et al. 2012). However, it is common to observe cases of species capable of occupying and proliferating in niches different from the native environments (Atwater et al. 2018), as for example the invasive plant species *Lantana camara* L. (Sharma et al. 2005; Guisan et al. 2014; Pack et al. 2022). On the other hand, it is also possible that in new environments, despite having climates similar to those occupied in native areas, some invasive species fail to become established. When this process occurs in an invaded area, it is called niche abandonment (Atwater et al. 2018). Finally, some invasive species may also occupy niches absent in their native areas; a process known as niche expansion (Atwater et al. 2018). Both niche abandonment and niche expansion should not be considered fundamental niche shifts, as they do not necessarily result from ecological and/or evolutionary processes (Atwater et al. 2018).

Ricinus communis, popularly known as castor bean, is a species listed as invasive in many areas of the world (e.g. Angola; Rejmánek et al. 2016; Reunion Island: Tassin et al. 2006). The origin of castor bean has been traced to northeast Africa, around the Ethiopian region (Seegeler 1983; Kumar et al. 2017; Naik 2018; Xu et al. 2021; Rojas-Sandoval and Acevedo 2022). This species is closely tied to human history, with evidence of its earliest known use dating back to the late Pleistocene (c. 24,000 years ago) (d'Errico et al. 2012). At Border Cave (South Africa), arrow poison applicators containing traces of ricinoleic and ricinelaidic acid as poisons for hunting purposes (d'Errico et al. 2012; Polito et al. 2019). Remains of ricin plants and oil have also been found inside sarcophagi, mainly of priests, around 4000 years old (Scarpa and Guerci 1982; Figueiral et al. 2021; Muraguri and Liu 2022). However, it is estimated that domestication of castor bean began 3200 years ago between East Africa and West Asia (Xu et al. 2021). It is first mentioned in the Ebers Papyrus, an Egyptian medical treatise that devotes an entire chapter to its medical applications (Polito et al. 2019). This text describes the use of its leaves, roots and seeds to relieve pain, stimulate hair growth, treat eczema, among many other purposes (Lobera 2020). During the domestication process, there was a selection of key agronomic traits for its use, such as the height of the plant, the diameter of the stem, the number of nodes or the weight and size of the seeds, thus beginning the process of separation from wild populations (Xu et al. 2021). It is estimated that approximately 2500 years ago, the domesticated form of castor bean reached Europe through trade, probably from Egypt (Xu et al. 2021). In Europe, castor bean was introduced and cultivated at least between the 14th and 16th centuries (Figueiral et al. 2021), the oldest herbarium sheet being the one preserved in the Herbarium ‘In Tibi’ (16th century; Stefanaki et al. 2019). Given its presence in Europe, its arrival in

the New World occurred with the arrival of European colonisers and traders during the 15th and 16th centuries (Xu et al. 2021; Muraguri and Liu 2022). However, there are exceptions such as its introduction to the island of Curaçao where it was introduced from Egypt and Palestine (Buurt 1999). Nowadays, it is widely exploited in India, China and the United States for industrial, cosmetic, medical and decorative purposes (Seegeler 1983; Kumar et al. 2017; Chouhan et al. 2021; Rojas-Sandoval and Acevedo 2022). Among its most notable uses are phytoremediation, given its ability to grow in soils contaminated by heavy metals; and bioenergy, as its oil can be used in the production of biodiesel, fertiliser, animal feed and as a lubricant for certain engines (Kumar et al. 2017; Naik 2018; Xu et al. 2021). Its close link with humans from ancient times to the present day has conditioned the global distribution of this species, which is cultivated on four continents. Despite its great economic attractiveness, the species poses a significant ecological risk due to its high invasive potential in many regions of the world (e.g., California, Taiwan, Zambia, Greece, Iran) (Gordon et al. 2011; Carmona-Galindo et al. 2013; Rojas-Sandoval and Acevedo 2022; Sohrabi et al. 2024). Its distribution is especially concentrated in tropical and subtropical regions (Seegeler 1983; Rojas-Sandoval and Acevedo 2022). Within these regions, it grows on well-drained substrates with wide pH ranges (from 4.5 to 8.3), being generally very adept at growing on any type of soil, except dense clay or swampy soils (Naik 2018). As an invader, it is frequently found on grasslands, croplands, disturbed lands and, especially, on roadsides (Rojas-Sandoval and Acevedo 2022). In the Iberian Peninsula, castor bean is cultivated as an ornamental, but it is naturalised in many areas, being very common in arid and semi-arid ecosystems, Mediterranean scrublands or even dunes (Rojas-Sandoval

and Acevedo 2022), in wastelands, nitrophilous grasslands and ruderal areas (Benedí 1997).

To date, there has been no detailed study of the climatic characteristics of the habitats invaded by castor bean. Understanding whether castor bean is limited to occupying environmental spaces similar to its native environment, or whether it is expanding its niche, is crucial for understanding, predicting and managing the spread of this species. Thus, the aim of this paper is to characterise the native (northeast Africa) and invaded (Iberian Peninsula) climate space of *R. communis* in order to determine whether there is niche overlap between the two areas and to identify regions of global invasive potential.

Methods

Obtaining species occurrence

To compare the native area of castor bean with the invaded area in the Iberian Peninsula, we used occurrences obtained through the Global Biodiversity Information Facility (GBIF) (GBIF.org 2020; GBIF.org 2023a, 2023b). The search was limited to human observations and herbarium specimens with coordinates. The inclusion of human observations is justified because *R. communis* is the only species in its genus (monotypic), it has a unique morphology, and is well known to the general public. For these reasons, misidentifications are highly unlikely. The range of occurrence records downloaded for the Iberian Peninsula and northeast Africa is 1849 to 2023 and 1932 to 2023, respectively. In addition, globally occurrences available from 1816 to 2020 were downloaded with these same criteria, for the calculation of the modelling success rate.

For the delimitation of occurrences in the native area, all countries within northeast Africa were chosen: Djibouti, Kenya, Somalia, Somaliland, Ethiopia and Eritrea. Occurrences for the Iberian Peninsula exclude the Atlantic islands of both Spain and Portugal. To clean worldwide data, all occurrences from areas reaching values below 4°C (Seegeler 1983; Falasca et al. 2012) were excluded, using Worldclim's BIO6 (Coldest Month Minimum Temperature) (Fick and Hijmans 2017). These occurrences were excluded because castor bean does not tolerate winter frosts, and is currently cultivated in areas where the temperature drops below 4°C. After the data cleaning process, 6848 occurrences were obtained for the Iberian Peninsula, 1360 for northeast Africa and 23217 worldwide. Fig. 1 shows the distribution of these occurrences in the Iberian Peninsula and the native range of the species (northeast Africa). Distribution maps were obtained using the R packages maptools, ggplot2, ggspatial and rnaturalearthdata in R version 4.4.0 (Wickham 2016; Bivand et al. 2023; Dunnington 2023; R Core Team 2024; South et al. 2024).

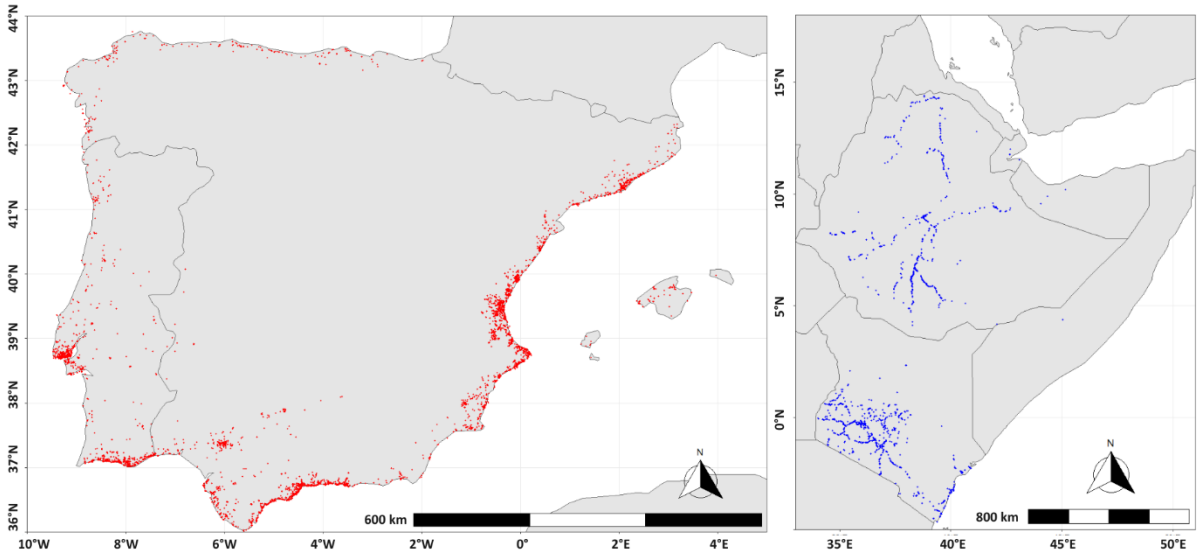

Figure 1. Distribution map of occurrences of *Ricinus communis* in the Iberian Peninsula (n = 6848) (left) and northeast Africa (n = 1360) (right) used in the characterisation and modelling analyses.

Obtaining environmental variables

To perform the characterisation and niche modelling analyses, we used the 19 environmental variables available in the Worldclim platform (Fick and Hijmans 2017). These data were obtained from R, using the getData function of the raster package (Hijmans 2023), with a resolution of 2.5 arcmin. Castor bean occurrences were used to extract their respective bioclimatic values with the sp and raster packages (Pebesma and Bivand 2005; Hijmans 2023). Study areas were delimited using the package maptools and the bioclimatic values of these areas were obtained with the raster package, which allows the transformation of the delimited climatic information into a dataframe.

Niche characterisation analysis

The castor bean niche characterisation was performed using occurrence records from both the native and invaded ranges, along with the 19 bioclimatic variables, through the ecospat package (Di Cola et al. 2017; Broennimann et al. 2023). First, a Principal Component Analysis (PCA) was performed using the dudi.pca function of the Ade4 package (Dray and Dufour 2007), based on climate data associated with occurrence records from the native and invaded regions. This analysis synthesises the matrix of bioclimatic variables into a reduced set of uncorrelated linear combinations (components), maximising the information retained in each (Abdi and Williams 2010; Broennimann et al. 2012). Within the ecospat package, the dudi.pca function provides a two-dimensional synthesis of bioclimatic variability across the study areas (Dray and Dufour 2007). The resulting components were used to represent the native and invaded niches (Fig. 2), applying the functions

ecospat.grid.clim.dyn and ecospat.plot.niche.dyn. To quantify niche overlap and dynamics, the functions ecospat.niche.overlap and ecospat.niche.dyn.index were employed, respectively. Niche dynamics were assessed through indices of expansion, stability and unfilling, which respectively represent: (i) the climatic space occupied in the invaded range but absent in the native niche (expansion); (ii) the shared climatic space between native and invaded occurrences (stability); and (iii) the climatic space present in the native range but not occupied in the invaded range (lack of occurrences, unfilling) (Guisan et al. 2014).

The degree of niche overlap was quantified using Schoener's D index, where a value of 0 indicates no niche overlap, while a value of 1 denotes complete niche identity (Warren et al. 2008). For the geographic projection of occurrence densities (Fig. 2C), the ecospat.grid.clim.dyn function was used in combination with the wrld_simpl map from the maptools package. Niche equivalency and similarity analyses were assessed using the functions ecospat.niche.equivalency.test and ecospat.niche.similarity.test, respectively. The niche equivalency test evaluates whether the observed niche overlap persists when occurrences from the native and invaded ranges are randomly reassigned (Warren et al. 2008; Broennimann et al. 2012; Di Cola et al. 2017). In contrast, the similarity test compares the observed overlap with that between the native niche and a randomly generated niche within the invaded range (Warren et al. 2008; Broennimann et al. 2012; Di Cola et al. 2017). To test for niche conservatism, the argument *higher* was specified in both analyses. Each test was repeated 100 times to ensure robust statistical inference and increase confidence in the acceptance or rejection of the null hypotheses.

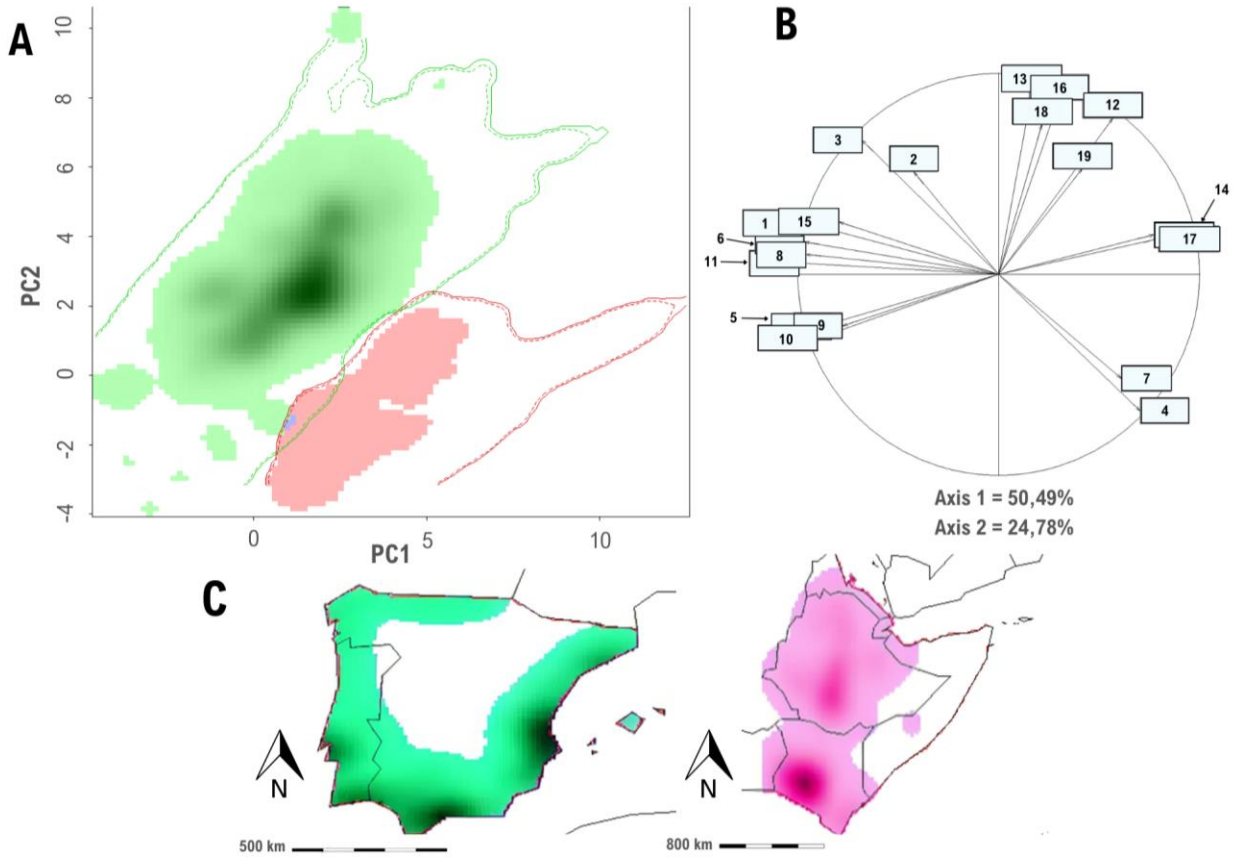

Figure 2. A, PCA of niche dynamics of *Ricinus communis* in the native range (pink area) versus the invaded range (green area), where the blue zone represents niche overlap and darker shades indicate occurrence density. **B,** Correlation circle showing the contribution of environmental variables (numbers indicate the BIO variable number as indicated in Table S1) to the first two principal axes (PC1 = 50.49%, PC2 = 24.78%). **C,** Projection of climatic space onto geographic space for the invaded area (green, left) and native area (pink, right).

Estimation of the probability of presence of Ricinus

To identify areas with a high probability of *Ricinus* presence that have not yet been invaded, niche models were developed using MaxEnt software version 3.4.4 (Phillips et al. 2024). Based on bioclimatic data, MaxEnt contrasts the environmental conditions of known occurrences with those of the broader study area, generating a predictive model to estimate potential distribution across other regions (Phillips and Dudík 2008; Broennimann et al. 2012). MaxEnt was chosen over other modeling

approaches due to its suitability for presence-only data and bioclimatic variables. Additionally, its deterministic nature ensures consistent results across runs, and it offers high computational efficiency (Guillera-Arroita et al. 2021). MaxEnt does not requires absent data, only the presence records used in the niche characterization analysis described above were included. Environmental layers were sourced from Worldclim (Fick and Hijmans 2017).

To reduce multicollinearity among environmental variables, we calculated the variance inflation factor (VIF) using Pearson correlations via the vif function from the usdm package in R (Naimi et al. 2014). Variables with VIF values greater than 3.9 were excluded from the analysis. The remaining environmental variables were used to build the MaxEnt models.

For the predictive projection, the entire land surface, excluding Antarctica, was selected as study area. The output format was set to C-log-log, a link function that translates raw values into interpretable probability of presence, and the output file type was specified as .bil to generate a raster layers compatible with QGIS v3.36.1 (QGIS Association 2024). Model parameters included a maximum of 500 iterations, the crossvalidate option for the replicated runs, and 10,000 background points. A random test percentage of 25% was applied, with the remaining 75% used for model training. To assess variable importance, the Jackknife test was performed, considering variables with a contribution greater than 15% as significant to the model. Model performance was evaluated using the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) curve, which plots sensitivity (true positive rate) on the *y* axis against 1-specificity (false positive rate) on the *x* axis (Phillips et al. 2006). The AUC measures the model's ability to distinguish between

suitable and unsuitable areas by comparing predicted suitability values for actual occurrences versus random locations (Phillips et al. 2006).

The global potential distribution map generated with occurrence data from the Iberian Peninsula (Fig. 2A) revealed low-probability regions where temperatures drop below 4ºC, conditions incompatible with *Ricinus* survival (Seegeler 1983; Falasca et al. 2012). To address this issue, the raster-type maps generated by MaxEnt were exported to QGIS (QGIS Association 2024). Within the software, two steps were applied: (i) we excluded areas with a predicted probability of occurrence below 50% were excluded; and (ii) we clipped the raster layer using BIO6 as a mask to filter unsuitable temperature zones. This procedure was applied to both native and invaded niche projections. To analyze the distribution by biogeographic region, the resulting probability maps were intersected with regional layers from the UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), based on Olson et al. (2001). Area extent calculations were performed in QGIS using the field calculator, applying the formula $area divided by 10,000 to convert square meters to hectares. These calculations were based on the WGS84 ellipsoid settings, yielding ellipsoidal surface area (QGIS Association 2024). Finally, all known global occurrences of *Ricinus* were compiled to evaluate model accuracy. Accuracy was calculated as the percentage of global occurrences (n = 23,217) falling within the predicted distribution polygons. Lastly, the spatial intersection between the native and the invaded niche models was determined using the “cut” function to assess overlap.

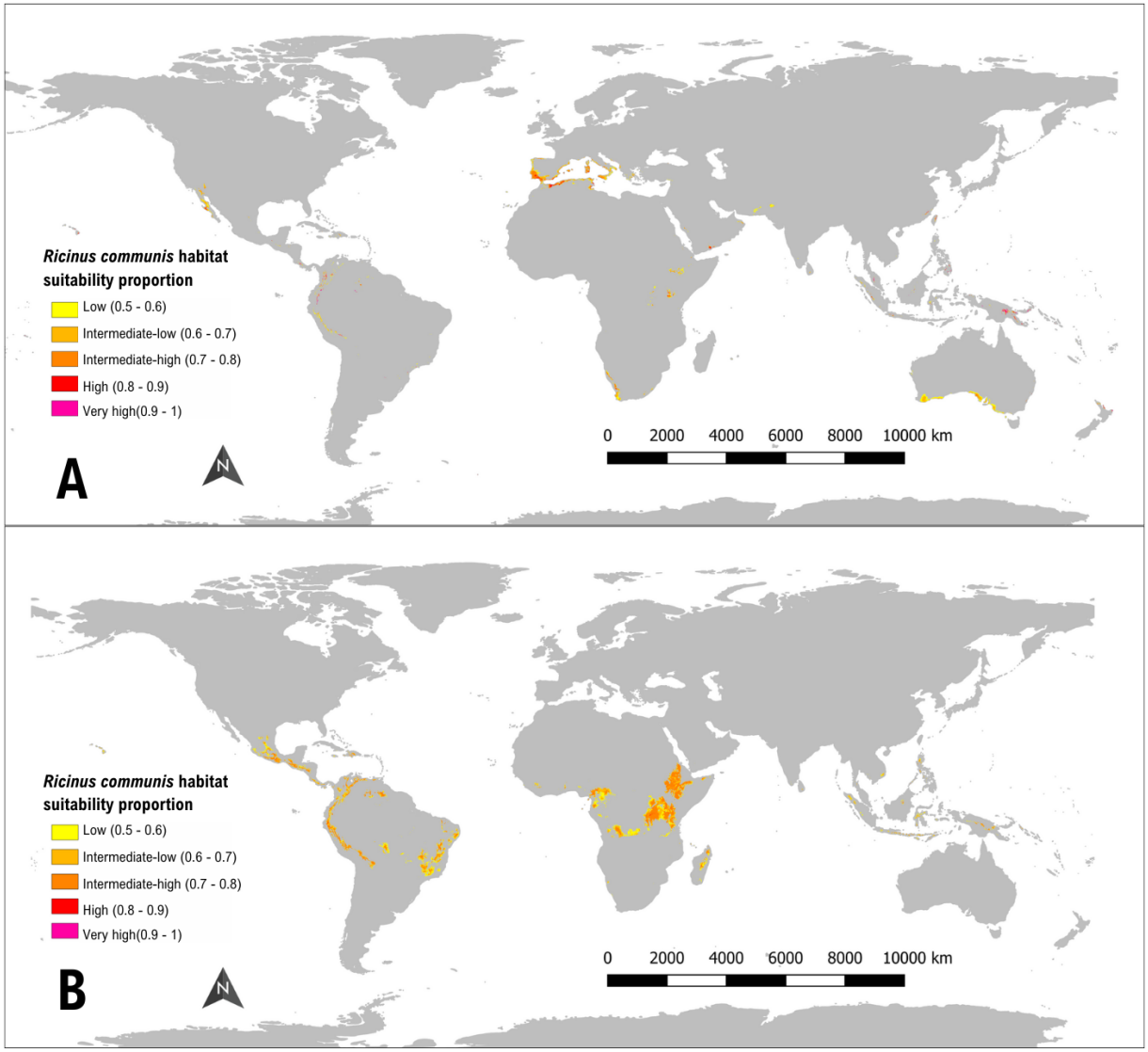

Figure 3. Predictive global distribution model of *Ricinus communis* based on occurrence records from: **A,** the Iberian Peninsula; and **B,** northeast Africa. Areas with high presence probability are shown in the high to very high probability range (0.8 to 1).

Estimation of environmental ranges

To estimate the ranges of the bioclimatic variables, the minimum, maximum, and mean values were calculated using R's default functions, while the mode was obtained using the mlv function from the modeest package (Poncet 2019). The graphical representation of these environmental ranges (Fig. 4) was generated using

the geom_boxplot function from the ggplot2 package (Wickham 2016), and the plots were arranged using the patchwork package (Pedersen 2024). To assess differences among the types of environmental ranges, an analysis of variance (ANOVA) was performed (Fig. 4).

Quantification of presence in biomes

To identify the biomes in which *R. communis* potentially occurs (Tables 2 and 3), vector layers from Olson et al. (2001) were used. In QGIS, biomes were assigned to both the modelled distribution areas and to regions with high occurrence probabilities (greater than 0.8). The area occupied by each biome was estimated, and the number of occurrences present within the modelled regions was calculated using the point-in-polygon counting function. The hit rate for each biome was defined as the ratio between the number of occurrences within the predicted area and biome, and the total number of occurrences recorded in that biome. Subsequently, the area occupied by each biome was then calculated, and the percentage of overlap was estimated as the area of intersection between each biome and the predicted distribution, divided by the sum of the occupied area of that biome in both models, expressed as a percentage (Tables 2 and 3).

Results

Distribution description

In northeast Africa, most of the available castor bean occurrences coincided with roadsides, showing a reticulate pattern of distribution (Fig. 1). Kenya and Ethiopia had the highest proportion of occurrences within the region. Djibouti had three

occurrences, as did Somaliland. Within Somalia only a single occurrence was found, while no records were found in Eritrea. The distribution of *R. communis* on the Iberian Peninsula (Fig. 1) reflected the specie's preference for coastal environments. Its presence was observed in the interior of the Iberian Peninsula through the Guadalquivir valley and around large cities such as Seville, Valencia, Lisbon and Barcelona.

Native and invaded niche characterisation

The graphical representation of the studied niches revealed minimal overlap (Schoener's D = 0.00165), represented by the blue area in Fig. 2A. The indices for expansion, stability and unfilling were 0.983, 0.0174 and 0, respectively. The *p-values* for equivalence and similarity analysis were 1 and 0.0396, respectively.

Quality of predictive models, choice and analysis of the contribution of variables

The variables with the lowest correlation (Tables 2 and 3) resulting from the VIF analysis were chosen for the predictive models. The variables that coincided in both environments after the selection of the analysis were BIO4 (seasonality of temperature), BIO8 (average temperature of the wettest quarter) and BIO14 (precipitation of the driest month). The predictive models for the native and invaded environment obtained high levels of performance, showing AUC values of 0.966 and 0.951, respectively.

Regarding the percentage contribution, for the Iberian Peninsula data, the environmental variables that contributed most to the model were BIO8, BIO15 (seasonality of precipitation) and BIO18 (precipitation in the warmest quarter), with values of 29.9%, 49.3% and 17.1%, respectively. Concerning the jackknife test,

BIO8 showed the greatest gain when used in isolation, being the environmental variable with the most useful information by itself and not present in the rest, in agreement with what was observed in the VIF analysis (Table 1). For northeast Africa, the environmental variables with the highest mean contributions were BIO3 (isothermality), BIO8 and BIO14, with values of 36.4%, 7.5% and 56.3%, respectively. BIO14 was the variable that most influenced the potential distribution. For the jackknife test, BIO3 proved to be the variable with the most useful information on its own with respect to the rest, which is in agreement with what was observed in the VIF analysis (Table 1). BIO8 was selected as a contributor as it had a high contribution value in the previous modelling and is therefore very useful for comparing the two models.

The ranges of the most contributing environmental variables (Fig. 4) were as follows. For northeast Africa, areas ranged from 37 to 88% isothermality (BIO3), with the mode at 84% and the mean at 77.5%; for the precipitation of the driest month (BIO14), the range was between 0 and 62 mm of rainfall, with a mean of 7.82 mm and mode of 1 mm; and for the mean temperature of the rainiest month (BIO8), the range was between 12.8°C and 33°C, with a mean of 19.6°C and a mode of 20.1°C. For the Iberian Peninsula, the coefficient of variation of rainfall seasonality (BIO15) ranged from 23% to 78%, with the mean at 55.5% and the mode at 64%; BIO8 ranged from 7.9°C to 20.5°C, with the mean at 14.5°C and the mode at 13.1°C; and BIO18 ranged from 15 to 255 mm, with the mean at 59.7 mm and the mode at 18 mm.

Table 1. Selected set of environmental variables along with their variance inflation factor (VIF) values for the Iberian Peninsula and northeast Africa of *Ricinus communis*. The correspondence to the variable BIO is indicated in Table S1.

Code	**Environmental variables**	**VIF values**	
		Iberian Peninsula	northeast Africa
BIO3	Isothermality (BIO2/BIO7) (×100)	-	1.07
BIO4	Temperature Seasonality (standard deviation ×100)	2.76	1.72
BIO7	Temperature Annual Range (BIO5-BIO6)	3.37	-
BIO8	Mean Temperature of Wettest Quarter	2.17	1.41
BIO12	Annual Precipitation	-	1.67
BIO14	Precipitation of Driest Month	2.43	1.51
BIO15	Precipitation Seasonality (Coefficient of Variation)	2.56	-
BIO18	Precipitation of Warmest Quarter	3.93	-

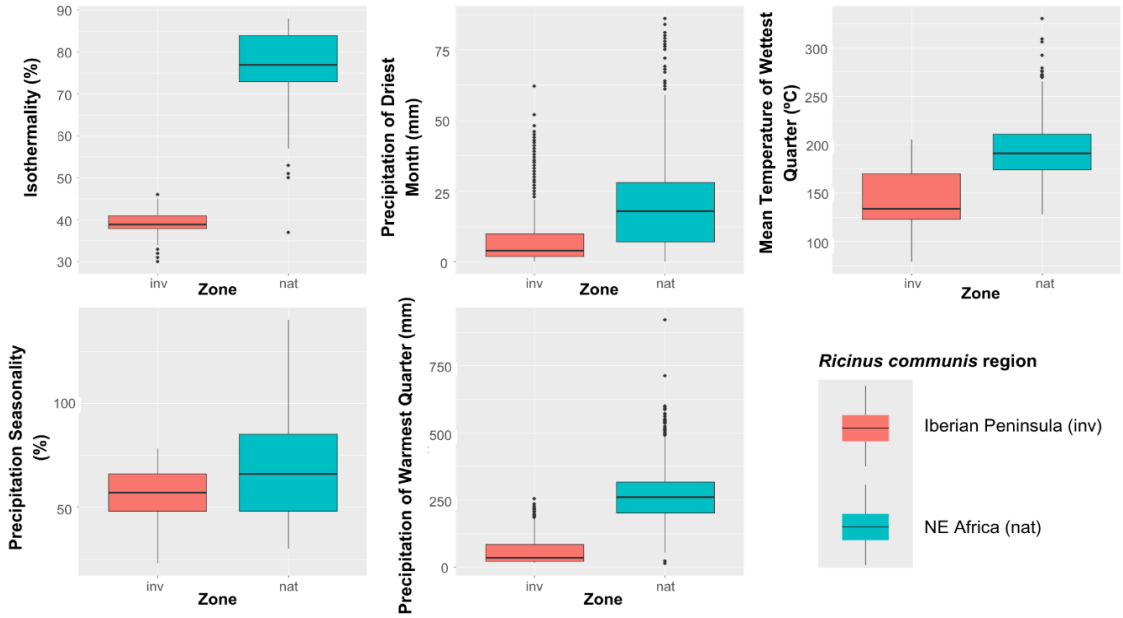

Figure 4. Ranges of the most influential bioclimatic variables in the predictive models for *Ricinus communis*. All inter-zone differences were statistically significant ($p < 0.001$).

Presence probability distribution with a modelling of Iberian Peninsula

The predictive map based on the data from the Iberian Peninsula (Fig. 3A) showed the following patterns: (i) The potential niche was concentrated in the Palaearctic region, occupying 33. 8 M ha, mainly in the western Mediterranean, highlighting small areas with a very high probability of occurrence in the Rif and the Adriatic Sea coast; (ii) in Australasia, an occupied area of 20 M ha highlighted regions of higher probability in New Guinea and northern New Zealand and an extensive region in southern Australia; (iii) in the Afrotropics, a region of 15 M ha included a small area in Kenya with a 90-100% probability; (iv) in the Neotropics, a total area of 11 M ha was recorded, associated to major mountain systems such as the Andes; (v) the Nearctic presented a region of 5.7 M ha, in the area around Baja California (Mexico) and California-Arizona (USA); (vi) the Indo-Malayan region

agglutinated 4.5 M ha, with the southern Philippines, Taiwan and peninsular Malaysia being the most important areas; (vii) finally, in the Oceanic bioregion, an area of 281,978 ha was recovered, with the Hawaiian archipelago constituting the largest part of the area.

Presence probability distribution with a modelling of northeast Africa

The following patterns resulted from the predictive model generated from the occurrences in northeast Africa: (i) the Afrotropics included the largest area of the model with 196.7 M ha, showing a mainly tropical pattern; (ii) the Neotropics covered a surface area of 72.8 M ha, with a distribution pattern mostly associated to the major neotropical mountain systems from Mexico to southern South America, as well as areas within the Brazilian Cerrado, the Caatinga and the interior forests of the state of Bahia; (iii) the Nearctic region described an area of 4.4 M ha; (iv) the Indo-Malayan region covered an area of 6.6 M ha; (v) Australasia had an area of 7 M ha; (vi) and finally, the Oceanic region had an area of 281,978 ha, predominantly in the Hawaiian archipelago.

Quantification of occupied biomes

From the quantification of the coincidences with the predicted surfaces and the identification of the biomes in the high probability areas (Tables 2 and 3), we obtained the following results: (i) in the modelling of the Iberian Peninsula, the total area occupied was 89.6 M ha and the biomes covering the largest area were Mediterranean forest and scrub, rainforest and xerophytic scrub; (ii) for the northeast Africa modelling, the total area covered was 346 M ha, with the main biomes being rainforest, tropical and subtropical grasslands, savannahs and shrublands, montane grasslands and shrublands, and subtropical coniferous forest.

Regarding the accuracy percentage (Fig. 5 and Tables 2 and 3): (i) the modeling of the Iberian Peninsula predicted a higher proportion of occurrences for the Mediterranean forest and shrubland biomes, mountain grasslands and shrublands, and temperate broadleaf and mixed forests (Table 2); (ii) the subtropical coniferous forest biomes, mountain grasslands and shrublands, tropical and subtropical grasslands, savannas and shrublands, and rainforest stood out as the biomes where the accuracy percentage was higher in the modeling of northeast Africa (Table 3); (iii) the accuracy percentage for the entire predictive area of the Iberian Peninsula was 18.9%, while for northeast Africa it was 13.6%. Regarding the intersection between both modelings (Table 4), the total occupied area covered 15.9 M ha.

Table 2. List of biomes and predicted occurrences (n = 4385) within high-probability zones resulting from the Iberian Peninsula occurrence modeling of *Ricinus communis*.

Biomes	Number of occurrences	Area occupied (M ha)	Accuracy rate (%)	Area occupied by high-probability zones (M ha)
Mangroves	0	0.0525	0	>0.01
Tropical and subtropical moist broadleaf forests	223	21	5.76	4.96
Montane grasslands and shrublands	22	4.2	14.4	0.331
Tropical and subtropical dry broadleaf forests	3	0.291	0.159	0.0235
Tropical and Subtropical Grasslands, Savannas, and Shrublands	43	1.37	1.53	0.0735
Tropical and subtropical coniferous forests	8	0.471	1.25	0.0178
Deserts and xeric shrublands	21	13.3	1.42	0.8
Temperate broadleaf and mixed forests	227	2.41	14.4	0.215
Temperate coniferous forest	14	0.503	3.28	0.018
Mediterranean forests, woodlands, and scrub	3820	45.6	42.4	2.25
Flooded grasslands and savannas	0	0.0541	0	0
Temperate grasslands, savannas, and shrublands	4	0.21	0.547	0
Tundra	0	>0.01	0	>0.01

Table 3. List of biomes and predicted occurrences (n = 3157) within high-probability zones resulting from the northeast Africa occurrence modeling of *Ricinus communis*.

Biomes	Number of occurrences	Area occupied (M ha)	Accuracy rate (%)	Area occupied by high-probability zones (M ha)
Tropical and subtropical dry broadleaf forests	274	12.6	14.5	0.0271
Tropical and subtropical moist broadleaf forests	1120	138	28.9	0.421
Tropical and subtropical coniferous forests	352	16.8	55.3	0
Deserts and xeric shrublands	212	17.6	14.3	0
Tropical and Subtropical Grasslands, Savannas, and Shrublands	937	126	33.4	0.165
Montane grasslands and shrublands	261	27.5	51.3	0.0143
Flooded grasslands and savannas	0	0.0346	0	0
Lakes	1	6.52	20	0

Table 4. List of biomes within the intersection areas of both models of *Ricinus communis* niche.

Biomes	**Area occupied (M ha)**	**Intersection percentage (%)**
Tropical and subtropical moist broadleaf forests	10.7	6.72
Montane grasslands and shrublands	3.07	9.66
Tropical and subtropical dry broadleaf forests	0.242	1.87
Tropical and Subtropical Grasslands, Savannas, and Shrublands	1.3	1.02
Tropical and subtropical coniferous forests	0.407	2.35
Deserts and xeric shrublands	0.15	0.486

Discussion

This is the first study to demonstrate that castor bean has expanded its climatic niche in an invaded area. Our results reveal a low overlap of the castor bean's climatic niche between the native area and the Iberian Peninsula (Schoener's D = 0.165%), with the niches being neither equivalent nor similar. The ability of castor bean to thrive in new environments (absent in its native area) suggests that it possesses traits responsible for a broad climatic tolerance. This facilitates its establishment in new settings in different biomes worldwide. The climatic plasticity of castor bean, combined with other characteristics such as rapid seed generation in its life cycle, mixed mating system and the presence of a nutrient-rich endosperm that supports germination and early developmental stages, supports a high invasive potential (Martins et al. 2011; Goyal et al. 2014; Muraguri and Liu 2022).

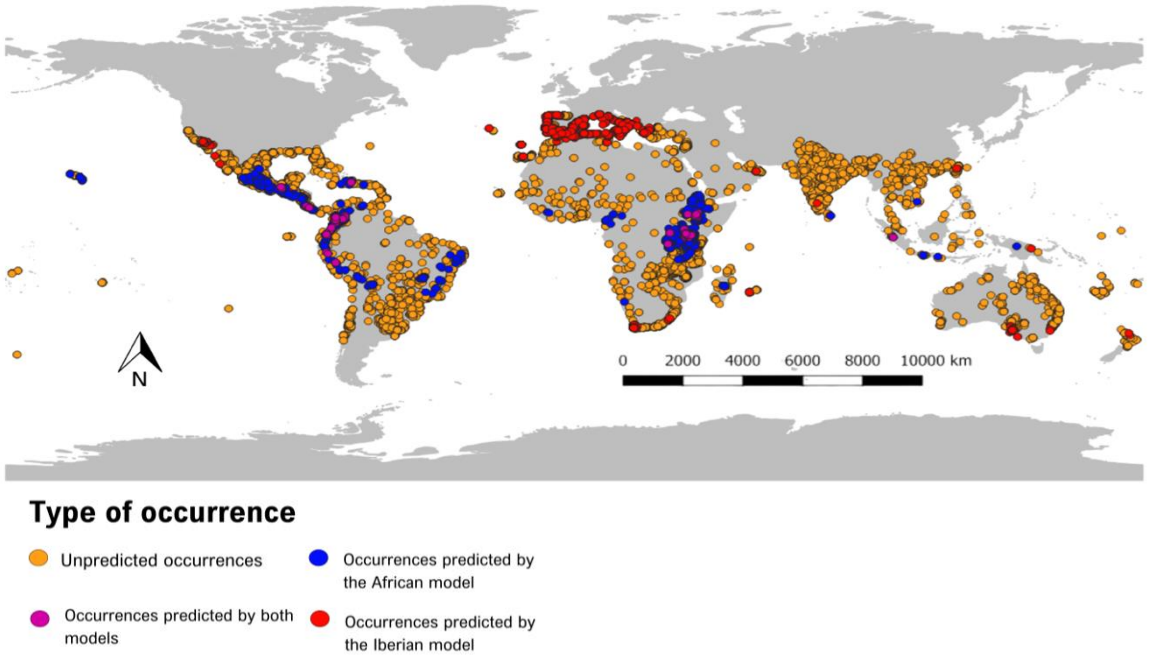

Figure 5. Map of actual recorded occurrence types of *Ricinus communis* (n = 23217) (GBIF.org 2020) corresponding to those described in Tables 2, 3, and 4.

Within the Iberian Peninsula, castor bean appears in environments with the mildest climates, persisting in areas with little to no winter frost, as it does not survive temperatures below 4ºC (Seegeler 1983; Falasca et al. 2012). In northeast Africa, it grows in tropical, subtropical, and semi-arid environments under mild conditions (Seegeler 1983; Rojas-Sandoval and Acevedo 2022). The niche stability between both regions, corresponding to 1.74%, represents the proportion of the niche shared by both environments where castor bean occurs (Guisan et al. 2014). Therefore, castor bean has expanded its niche, compared to the native area, after its introduction into the Iberian Peninsula, possibly due to favorable biotic and abiotic interactions in the region (Atwater et al. 2018). Despite the low value of stability, a few populations maintain similar climatic conditions in both niches.

The results of the niche characterization in the native and invaded areas indicate an extraordinary niche expansion with 98.3% of occurrences found in environments that are nonexistent in the native area. At the same time, the niche unfilling index is 0, indicating that all niches in the Iberian Peninsula with climatic conditions similar to those in the native area have been occupied by castor bean. Low unfilling values indicate old introductions (Guisan et al. 2014; Atwater et al. 2018), suggesting a long history of establishment of castor bean in the Iberian Peninsula. The low unfilling index could also indicate a long-term naturalization process in this area. One of the oldest pieces of evidence of castor bean naturalization in the Iberian Peninsula comes from a specimen collected by Cavanilles 231 years ago in Sagunto (Valencia), deposited in the herbarium MA of the Real Jardín Botánico (RJB), in

Madrid. In Cavanilles' field diary, kept in the historical archives of the RJB, he noted that the plant was growing naturally in the area.

Castor bean is a predominantly tropical species, highly sensitive to low temperatures and winter frosts. In northeast Africa, the predictive distribution model identified isothermality (BIO3) and precipitation of the driest month (BIO14) as the most influential environmental variables. Isothermality measures the ratio between daily temperature variation and annual temperature range (O'Donnell and Ignizio 2012). A value of 100% implies that daily and annual temperature range are equal, while lower values reflect greater seasonal variation relative to daily changes (O'Donnell and Ignizio 2012). In its native range, castor bean typically occurs in areas with isothermality around 77.5% (Fig. 4), consistent with its preference for stable tropical climates. This supports the idea that the species avoids environments with high temperature variation, thriving instead under relatively stable environmental conditions. The second most important variable in the model corresponds to precipitation during the driest month (BIO14), with values around 7.82 mm (Fig. 4). This suggests that drought periods play a key role in shaping the distribution of *R. communis* as the species can tolerate low precipitation during the driest part of the year. A previous niche modeling study by Xu et al. (2021), based on only 82 global occurrences, identified mean annual temperature (BIO1) and annual precipitation (BIO12) as the most relevant predictors. In contrast, the present study significantly expands the dataset, incorporating 1360 occurrences from the native range and 6848 from the invaded range, although it focuses on modeling only two specific regions.

In the predictive model for the Iberian Peninsula, the most influential environmental variables were BIO15 (precipitation seasonality), BIO8 (mean temperature of the wettest quarter), and BIO18 (precipitation of the warmest quarter). BIO15 revealed that the occurrences used in the model span a wide range of values, with most concentrated around 64%, indicating moderate seasonal variation in precipitation. This aligns with the Mediterranean climate, characterized by a warm, dry period followed by a cooler, rainy season (Ballesteros et al. 2015). However, the duration and intensity of these phases vary depending on geographic location and orography, resulting in high interannual variability (Ballesteros et al. 2015). Specifically, the Mediterranean coastal zone, where castor bean is mostly distributed (Fig. 1), exhibit marked precipitation gradients both latitudinally and longitudinally (González-Hidalgo et al. 2009). Thus, in the Iberian Peninsula, castor bean tend to occupy areas with intermediate levels of precipitation variability. The second most contributing variable, BIO8 (29.9%), corresponds to the mean temperature of the wettest quarter. In the Iberian model, this variable shows a narrower range in the native environment, with most occurrences at 13.1ºC (Fig. 4). Despite this lower temperature, the result is consistent with the warm, humid, and mild conditions typical of the Mediterranean coast (Seager et al. 2019). The presence of castor bean in areas with cooler wet-season temperatures compared to its native range suggest a degree of climatic niche expansion.

Precipitation of the warmest month (BIO18) emerged as a relevant variable in the Iberian model, reflecting the characteristic summer drought of the Mediterranean climate. This variable contributed 17.1% to the model and exhibited a wide range of values, although most of the occurrences were associated with low precipitation values (Fig. 4). These values are comparable to those observed for BIO14

(precipitation of the driest month) in northeast Africa, suggesting that *R. communis* is capable of establishing in drought-prone environments. This adaptability may be explained by its early and vigorous growth response under water stress, efficient stomatal regulation that maintains a high net CO_2 fixation rate (Sausen and Rosa 2010) and the development of a robust root system (Seegeler 1983).

The modeling results of occurrences in the Iberian Peninsula (Fig. 3A) highlight the western Mediterranean region as the area with the greatest extent of occurrence probability. The probability of establishment of castor bean in Australasia, the Afrotropics, and the Neotropics is also high. Within these regions, rainforest stands out as the biome with the largest area of high probability of occurrence (4.96 M ha). At the same time, there is also a trend toward subtropical environments, such as xeric shrublands, where the predictive area occupied is extensive (13.3 M ha), although the area with high probability (0.800 M ha) is low.

The distribution model based on occurrences in northeast Africa (Fig. 3B) shows a pantropical disjunction, with most suitable areas located in tropical regions of Africa, South America, and Asia. A significant proportion of the predicted distribution falls within the rainforest biome (138 M ha), with 0.421 M ha classified as high-probability zones. This biome, characterized by consistently high temperatures and evenly distributed rainfall throughout the year, aligns with the isothermality values observed in the native range (BIO3, mean = 77.5%). The second most prominent biome is tropical and subtropical grasslands, savannas, and shrublands, covering 126 M ha, with 0.165 M ha identified as high-probability areas. These environments correspond well with the ecological preferences described in the literature (Seegeler 1983) and are consistent with the results of this study. Interestingly, the model based on African

occurrences did not predict suitable areas within the Palearctic region, unlike the Iberian model, which did identify potential zones in the native range. This discrepancy may be attributed to the domestication process, during which varieties of castor bean cultivated in Europe were likely selected for their tolerance to the region's climatic conditions present there.

Overall, our results show that castor bean has expanded its habitats into environments that native populations apparently cannot occupy. A similar pattern has also been found in other plant species, such as the genus *Oryza* L. (Lin et al. 2015). While in northeast Africa castor bean appears to occur a limited number of biomes (8), in the invaded environment it is able to colonize a greater number of biomes (14) than in its native area. This seems to indicate that castor bean is capable of diversifying the environments it occupies when it is an invasive species, while in its native environment, it is restricted to narrower environmental settings. In this way, the intersection zones exhibit more tropical than Mediterranean characteristics.

The overlap between the two predictive models is minimal (3.65%), reinforcing the hypothesis of climate niche expansion in *R. communis*. Among the biomes where overlap was detected (Table 4), none exceeded 10%. The biome with the greatest overlap was mountain grasslands and shrublands, while rainforest represented the largest area of high occurrence probability.

From climatic characterization to predictive modeling, the evidence consistently suggest that *R. communis* has expanded its niche. This expansion is likely facilitated by its broad climatic tolerance combined with human-mediated dispersal. Key traits of the species that could explain its ability to establish in diverse environments

include its high phenotypic plasticity and capacity to undergo morphological changes in response to environmental variation (Muraguri et al. 2020; Xu et al. 2021). Phenotypic plasticity would allow the species to establish across a wide range of environments, effectively invading them (Goyal et al. 2014). This trait is not exclusive to castor bean, as there are many more examples of plant species such as *Carpobrotus edulis* (L.) L.Bolus, *Lantana camara*, or *Ageratina adenophora* (Spreng.) R.M.King & H.Rob. (Sharma et al. 2005; Datta et al. 2019; Campoy et al. 2021). In the case of *R. communis*, its ability to modulate vegetative and reproductive traits enhances its survival and establishment in different habitat types (Goyal et al. 2014).

There are limitations that could influence our results, such as insufficient sampling in the native range or the use of occurrences concentrated only along roadsides. One solution would be to conduct intensive, homogeneous sampling across the native range, including natural areas, and repeat the niche characterization and modeling (Ramírez-Albores et al. 2016). Furthermore, the model presents tiny areas in biomes like paramo or tundra in the Neotropics, which are ecologically unlikely for *Ricinus* to occur in these regions. These anomalies could be due to two main reasons: (1) there are rare areas in these biomes without temperatures lower than 4ºC; or (2) raster layers (BIO6) doesn't exclude these areas where truly *R. communis* cannot survive.

Regarding the effect of species identification errors in our analyses, *R. communis* is a well known plant, easily identifiable, and it is seldom confused with other species. For this reason, we believe that the inclusion of misidentifications from human observations GBIF records has a null impact on our results (Figure S1).

The vast majority of authors designate northeast Africa as the native range of *R. communis*, however this fact has yet to be tested using molecular evidence. Due to the uncertainty about the size and limits of the native area of castor bean in tropical Africa, the area selected in this study may have been too extensive or, conversely, may have excluded countries such as Tanzania, Uganda, South Sudan, and/or Sudan. A population genetic study using an adequate sampling will be needed to corroborate that northeast Africa corresponds to the area with the greatest genetic diversity, which in turn will support its designation as native area of *R. communis*.

Ricinus communis has successfully expanded its niche in the Iberian Peninsula compared to its native range. This climatic plasticity suggests that castor bean may exhibit high invasive potential, while simultaneously complicating efforts to predict potential invasion areas. The ability of invasive species to modify and broaden their niche (Atwater et al. 2018; Aravind et al. 2022; Pack et al. 2022) underscores the need to study their climatic niches to improve management and prevention of biological invasions.

Conclusion

Ricinus communis has successfully expanded its ecological niche in the Iberian Peninsula beyond its native range. This climatic plasticity of castor bean indicates that it may have a high invasive capacity, which complicates efforts to predict areas at risk of invasion. Therefore, a global assessment if needed to identify regions where the species remains stable versus those where it is expanding, using worldwide occurrence records and comparing invaded and native ranges, as done in this study. The ability of invasive species to shift and broaden their niches (Atwater et al., 2018; Pack et al., 2022; Aravind et al., 2022) reveals the need of analyzing

their climatic requirements to support management strategies and prevent biological invasions.

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Author contributions statement

NEL and TV designed the research; NEL and TV collected, processed and analyzed the data and wrote the R code. NEL led the writing of the original draft with contributions from all authors. TV, RR and IS contributed through supervision and review and editing of the manuscript, and RR and IS contributed to funding acquisition. All authors discussed the results and approved the final version of the manuscript.

Data Accessibility Statement

Code and cleaned dataset used for the analyses are available in: https://github.com/necharren/Characterisation_modelling_Ricinus.

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Supplementary files

Table S1. Worldclim environmental variables used.

Bioclimatic variables	Code
Annual Mean Temperature	BIO1
Mean Diurnal Range (Mean of monthly (max temp - min temp))	BIO2
Isothermality (BIO2/BIO7) (×100)	BIO3
Temperature Seasonality (standard deviation ×100)	BIO4
Max Temperature of Warmest Month	BIO5
Min Temperature of Coldest Month	BIO6
Temperature Annual Range (BIO5-BIO6)	BIO7
Mean Temperature of Wettest Quarter	BIO8
Mean Temperature of Driest Quarter	BIO9
Mean Temperature of Warmest Quarter	BIO10
Mean Temperature of Coldest Quarter	BIO11
Annual Precipitation	BIO12
Precipitation of Wettest Month	BIO13
Precipitation of Driest Month	BIO14
Precipitation Seasonality (Coefficient of Variation)	BIO15
Precipitation of Wettest Quarter	BIO16
Precipitation of Driest Quarter	BIO17
Precipitation of Warmest Quarter	BIO18
Precipitation of Coldest Quarter	BIO19

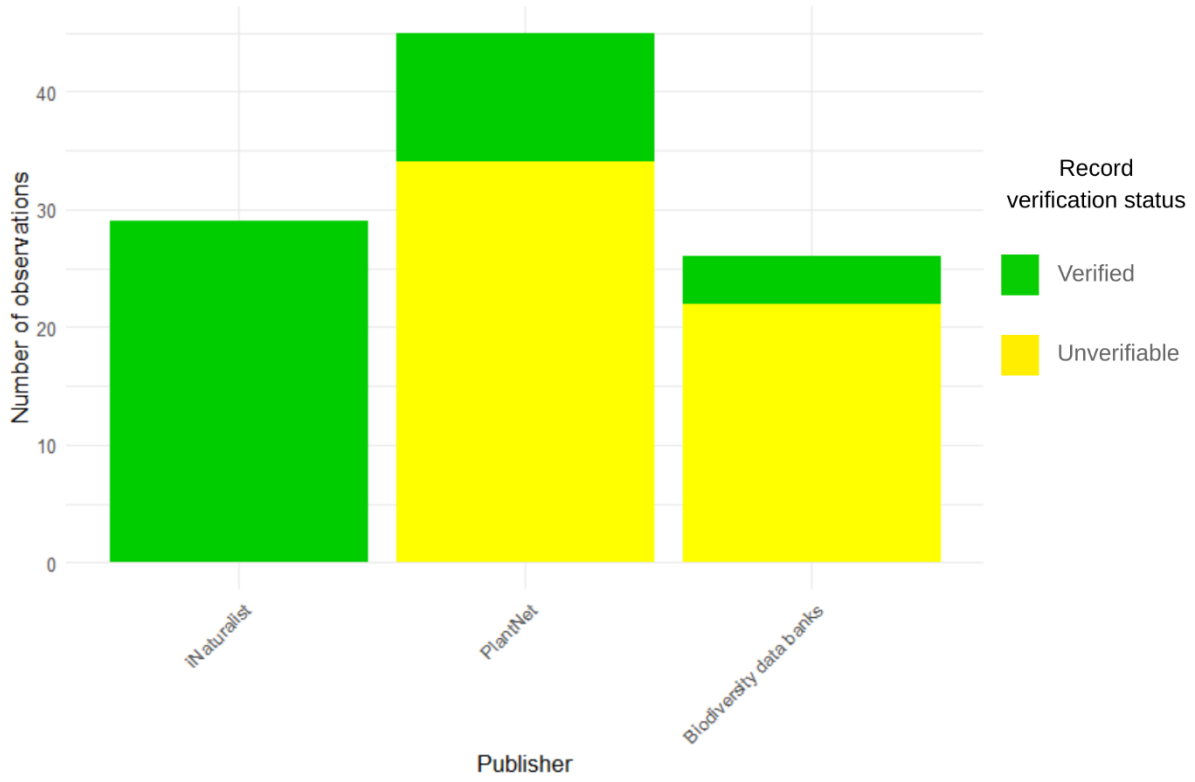

Figure S1. Review histogram of human observation records. A random sample of 100 records from GBIF.org (2020) was manually reviewed using the information available on GBIF and Google Maps Street View. The random observations were grouped by data publisher, consisting of 26 from Biodiversity data banks, 45 from PlantNet, and 29 from iNaturalist. Of these, 44 records were confirmed as correctly identified, while 56 lacked multimedia evidence and could not be verified through Street View. No misidentified records were found in the random sample.