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ORIGINAL PAPER

Climatic niche shifts along the worldwide expansion of jimsonweed (*Datura stramonium* L.)

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Abstract Biological invasions are one of the main drivers of global change. The European arrival to America in the late fifteenth century, and subsequent new trade routes, were critical events in the introduction of alien species, which have been increasing rapidly since the seventeenth century. In this study, we examine the global distribution and model the climatic niche of *Datura stramonium*, a cosmopolitan noxious weed. *D. stramonium* is of Mesoamerican origin and was introduced to Europe 450 years ago, thus is an illustrative case of the invasion associated with this colonization process. Analyzing *D. stramonium* occurrences and climatic data from global databases, we fit models in geographical and climatic space to determine if the species has undergone climatic niche shifts during its worldwide colonization process. We address the relationship between niche dynamics and residence time in *D. stramonium*, and we identify climatically suitable areas that show high risk of being colonized in the near future, which could help prevent invasion. In its non-native area, *D. stramonium* occupies climates similar to the native range (43% niche stability) but has also expanded remarkably into cooler climates (57% niche expansion). Niche unfilling is negligible (1%) when considering the non-native area globally. Low levels of niche unfilling in *D. stramonium* do not appear to be related to longer residence time but may instead be linked to a closer climate match between the native and non-native ranges. The large niche expansion towards cooler climates in three non-native ranges (Europe, North America and Asia) is associated with a remarkable increase in the frequency of low temperatures in the available climate compared to the native range. Despite a very long residence time, the species may still expand its distribution, notably in the warm zones in the non-native area.

Keywords Biological invasion · *Datura* · Ecological niche · Historical records · Human-mediated introductions · Niche modeling · Residence time

Introduction

Colonization of new territories by alien species is often associated with human movements (Hulme 2009). Alien species introductions have been increasing rapidly since the seventeenth century, leading to the establishment and naturalization of many species out of their native area (Vilà et al. 2008a, b). In many cases, those alien species expand massively,

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threat local biodiversity and cause huge economic losses, becoming weeds (Haubrock et al. 2021; Vilà et al. 2006). Success in the establishment of alien species depends on whether the new local environmental conditions and biotic interactions (pollination, competition, etc.) allow a species to reproduce. The time since colonization (residence time) and propagule pressure strongly influence the ability of alien species to expand their geographic range across suitable climatic conditions in the non-native area (Gassó et al. 2010; Lockwood et al. 2005). Suitable climatic conditions are usually more critical than other more local factors (e.g., edaphic) because new sites are usually very altered locally (Chytrý et al. 2008).

Species distribution and environmental niche models are useful tools to better understand the dynamics of alien species. For example, these models allow comparing the range of environmental conditions, usually climatic, occupied in native and non-native areas and detecting niche shifts associated with the colonization process. These models can also be used to assess invasion risk and spread potential across geographical areas (Peterson et al. 2011). Although niche conservatism is a premise of niche modelling (Peterson 2011; Wiens et al. 2010) and implies that a species will occupy in the non-native range a similar climate as in its native range, niche comparison studies for introduced species have found contrasting results so far, with abundant examples of both niche stability across species ranges, niche expansion in the non-native range, and niche unfilling (i.e., failure to colonize suitable climates in the non-native range) (Bates & Bertelsmeier 2021; Pearman et al. 2008; Petitpierre et al. 2012).

The relationship between niche dynamics and residence time has been explored (Herrando-Moraira et al. 2019), showing that niche unfilling typically decreases with residence time in the introduced range, as could be expected. However, the link between niche expansion and residence time is not straightforward, depending first on the ability to subsist in new climates. There is not much evidence that niche shifts necessarily increase with residence time, according to Petitpierre et al. (2012) and Liu et al. (2017). A positive relation was found by Li et al. (2014), but other studies found, unexpectedly, a negative relation between niche shifts and residence time (Early & Sax 2014; C. Liu et al. 2020). There are probably historical contingencies and biological features of each species, such as short life-span and rapid generation time, which in part determine the probability of niche shifts (Baker 1974; Sutherland 2004).

Datura stramonium is a cosmopolitan (invasive) annual weed whose native area is presumably situated in Mexico, southwestern USA, and Central America (Luna-Cavazos & Bye 2011; Symon & Haegi 1991). It is currently present in almost all the regions of the world with temperate and warm climates (Sanz Elorza et al. 2004). This ruderal weed grows in disturbed habitats like roadsides, cultivated fields, and riverbanks (Núñez-Farfán, 1995). The first introduction of *D. stramonium* in Europe goes back to the sixteenth century, when it probably entered through Spain (Colonna 1592; López Piñero & Pardo Tomás, 1996). This region had then considerable exchanges with America, which promoted the entrance of a large number of foreign species (Sanz Elorza et al. 2004). It was introduced deliberately as a medicinal (and psychotropic) plant traditionally used in Mexico and soon was cultivated in European botanical gardens and in fields for medicinal use (Gerard 1597). Besides the deliberate introductions, the species underwent later repeated unintentional introductions into Europe as a contaminant of imported grains, especially during the twentieth century (Danielsen & Ouren 1961; Ouren 1978) from the USA where the species was introduced in the 17th (in East USA) (Clements et al. 2004; Weaver & Warwick 1984). The time of introduction to other continents is unclear and can be challenging to establish, as other species of *Datura*, with similar uses and common names, have been used traditionally in distant regions: *D. ferox*, native of South America, or *D. metel*, introduced to Asia at least in the sixteenth century (Orta 1891).

Datura stramonium expansion is of public health concern due to its content of dangerous tropane alkaloids, typical of the Solanaceae family (Evans 1979). As a ruderal weed that prefers loose and fresh soil, it often appears associated with edible crops like corn, buckwheat, soybeans or tomatoes, and has become a very important summer crop weed (Benvenuti 2003). It can be harvested accidentally with the crops (Kessler 2015; PROFEL 2020); indeed, tropane alkaloids from *Datura* have been detected in processed food on several occasions (Cirlini et al. 2018; Mulder et al. 2016). In the last decades, numerous intoxications have been reported in Europe and Africa after consumption of contaminated food (Fretz et al. 2007; Onen et al. 2002; Perharič et al. 2013) or through

recreational use. Recently, a massive intoxication in Uganda (Abia et al. 2021; Mutebi et al. 2022) affecting more than 300 people and causing five deaths led to a joint report by the *World Health Organization* and the *Food and Agriculture Organization of the United Nations (FAO & WHO,* 2020*)* assessing the risk of alkaloid exposure by consuming food contaminated by *Datura* seeds. Although there are no available data on the economic costs provoked by these public health problems or on the cost of eradicating this weed, they can be assumed to be very high.

Because of *D. stramonium*'s impact on human populations, it has frequently been reported in different botanical sources and in natural history collections through time, since the start of intercontinental trade. Thus, it is an ideal model system for ascertaining the dynamics of its worldwide expansion through its colonization in continents at different periods. Despite *D. stramonium* potential danger to human societies, its climatic potential expansion has not previously been addressed at a global nor regional scale. In this study, we examine the global distribution and the realized climatic niche of *D. stramonium* in its native and non-native areas, with the aim to better understand (i) if the species has undergone climatic niche shifts during its colonization process that have helped it to spread across continents, (ii) address the relationship between niche dynamics and residence time in *D. stramonium*, and (iii) identify climatically suitable areas that show a high risk of being colonized in the near future. The long time since the first introduction of *D. stramonium* into the non-native area and the many accidental dispersal events by humans induce us to hypothesize that realized niche shifts are likely in this species. In addition, delineating areas of potential spread can help anticipate invasion and develop guidelines to prevent further damage.

Methods

Study area

Native range

The native area of *Datura stramonium* extends over Mexico, southwestern USA, and Central America (Luna-Cavazos & Bye 2011; Symon & Haegi 1991; Weaver & Warwick 1984) (Fig. 1). The exact limits of the native range are not precisely known, as

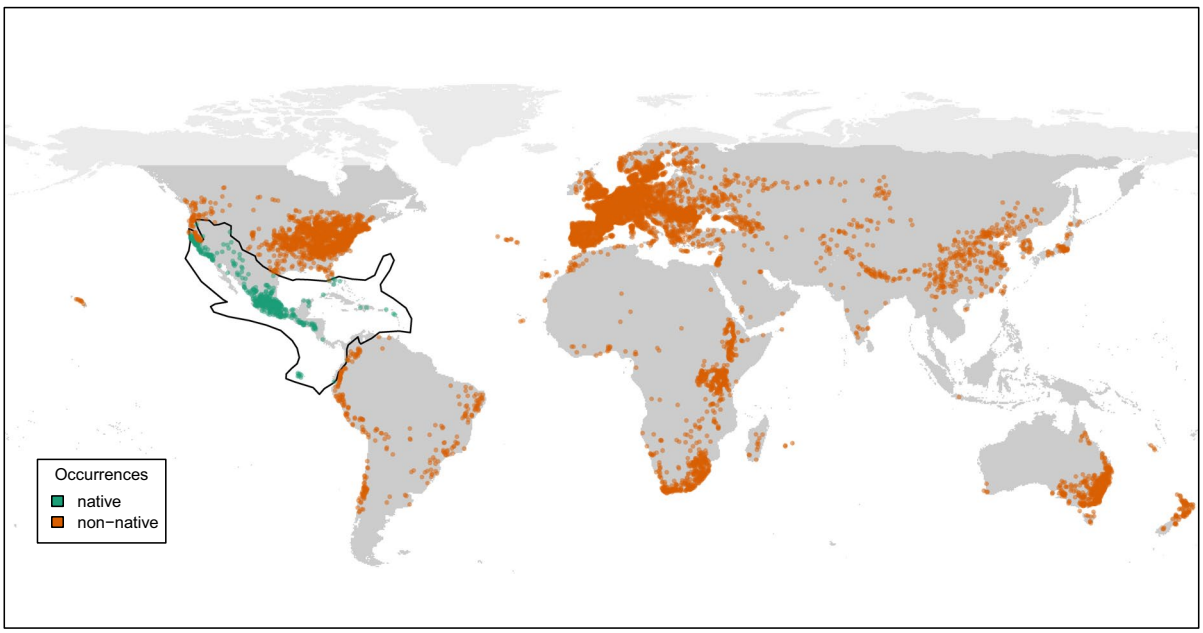

Fig. 1 Native (enclosed by a black line) and non-native range (medium grey) of *Datura stramonium*. Native occurrences are in green, non-native occurrences are in orange. Arctic regions (in light grey) were excluded as no occurrence of *D. stramonium* has been recorded there

the species has probably been spreading along the American continent for centuries, assisted by human introductions associated to crop development. Here we used Takhtajan's delimitation of floristic regions (Takhtajan 1986; Rodríguez-Sánchez 2023), one of the most recognized and widely used systems of biogeographic regionalization for land plants, as a guide to approximate *D. stramonium* native range. In particular, we considered Takhtajan's Madrean and Caribbean regions, spread along southwestern USA, Mexico, Central America, and the Caribbean (Fig. 1), as the accessible area (Barve et al. 2011) in *D. stramonium*'s native range.

Non-native range

Datura stramonium is nowadays a cosmopolitan weed spread over all continents (Fig. 1). Hence, for the non-native range, we considered the whole world but excluded the Arctic (as defined in Murray et al. 1998) and Antarctic regions, where no occurrence of *D. stramonium* has ever been recorded. We performed analyses of the non-native range at global and continent-level. The limit between Europe and Asia was set on the N-S spread Ural Mountains, cutting along the averaged 59.3º E longitude on Russia.

Occurrences

We retrieved occurrences of *Datura stramonium* from the Global Biodiversity Information Facility (124,822 records; GBIF.org (24 April 2025) GBIF Occurrence Download https://doi.org/10.15468/dl.5unuhj). From 121,744 records with coordinates, 95% were based on botanical inventories and 5% on herbarium specimens. We selected records from the period 1950–2025 to be compatible with the available period of the climatic variables. The data were cleaned to remove records from a large citizen science dataset (Pl@ntnet), as they exacerbated the sampling bias in Europe. Cultivated occurrences or located in gardens were also removed. Finally, occurrences located on centroids (countries/regions), capitals, botanical institutes, in seas, or with erroneous coordinates (zeros/equals) were filtered with the R package *CoordinateCleaner* v3.0 (Zizka et al. 2019).

In order to reduce spatial sampling bias, we subsampled the occurrences (Boria et al. 2014; Fourcade et al. 2014) to retain only locations separated at least 20 km apart, using the function thin in the *spThin* R package (Aiello-Lammens et al. 2015). This spatial thinning managed to reduce the spatial sampling bias and produced a final dataset of 7444 occurrences: 479 native, 6965 non-native (1511 in North America, 257 in South America, 3348 in Europe, 754 in Africa, 648 in Asia, 447 in Oceania) (Fig. 1), which were used in all subsequent analyses.

Climatic data

We extracted 19 climatic variables and selected five climatic variables from the WorldClim database 2.1 (Fick & Hijmans 2017) at 5-min spatial resolution: bio1 (annual mean temperature), bio2 (mean diurnal temperature range), bio7 (temperature annual range), bio12 (annual precipitation) and bio17 (precipitation of annual driest quarter). These variables were chosen upon statistical and ecological criteria (Mod et al. 2016), as they had low correlation among them and can discriminate between different macroclimates (warm/cold and dry/wet with varying degrees of seasonality and continentality) occurring across *D. stramonium* distribution.

Niche comparison in environmental space

We compared the climatic niche of native and non-native populations with the *ecospat* R package (Broennimann et al. 2025) by plotting a smoothed density of the occurrences over an environmental space defined by the first two axes of a principal components analysis (PCA) of the climatic variables from the whole study area (Broennimann et al. 2012). First, we analyzed the non-native niche as a whole, then each of the non-native ranges in continents separately, plotting them on the global PCA.

This analysis allowed us to quantify niche overlap among native and non-native ranges, disentangling the amount of niche stability (climatic conditions occupied in both the native and non-native ranges), niche unfilling (climatic conditions occupied in the native but not in the non-native range), and niche expansion (new climates only occupied in the non-native range). Measures of stability and expansion were expressed as fractions of the non-native niche, while unfilling was expressed as a fraction of the native niche (Guisan et al. 2014). All these values were measured by considering only the 90th

percentile of the ecological space common to both ranges and were corrected by accounting for occurrence density (see function ecospat.niche.dyn.index in *ecospat* R package). In addition, measures of pioneering (part of the non-native niche situated in no-analogue climate) were established as a fraction of the non-native niche.

We also tested for niche similarity following Warren et al. (2008). For this test, the observed overlap is compared to a null distribution of simulated overlap values obtained by shifting alternately both niches randomly in the climatic space 500 times. The alternative hypothesis states that the niches are more similar than random.

Finally, after extracting the climatic variables at the occurrence locations, we compared their distribution between the native and non-native occurrences globally and in each continent. As data were not normally distributed, we used a non-parametric Mann–Whitney test through the pairwise.wilcox.test function (*stats* package in R) with a Bonferroni correction. These distributions were visualized using histograms. We also extracted the climatic variables at the background locations sampled in the Maxent model (see below), selecting those who contributed most to PC1 and PC2. We compared their relative availability between native and non-native ranges by plotting histograms. This allowed us to assess whether potential difference between native and non-native niches could be driven by differences in climate availability.

Niche modeling and geographic projections

We also modeled the niche of native and non-native populations separately using maximum-entropy modeling, *Maxent* (Phillips 2017; Phillips et al. 2006) through the *Wallace* application (Kass et al. 2023).

We used the *ENMeval* package (Kass et al. 2021) to split occurrences into two sets using the 'Checkerboard1' partition method. This partition method splits occurrences according to their position on a checkerboard overlaid to the grid cells and creates two occurrence sets. One set coincides with the "black" squares of the checkerboard, the other with the "white" squares. We aggregated ten by ten grid cells to create each checkerboard square (i.e., about 100×100 km) to ensure more spatial independence between both sets. They were used in turn to train and test the model. We used 10,000 random points to capture the background climatic conditions in each range.

We fit 20 different models with different combinations of feature classes (linear, quadratic, hinge) and values of the regularization multiplier (from 1 to 3, with increments of 0.5; Radosavljevic & Anderson 2014). The different feature classes define the shape of the modeled response curves (Phillips 2017; Phillips et al. 2006). Higher regularization multiplier implies smoother responses and simpler models (Merow et al. 2013). We set the response curves to zero beyond the range of the training data in order to avoid extrapolating into unknown climatic conditions (particularly when projecting the native models onto the non-native area). For each combination of feature classes, *ENMeval* calculated evaluation metrics using training and testing bins in turn, as well as a global AIC and AUC based on pooled occurrences. Finally, the map prediction was done using pooled occurrences.

We evaluated and selected the best models based on a combination of coherence and ecological realism of the fitted response curves, Akaike Information Criterion (AIC) comparisons (Burnham & Anderson, 2002; Warren & Seifert 2011), and assessment of calibration using the continuous Boyce Index (Hirzel et al. 2006) through the ecospat.boyce function. This index assesses the quality of the model by comparing, along different suitability intervals, the distribution of test presences with a random distribution. The result is an index ranging from -1 to 1, where 1 indicates a good model, 0 a model not better than random, and -1 an erroneous model. We fitted models to both native and non-native ranges and projected onto each other to visualize potentially suitable areas still not occupied, as well as new areas that have been colonized parallel to niche expansion.

Estimation of residence time in the non-native area

In order to estimate the residence time in the different territories of the non-native area, we extracted all the herbarium specimen information prior to 1900 from the GBIF database (GBIF.org (31 October 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.gt8ay3). Then, we selected amongst these data the oldest records for each continent and, whenever possible, country. We cross-checked these records with the Alien Species First

Records Database (Seebens 2023; Seebens et al. 2018) and other references mentioned hereafter to support our residence-time estimates. Although actual introductions might have been older, these are the most reliable estimates available of the earliest presence of the species in each continent.

Datura stramonium time of residence widely differs in the different continents. It was introduced about 450 years ago in Europe (Sanz Elorza et al. 2004) and has been present in North America, beyond the native area, for nearly 300 years: *D. stramonium* was included in Flora Virginica (USA) in 1739 (Clayton & Gronovius 1739) but could have occurred in Virginia by 1616 (Avery et al. 1959). However, in the rest of the world (South America, Africa, Asia, Oceania), *D. stramonium* has only been reported with certainty for the last 200–250 years approximately. In South America, the earliest herbarium specimens were collected in the 1780s in Peru. The subsequent records, between the 1830s and the 1860s, were also from the west coast: Peru, Chile, Ecuador, and Colombia. It was not until 1867 that *D. stramonium* was sampled on the coast in Argentina and in 1872 in Brazil. In Africa, the oldest record is from 1775 in South Africa (Thunberg 1794), but most of the oldest herbarium specimens, from the 1830s–1840s, are from Northern Africa (Algeria) and the Horn of Africa (Sudan, Ethiopia). In Asia, the oldest record we are aware of is from 1776 in Nagasaki, Japan (Thunberg 1784). The oldest continental Asian herbarium specimens, to our knowledge, are from the nineteenth century (1809 Pakistan, 1831 India, 1859 China). According to the Alien invasive flora of China (Ma et al. 2020), *D. stramonium* was known in China by the late sixteenth century, as documented in the Ming Dynasty *Compendium of Materia Medica*. However, this work did not distinguish among different *Datura* species, and the record may therefore refer to *D. metel,* which has been used in traditional Chinese medicine since that time. In Oceania, the oldest herbarium specimen is from 1801 in Port-Jackson (Australia).

The oldest records in America, Africa, Asia, and Oceania are all located in coastal countries. It is probably linked to the history of the scientific exploration in the Age of Enlightenment and also high occupancy by the colonizers.

Results

Niche modeling in climatic space

The first two axes of the principal components analysis with the five climatic variables explained 82.8% of the climate variability (Fig. 2). The first axis mostly describes the precipitation regime and the temperature seasonality (higher values represent drier and more seasonal climates), while the second axis represents the temperature gradient and the diurnal temperature range (higher values represent warmer climates along with increased diurnal range). Diurnal temperature range was almost equally correlated with both PC1 and PC2, although it contributed little to PC1.

Niche overlap between the native and non-native ranges considering the global area was low (Schoener's D = 0.225). *Datura stramonium* has globally expanded remarkably into cooler climates (57% niche expansion) but occupies similar precipitation regimes in the non-native range (43% niche stability). There was a small amount (1%) of niche unfilling as the warmest climates were only occupied in the native niche (Fig. 2). The similarity between native and non-native climatic niches was marginally significant (p-value = 0.054).

In South America and Africa, *D. stramonium* notably conserved its climatic niche. In both cases, stability was higher than 90% and unfilling was very low (0.02–0.06) (Table 1). There was low niche expansion in South America (0.08) but it was negligible in Africa (0.003). Pioneering was null or extremely low (0.02) (Table 1). Niches in both continents were significantly similar to the native niche. Schoener's D (Warren et al. 2008), which ranges from 0 (no overlap) to 1 (complete overlap), was higher than in the other continents (D > 0.4, $p = 0.010$ and 0.016).

In North America, Europe and Asia, *D. stramonium* highly expanded into analogue (expansion: 0.6–0.84) and no-analogue climates (pioneering: 0.23–0.52). Niche stability was low in North America and Europe, but substantial in Asia. Asia had actually the highest niche breadth of all continents, but also the broadest available climate in the climatic space. Niche unfilling was low in Asia and Europe (0.05–0.09), but it reached 0.23 in North America.

In Oceania, *D. stramonium* conserved and expanded its climatic niche at the same time. Stability

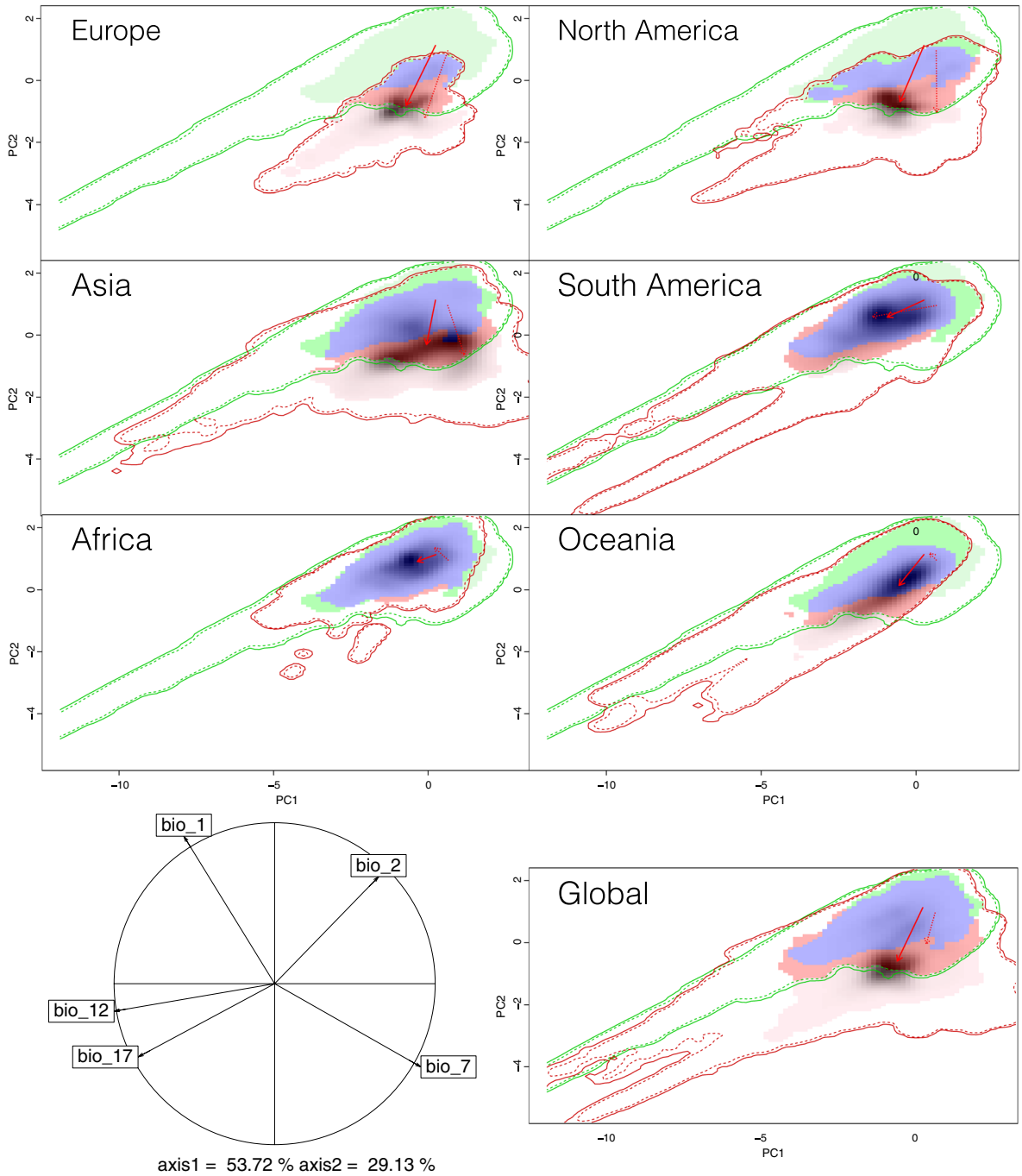

Fig. 2 Niche overlap in the climatic space. Green and red lines show available climates in the native and non-native ranges, respectively. Niche stability (the overlap) is shown in blue, unfilling in green, and expansion in red. Niche space in no-analogue climates is shown in light green (abandonment, not considered in this study) and pink (pioneering). The dashed red arrow shows the shift of the centroid of the available environment between native and non-native ranges. The solid red arrow shows the shift of the centroid of the occurrence density. The dark shade represents the occurrence density in the non-native range. The solid and dashed lines represent 100% and 90% of the available climate. Climatic variables used to define the climatic space: bio1 (annual mean temperature), bio2 (mean diurnal temperature range), bio7 (temperature annual range), bio12 (annual precipitation) and bio17 (precipitation of driest quarter)

Table 1 Overlap values for each native vs non-native range comparison. Stability and expansion are expressed as fractions of the non-native niche, and unfilling as fractions of the native niche. Measures of pioneering (part of the non-native niche situated in no-analogue climate) are established as a fraction of the non-native niche, including both analogue and no-analogue climates. Niche overlap (Schoener's D) is measured considering the whole available ecological space and is corrected by both occurrence density and environment density. Niches significantly similar to the native niche are marked as * $p<0.05$ and ** $p<0.01$

Continent	N	Stability	Expansion	Unfilling	Pioneering	Schoener's D (Niche overlap)	Niche similarity (p-value)
North America	1511	0.156	0.844	0.226	0.359	0.186	0.038*
South America	257	0.922	0.078	0.057	0.017	0.496	0.010**
Europe	3348	0.177	0.823	0.049	0.524	0.129	0.040*
Africa	754	0.997	0.003	0.024	0	0.436	0.016*
Asia	648	0.400	0.600	0.088	0.234	0.238	0.030*
Oceania	447	0.744	0.256	0.290	0.108	0.192	0.136
Global non-native	6965	0.430	0.570	0.012	0.357	0.225	0.054

was larger than expansion, but there was substantial unfilling (0.29) which caused the niche to differ from the native niche (similarity test $p=0.136$). In addition, there was a low level of pioneering.

In all continents except Oceania, niches were significantly more similar to the native niche than random although overlap values were low for Europe, North America and Asia (D: 0.13, 0.19 and 0.24, respectively).

In North America, Europe and Asia, the centroid of the occurrences was located out of the occupied climate in the native range, showing a remarkable niche shift in these continents, in contrast with Oceania, South America and Africa, which showed higher niche conservatism. Europe showed the largest value of pioneering niche in no-analogue climates (52%).

Analysis of climatic variation between native and global non-native areas at the occurrence locations showed that all variables except bio12 (annual precipitation) had significantly different distributions. When considering the non-native range as separate continents, bio2 (diurnal temperature range) and bio17 (precipitation of the driest quarter) differed from the native range in all continents (Fig. 3, Table S1 suppl.). Bio2 (diurnal temperature range) was significantly higher in the native range ($p<2e\text{-}16$), while bio17 (precipitation of driest quarter) was significantly lower in the native range ($p=6.2e\text{-}05$ to $<2e\text{-}16$). Europe and North America were the continents where variables were the most dissimilar to the native area: all variables had significantly different distributions, although difference for bio12 in Europe was low (see Fig. 3). In South America, Africa and Oceania, variables were more similar to the native range.

Histograms of the variables contributing most to PC1 (bio12) and PC2 (bio1), at background locations, showed that bio1 (annual mean temperature) had a very different distribution in North America, Europe and Asia, than in the native range (Fig. 4). The frequency of low temperatures was higher in these three continents than in the native range, and the average annual mean temperature was much lower than in the native range. Bio12 distribution (annual precipitation) was globally more similar between native and non-native ranges.

Niche modeling in the geographic space

Niche models using Maxent achieved a very good ability to predict *Datura stramonium* distribution (Fig. 5 and Table 2: Boyce index = 0.98 and 1 in the native and non-native ranges, respectively). The best native model was built with a hinge feature only and the response curves were smoothed by a regularization multiplier of 2.5. The best non-native model combined linear, quadratic and hinge features, and a regularization multiplier value of 1.

Reciprocal projection performed unevenly (Table 2). According to the Boyce index, the projection of the native model onto the non-native range had good predictive power (Boyce index = 0.82), and the projection of the non-native model onto the native range performed well (Boyce index = 0.95).

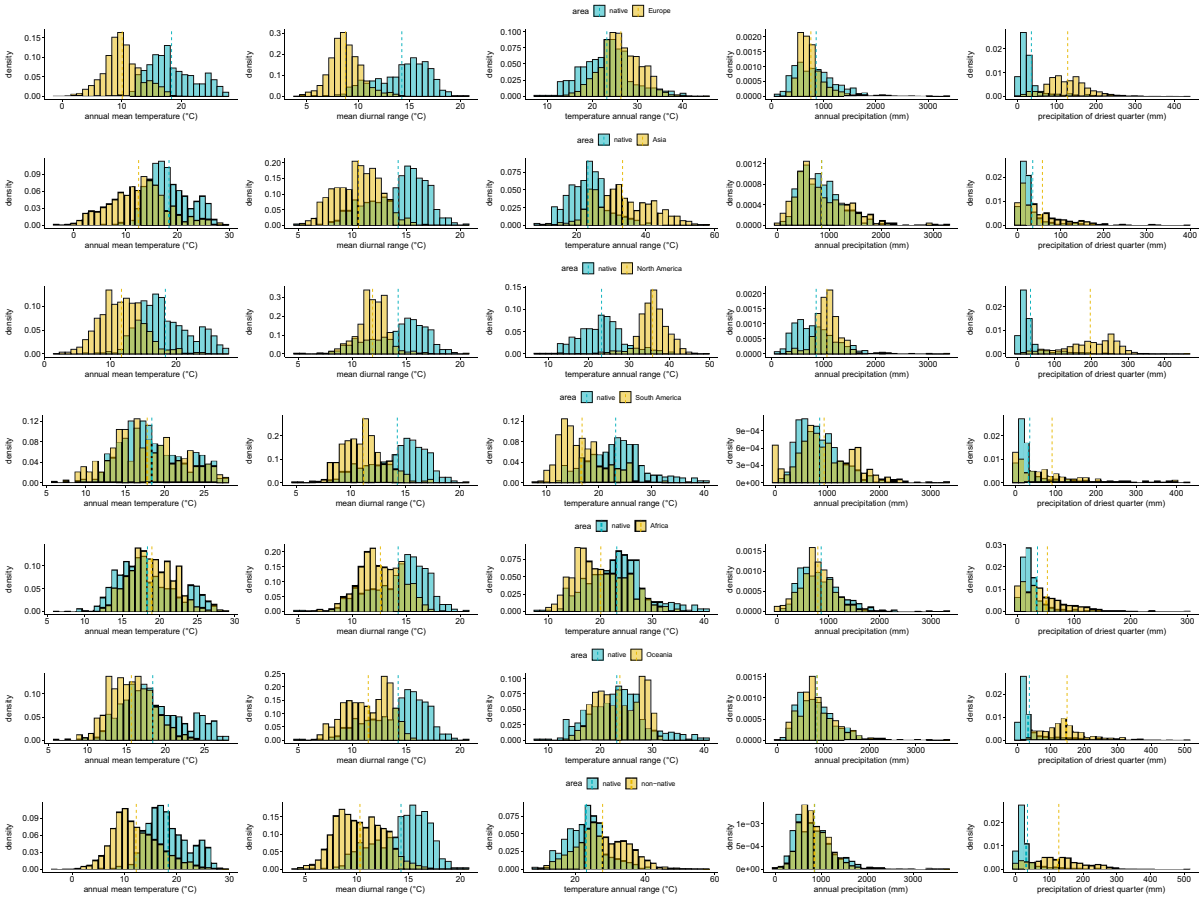

Fig. 3 Comparison of the five climatic variables across the native and non-native ranges of *Datura stramonium*. Climatic variables at the occurrence locations in each range are compared in density plots. The mean value at each range is represented as a dashed line

Nevertheless, the evaluation through the 10 percent Omission Rate thresholding revealed a low to moderate performance in both projections (40% and 43% omitted occurrences in respective projections). Some mismatch in reciprocal distribution projections is expected given the realized niche shift towards colder climates in the non-native range (Figs. 2, 5).

According to the native model (Fig. 6 a), the regions of high suitability in the native area corresponded to the Sierra Madre, which extends over Mexico and Central America; the Transversal neovolcanic System, the Mexican High Plateau and the Western and Southern Pacific Mexican coasts; and the Mediterranean climate in California (USA). Globally, high climatic suitability areas were consistent with the observed native distribution, although only a few occurrences were reported in the Western Sierra Madre, and some occurrences were found in a desert with very low suitability, along rivers.

In the non-native area, high suitability regions according to the non-native model covered large territories of North America, Europe and China (Fig. 6 d). In the southern hemisphere, high suitability was more restricted and mostly concentrated in the basin south of Rio de la Plata and in high-elevation areas in South America and Africa, as well as along the Australian coast. *Datura stramonium* was still lacking in large areas predicted as climatically suitable considering the projection of the native model onto the non-native area, mostly in warm regions from South America and Africa (Fig. 6 b).

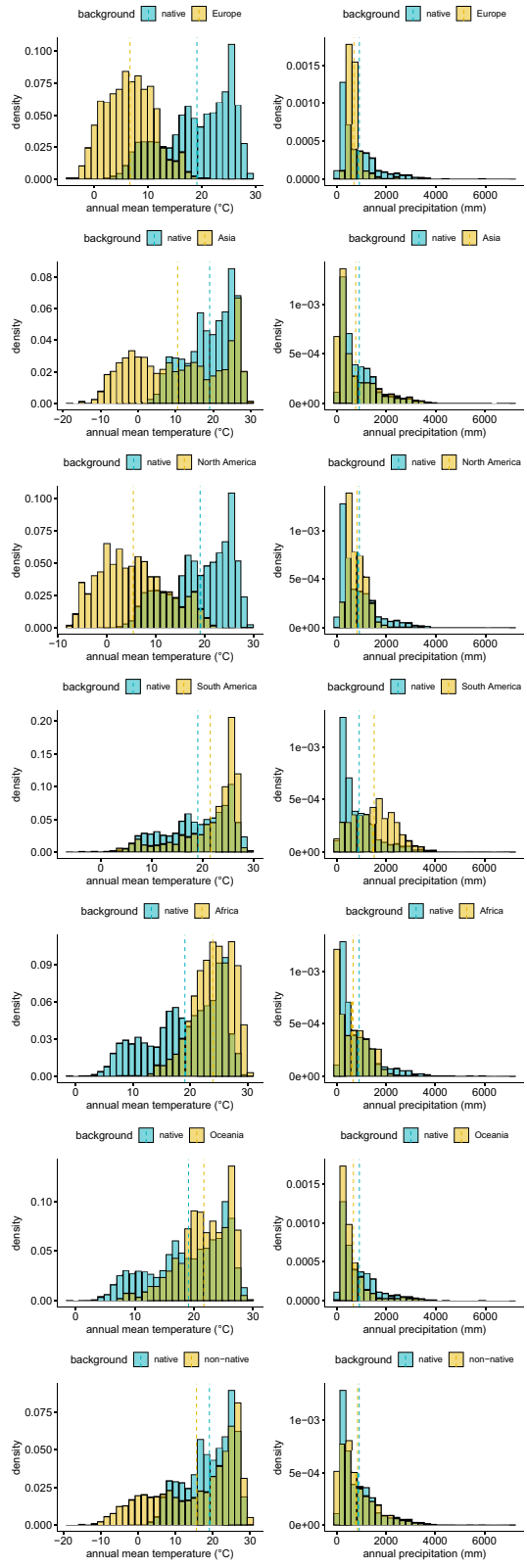

Fig. 4 Comparison of available climates across the native and non-native ranges of *Datura stramonium*. Bio12 (annual precipitation) and bio1 (annual mean temperature) at background locations in each range are compared in density plots. The mean value at each range is represented as a dashed line

Residence time in the non-native area

Residence time varied across continents in the non-native range, from the longest in Europe (ca. 450 years) to the shortest in Oceania (ca. 225 years), with intermediate values observed in North America, Africa, Asia, and South America (Table S2 supplementary material). The relationship between residence time and niche metrics showed variable patterns (Fig. S1 supplementary material).

Discussion

In this study, we used niche modeling to assess changes in the realized climatic niche between native and non-native *Datura stramonium* ranges that could have facilitated the species colonization worldwide. To do so, we compared the distribution of climatic environments occupied by the species in both the native and non-native ranges and performed reciprocal projections in geographical space to assess how much climatic niche shifts occurred during the invasion process.

We found that *D. stramonium* has expanded its climatic niche, colonizing significantly cooler environments worldwide than occupied in its native range in Mexico, Central America, and the Caribbean. The observed climatic niche shift occurred along a temperature, but not precipitation, gradient: *Datura stramonium* still preferentially occupies regions with moderate precipitation and is absent from very cold and non-seasonal heavily rainy regions (Fig. 2). According to niche models evaluated across the geographic range, *D. stramonium* remains absent from large areas predicted to be climatically suitable, particularly in the warm regions of South America and Africa. These areas could represent potential sites of invasion. The species might already be present there, but we might be lacking occurrence data there due to scarcity, limited sampling or reporting (Jiménez-Valverde et al. 2011).

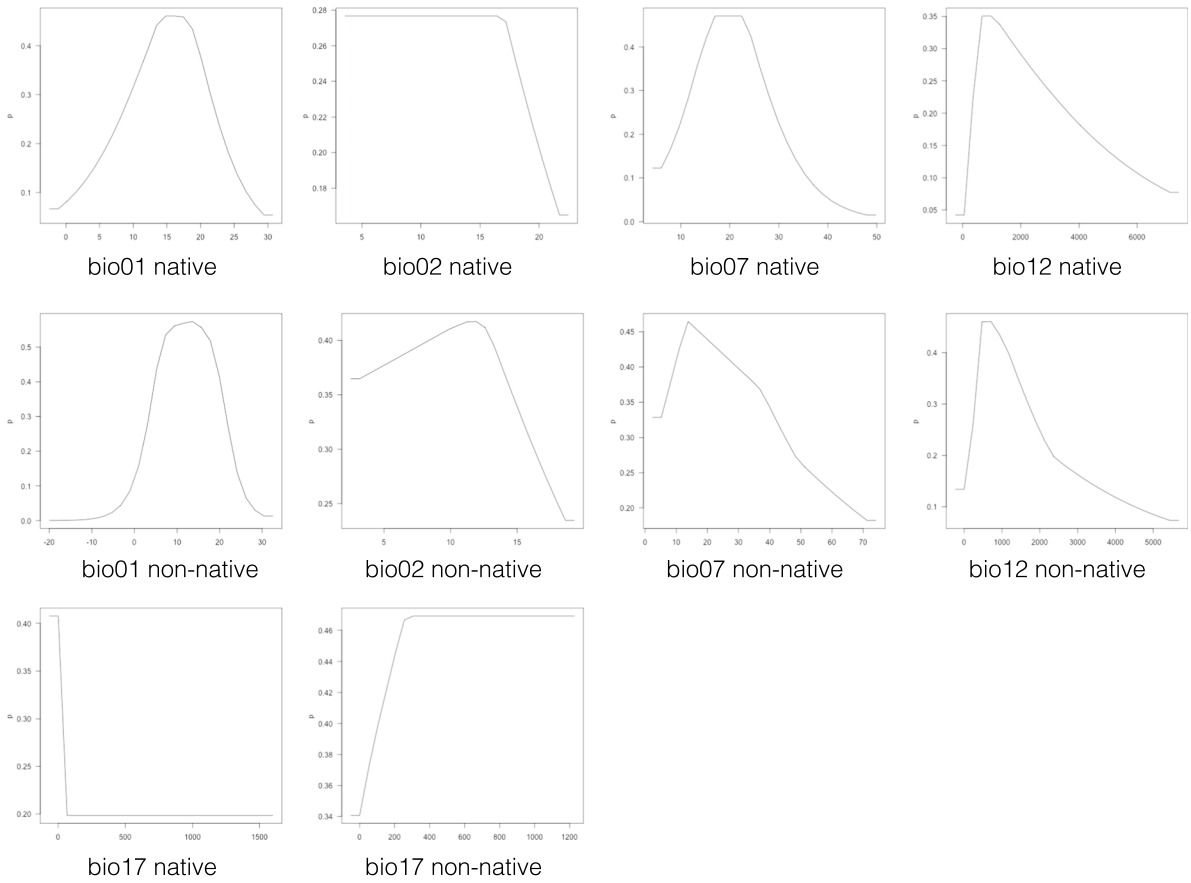

Fig. 5 Response curves of native and non-native niche models

Table 2 Evaluation metrics for native and non-native models, including metrics for projection onto non-native and native areas respectively

	Boyce Index	AUC	Omission Rate 10 percentile	Boyce Index proj	Omission Rate 10 percentile proj
Native model	0.977	0.857	0.117	0.822	0.408
Non-native model	1	0.911	0.101	0.951	0.430

Niche dynamics and residence time

There were strong differences in the niche dynamics between continents, with niche unfilling going from 2 to 29% and niche expansion from 0 to 84%, considering only the niche in analogue climates.

North America and Oceania had markedly larger niche unfilling (23% and 29%). The more recent introduction into Oceania (ca. 225 years) could explain the partial filling of suitable environments, but *D. stramonium* has been reported in North America for nearly 300 years, or possibly up to 400 years. In the latter, intense crop pest management might have much precluded the widespread occurrence of *D. stramonium* (Teasdale et al. 2019; Zimdahl 2010), since it was increasingly reported as a weed after 1950s (Clements et al. 2004).

Low unfilling was not consistently linked to longer residence time. Additionally, the continents on which *D. stramonium* occupied most of its original climatic niche (unfilling < 10%), did not show consistent patterns of niche expansion: South America and Africa

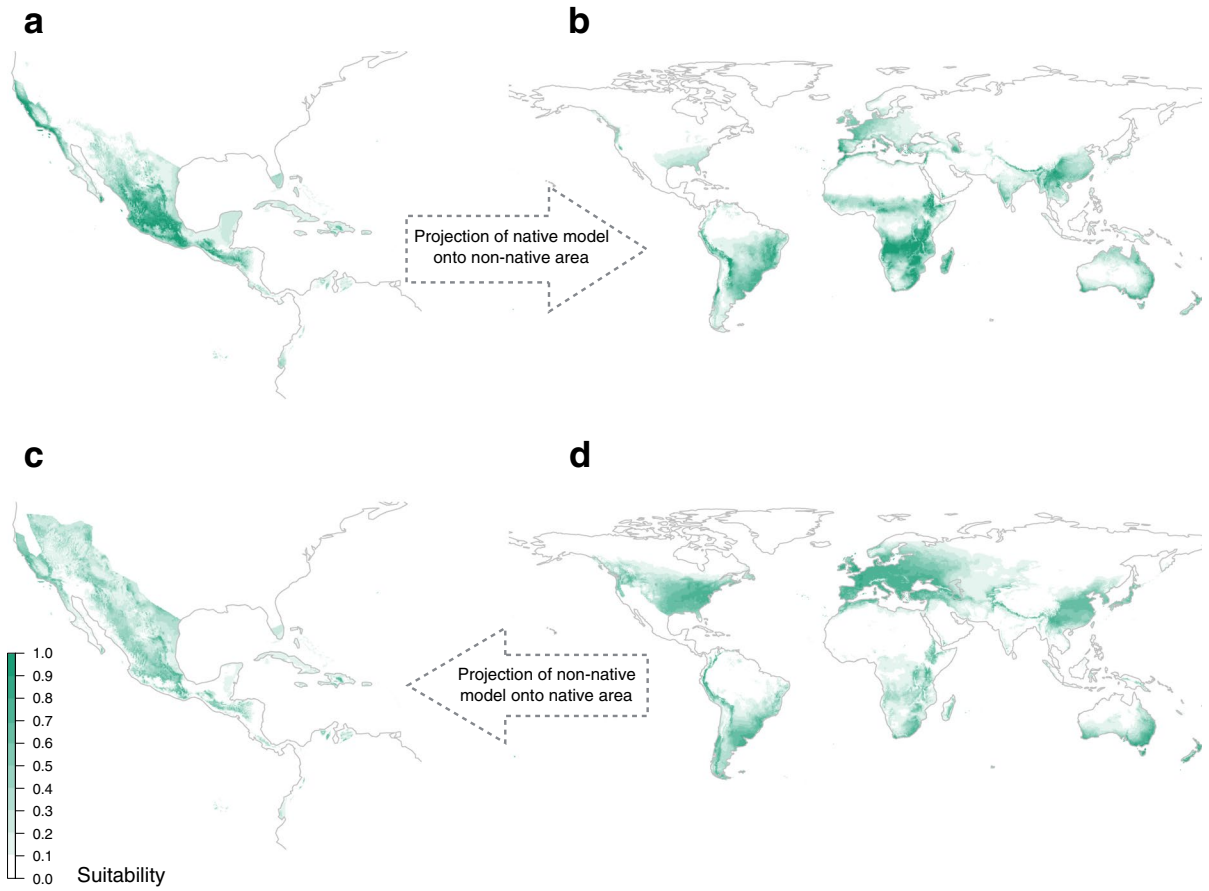

Fig. 6 (**a**) Geographical projection of the native niche model. (**b**) Geographical projection of the model calibrated in the native range and projected onto the non-native range. (**c**) Geographical projection of the model calibrated in the non-native range and projected onto the native range. (**d**) Geographical projection of the non-native niche model

displayed minimal expansion (0–8%), whereas Asia and Europe showed high expansion (60% and 82%). Nevertheless, very high expansion (> 82%) was associated with a longer residence time (Fig. S1 supplementary material), as observed in Europe and North America (300–450 years). In Asia, where the timing of introduction is uncertain, the substantial expansion (63%) may be linked to the wide range of available climatic conditions.

Low levels of niche unfilling in continents with shorter residence time may reflect a closer climate match between native and non-native ranges, like in Africa, South America and Asia (see Fig. 2). In Oceania, with a climate quite similar to the native range but an important niche unfilling (Fig. S2 supplementary material), *D. stramonium* could still be in the process of occupying the niche. Perhaps the isolated pattern of these territories and the concern about biological invasions are precluding the spread there (Julien et al. 2007; Meadly 1956).

Niche shifts in invasive species: the role of available climates

A large part of the available climate in the non-native range is not analogue to the native range (see Fig. 2). Several studies suggest that shifts are related to no-analogue climates between ranges (Petitpierre et al. 2012) or to an imbalance in climate availability (climate centroid shift) even though occupied climates may be overlapping (Atwater et al. 2018). In *D. stramonium* we found that the large niche expansion towards cooler climates in three non-native ranges (Europe, North America and Asia), as well as their

substantial pioneering, was associated with an important increase in the frequency of low temperatures compared to the native range. This supports the idea that an imbalance in the frequency of available climates may drive a niche shift, while it emphasizes the need to characterize the frequency of the available and occupied climate when analyzing niche shifts. The expansion in Oceania cannot be associated to colder climates, as the mean annual temperature in those climates is higher than in the native range, but it is moderate compared to the high expansion in Europe, North America and Asia.

Despite the large niche expansion in Europe, North America and Asia (Fig. 2), the native and non-native climatic niches in these continents were still statistically more similar than expected by chance ($p < 0.05$). In fact, according to Bates & Bertelsmeier´s review (2021), half of the species examined that had similar niches under a similarity test showed a niche shift. Thus, instead of deciding whether or not a niche is conserved, it seems appropriate to consider different aspects of the climatic niche, examining the different ways in which niches may differ (as the frequency of the occupied climate, and the frequency of the available climate) and what this entails for species distributions (Wiens & Graham 2005).

Niche shifts in invasive species: the role of species' traits

In addition to changes in climate availability, there are intrinsic characteristics of plant species that may be linked to niche shifts. Reported traits of *Datura stramonium* like high dispersibility (human-mediated), early germination and rapid growth, self-compatibility, and persistent seed bank (Benvenuti 2007, Dorado et al. 2009, Motten et Antonovics 1992, Reisman-Berman et al. 1991, Weaver & Warwick 1984), among others, are related to the success of alien invasive plants (Baker 1965). Although invasion may not involve a niche shift, and vice versa, the traits related to invasiveness can favor a climatic niche shift by promoting the establishment of the species in new areas, be by adaptative directional selection or simply by selected phenotypic plasticity (Clements & Ditommaso 2011). A key trait of *D. stramonium* that could have favored its niche shift and worldwide expansion is its annual life cycle throughout its native and invaded range. In the temperate non-native area, having a short life cycle (4–5 months) allows *D. stramonium* to avoid the cold stress in winter and seedling mortality due to late frosts. *Datura stramonium* is self-compatible and has a mixed mating system although selfing predominates (Motten & Antonovics 1992; Motten & Stone 2000). According to Levin (2010), in addition to reproductive assurance, self-fertilization in colonizing populations acts as a barrier for pollen flow from core populations, which can promote the adaptation to a different environment.

Herbivory and traits related with resistance and/or resilience to herbivores may also be related to range expansion in invasive plants, when these are released from herbivore consumption (the Enemy Release Hypothesis, Keane & Crawley 2002). Actually, *D. stramonium* populations in Spain are much less damaged than native populations in Mexico (Valverde et al. 2015), and their alkaloid concentration is 20–40 times lower (Castillo et al. 2019). However, these plants have not lost the capacity to produce alkaloids, which suggests some plasticity in this trait (Núñez-Farfán et al. 2024). In other cases, adaptive directional selection has been demonstrated in specific parts of the invaded range in traits related with invasive ability of *D. stramonium* populations: shorter time to flowering, heavier seeds with larger cotyledons that favor faster growth in Canada in comparison with southern populations (Weaver et al. 1985), as may happen with North American populations with reduced herkogamy (stigma-anther separation) leading to higher selfing rate (Motten & Stone 2000), assuring seed set. All these changes affect invasive vs native populations, but their prevalence throughout the world range remains to be explored.

Occurrences in zero suitability areas: the role of microhabitats and irrigation

Datura stramonium occurrences reported in extremely arid environments, with virtually zero suitability according to the climatic niche model, could be explained by microhabitats. Microhabitats play a crucial role for ruderal *D. stramonium* given its need for disturbance and water. In addition to ruderal habitats like roadsides and wastelands, river edges and irrigated fields are generally associated with *D. stramonium* occurrences, as it was reported for many Mediterranean invasive species growing in summer (Lloret et al. 2005). River edges are frequently

occupied by the species in both native and non-native areas, while irrigated summer crops are highly associated with non-native *D. stramonium* occurrences (Follak et al. 2017). In the native area, *D. stramonium* is usually not found in cultivated fields (J. Núñez-Farfán, pers. comm.), being at most present in the field margins. Although few occurrences were reported in arid places, irrigated areas should not be neglected as a possible way to expand *D. stramonium* range and climatic niche, as irrigation in summer crops can compensate for water stress when precipitation is not sufficient or not at the right time in the case of a marked precipitation seasonality (Fig. S3 supplementary material) (Godoy et al. 2009; Lloret et al. 2005; Vilà et al. 2008a, b). Including these local factors could be critical to improving risk assessment (Chambers et al. 2014) by mapping the areas of potential range expansion accounting for irrigation, particularly in drier climates.

Conclusions

In conclusion, *D. stramonium* niche expansion into cooler climates appears to be driven by an imbalance in the frequency of available climates between the native and non-native ranges, with proportionally more areas of low temperatures in the non-native range. Species traits like the annual life cycle, the early-season emergence and rapid growth, and the persistent seed bank, may have facilitated *D. stramonium* establishment in areas cooler than the native area, as well as self-fertility in locations lacking its specialized pollinators. Low levels of niche unfilling in *D. stramonium* do not appear to be related to longer residence times but may instead be linked to a closer climate match between the native and non-native ranges.

The dependence on microhabitats created by humans is very strong in the non-native area (irrigated crops, disturbed areas) and the global distribution may be contingent on the availability of these habitats. This narrow dependence could be stronger than the available macroclimate, as occurrences were found outside the niche limits. This suggests that predicting the distribution of *D. stramonium* at more local scales cannot rely on macroclimatic data alone and should include irrigation and disturbance variables.

Despite a very long residence time, there are still areas that could be in the colonization process, and the species may still expand its distribution, notably in the warm zones in the non-native area.

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Author contributions J.A. conceived the study. C.V.J. collected the data, performed the analyses with supervision of F.R.S. and wrote the manuscript with contributions of F.R.S. and J.A. All authors reviewed and approved the final version of the manuscript.

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Data availability The climatic data are available via the WorldClim database (https://www.worldclim.org/data/worldclim21.html), and the *Datura stramonium* occurrences were obtained from the Global Biodiversity Information Facility (https://doi.org/10.15468/dl.5unuhj).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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