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ORIGINAL PAPER

High potential for *Brassica tournefortii* spread in North American introduced range, despite highly conserved niche

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Abstract Identifying areas vulnerable to the spread of invasive species is critical for designing effective management plans. Species distribution modeling is commonly used to predict species suitable habitat. However, invasive species may not be in equilibrium with environmental conditions within the introduced range, leading to inaccurate predictions. We focused on *Brassica tournefortii* to (1) assess the role of niche dynamics, (2) identify environmental drivers facilitating spread, and (3) identify suitable habitat within currently un-invaded areas in North America (introduced range) by quantifying the realized niche in its home range (Mediterranean basin and Middle East) and introduced range. *Brassica tournefortii* continues to expand its distribution within North America, threatening native species and altering ecosystem dynamics through invasion. We found that *Brassica tournefortii* has a highly conserved environmental niche, driven primarily by warm and dry climates with resource-limited soils. Despite high niche stability, we detected environmental non-equilibrium between the ranges, with 55% niche unfilling and 1% expansion into more arid and resource-limited environments within the introduced range. Our distribution models also highlighted invadable regions in the introduced range where this species is not found currently, indicating opportunities for this species to continue to spread within North America, and suggesting that previous estimates may underestimate areas at risk for invasion. To improve spatial predictions of the potential spread of invasive species, we must consider the role that niche dynamics and environmental equilibrium play during biological invasions.

Keywords Invasive species · SDM · Niche dynamics · Niche shifts · Niche stability · COUE

Introduction

Identifying areas at risk for the potential spread of invasive species is essential for prioritizing invader management and prevention efforts to reduce an invader's ecological impacts. Species distribution

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modeling (SDM) is one important tool that can forecast invader spread by creating spatial predictions of species suitable habitat and identifying important drivers of species distributions (Franklin 2010). However, when species are introduced to novel areas, a variety of niche dynamics can emerge depending on whether the introduced area matches or differs from the environmental conditions of a species' native range (Broennimann et al. 2012; Atwater et al. 2018). A species' niche may be consistent between the native and introduced ranges (i.e., niche conservatism or stability), or a species niche may experience a shift to match environmental conditions in its introduced range. Many studies often assume this and fail to account for potential niche shifts within the introduced range. Failure to account for niche shifts can lead to underestimating suitable habitat within the introduced range, limiting our ability to predict invader spread and successfully manage invaders (Pili et al. 2020).

Evidence for niche shift dynamics between species' native and introduced ranges is equivocal. Some studies support that niche shifts are rare (Petitpierre et al. 2012) and focus on dynamics of how a species occupies similar niche space between the native and introduced range. Within this niche conservatism approach, a species may exhibit a suite of potential dynamics (Fig. 1): (1) where they occupy the same suitable habitat in both ranges (i.e., stability), (2) where they fail to occupy suitable habitat in the introduced range that is occupied in the native range (i.e., unfilling) or (3) where they are occupying suitable habitat in the introduced range that is not occupied in the native range (i.e., expansion) (Atwater et al. 2018). Unfilling is important for predicting the spread of species since these conditions are considered suitable for the species but are unoccupied, perhaps due to limitations in dispersal or lag effects in spread (Qiao et al. 2017). Moreover, niche unfilling may occur among species that are not in equilibrium with their environment (i.e., species-environment non-equilibrium). Expansion, conversely, can be due to changes in biotic pressures (i.e., enemy release hypothesis), physiological adaptations, or high phenotypic plasticity of the invader in the introduced range (Atwater et al. 2018). Conversely, other studies support that niche shifts are relatively common among invasive species (Atwater et al. 2018), showing that in models comparing the climatic niche of species' native and introduced ranges, shifts are often dependent on the species growth forms and traits (Wang and Wan 2021; Vásquez-Valderrama et al. 2022). When the underlying niche conservatism and species-environment equilibrium assumptions are violated, this can lead to underestimating the spread of invasive species and reduced spatial transferability (Mainali et al. 2015; Andrade et al. 2019; Liu et al. 2022), thus limiting the applicability of SDMs for invasive species management.

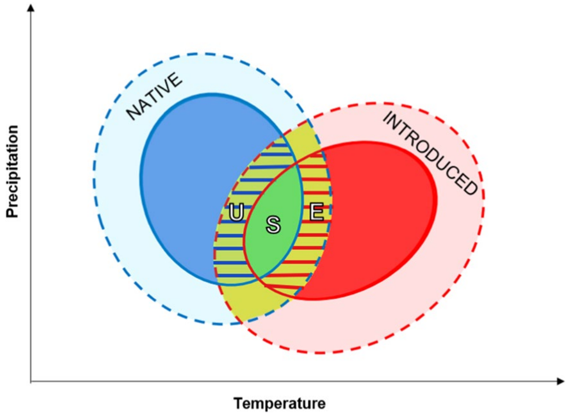

Fig. 1 Conceptual figure of niche dynamics. Dashed lines indicate available climate, solid lines indicate occupied environmental conditions (realized niche). Blue represents the native range, red represents the introduced range, yellow and green represent analogous climate between ranges. (U) Niche unfilling is the proportion of analogous conditions that are occupied in the native range, but not occupied in the introduced range, (S) Niche stability is the proportion of overlapping analogous conditions that are occupied in both the native and introduced ranges, (E) Niche expansion is the proportion of the realized niche in the invaded range that is available, but not occupied in the native range. Figure adapted from Guisan et al. (2014) and Atwater et al. (2018)

With this in mind, researchers have emphasized that the approach used to model invasive species distributions matters and should be standardized to include the native and introduced ranges to facilitate comparisons between studies and improve spatial predictions (Broennimann and Guisan 2008; Guisan et al. 2014; Di Cola et al. 2017). Yet, spatial predictions for invasive species continue to rely on data from the introduced range only (Kariyawasam et al. 2019; Jarnevich et al. 2022). For species that are continuously spreading and have broad distributional ranges, using a subset of available data for model training may result in inaccurate model predictions

(Yates et al. 2018), particularly if the niche conservatism or species-environment assumptions are violated (Foster et al. 2022). Hence, the importance of incorporating occurrence data from the native and introduced ranges when modeling distributions of invasive species.

Our ability to detect shifts is improved when we expand beyond models that only use climatic predictors. Edaphic factors such as soil texture and nutrient availability (Ulrich et al. 2014; Maestre et al. 2021) are also major factors related to plant distributions and can contribute valuable information as to what is driving the establishment and spread of a species but are not regularly included in SDMs. In one study, Velazco et al. (2017) found that distribution models that included both edaphic and climatic variables as predictors improved model accuracy compared to models that only included climatic predictors. Additionally, defining the species fundamental niche (i.e., full range of environmental conditions a species can theoretically live in) is often unfeasible, emphasizing the importance of studying niche shifts within analogous environments in order to capture changes within the realized niche (e.g., environmental conditions that a species currently occupies). Disentangling dynamics comparing non-analogous environments is challenging with only information on the species occupied (realized) niche. Capturing broader species-environment relationships beyond climate may help further delimit invasive species establishment and spread patterns.

Brassica tournefortii (Brassicaceae; sahara mustard) is an herbaceous winter-annual forb native to the Mediterranean basin and parts of the Middle East. This species was accidentally introduced into North America through California's date palm tree trade in 1920 (Sanders and Minnich 2000). Despite the early introduction year, this species has only more recently (within the past 2–3 decades) started rapidly expanding across southwestern United States and Northern Mexico, altering ecosystem dynamics in the process (Winkler et al. 2018). This invader reduces native plant flowering and fruiting within the Colorado desert by 80–90% in sand dune communities, threatening many endemic plants (Barrows et al. 2009). Additionally, *Brassica tournefortii* has been linked to changes in community structure by reducing plant and arthropod richness and abundance within drylands (Van Tassel et al. 2014). With the distribution of this species continuing to spread, efforts to model spread are critical to help invasive plant management minimize any further impacts.

Species distribution models have been developed to understand the drivers of *Brassica tournefortii's* spread and improve the management of this species. However, those models have either been limited to regional scales (Berry et al. 2014; Sanchez-Flores, 2007), have primarily focused on climatic factors (Curtis and Bradley 2015), and all except Li et al. (2015) have used occurrence points from only the introduced range of the species to calibrate their models. Additionally, this species can adjust certain physiological traits such as phenology and investment in reproductive structures to match environmental drivers in the North American introduced range (Marushia et al. 2010; Winkler et al. 2018), making it an exceptional study system to test the niche conservatism and species-environment relationships that are important to modeling invasive plant species distributions.

Here, we use a global biogeographic approach to assess the potential spread of *Brassica tournefortii* in its North American introduced range. We first assess underlying niche dynamics and ask (1) Is *B. tournefortii's* environmental niche conserved within its North American introduced range? and (2) What climatic and edaphic factors are shaping the distribution of *B. tournefortii*'s environmental niche within its introduced range? Lastly, we forecast invasion potential and ask 3) What un-invaded areas within the North American introduced range support suitable habitat for *B. tournefortii*? Answering these questions will provide a more holistic understanding of the variables driving the spread of the species and improve the accuracy of spatial predictions to be used for invasive species management.

Methods

Species records

We retrieved 12,620 global occurrence records in both *Brassica tournefortii's* native range and North American introduced range using four databases: Global Biodiversity Information Facility (GBIF.org, https://doi.org/10.15468/dl.4fmk2n), SEInet (biodiversity data accessed through Data Portal, http//:swbiodiversity.org/index.php, 2022–03-14), Integrated Digitized Biocollections (https://www.idigbio.org/portal, 2016) and research-grade occurrence points from iNaturalist (https://doi.org/10.15468/dl.wbw2pe) from 1950 to 2022. Occurrence data were cleaned using the 'bdc' package in R (Ribeiro et al. 2022) by georeferencing records, removing duplicates, adding a geographic correction filter to remove records within 3 km of capital city and province/state centroids, records within 10 km around country centroids, records within 111 km of the GBIF headquarter, records within 100 m of zoo and herbaria to exclude cultivated occurrences, and lastly applied a 0.1 distance in decimal degrees buffer around the country records for coordinate precision. After the filters were applied, we identified 8138 unique occurrence points (native range = 517; introduced = 7620).

Environmental variables

To assess the factors shaping the distribution of *B. tournefortii*, we focused on environmental variables that are important drivers of plant community dynamics in drylands, where this species commonly invades (Williams et al. 2012). Since this species is an annual winter forb (germinating in response to cold-season precipitation), bioclimatic variables were selected to capture intra-annual seasonality and annual average temperature and precipitation during the winter growing season (Table 1). We also selected edaphic variables important to plant establishment and growth dynamics. Bioclimatic factors averaged from 1950–2000 were downloaded at a 1 km spatial resolution from the WorldClim database, version 2.1 (Hijmans et al. 2005), and the edaphic variables were retrieved from the ISRIC World Soil Information database at a 250 m resolution (Poggio et al. 2021). Since predictors varied in resolution, we used a bilinear interpolation method, which calculated a weighted average of nearby cells to resample the original soil layers to create a common resolution of 1 km. We performed a correlation analysis among bioclimatic and edaphic variables to detect pairs with a high correlation > |0.75|, resulting in 12 uncorrelated predictor variables. These included six bioclimatic variables and six edaphic variables (Table 1).

Data analysis: niche dynamics

To assess the role of niche dynamics in facilitating the spread of *B. tournefortii* in North America, we first limited the model training areas and study extent to the World Wildlife Fund's terrestrial ecoregions (Olson et al. 2001) found within the native range of the species and containing occurrence data (Table 2). These included (1) temperate conifer forests, (2) temperate grasslands, savannas, and shrublands, (3) Mediterranean forests, woodlands, and scrub, and (4) deserts and xeric shrublands (Fig. 2). To quantify the environmental niche of the native and North American introduced ranges that are within the ecoregions found in the native area, we used the Centroid shift, Overlap, Unfilling, and Expansion (COUE) methodological framework (Broennimann et al. 2012) in the 'ecospat' package in R (Di Cola et al. 2017). To assess the contribution of our 12 variables to the environmental niche, we ran a Principal Component Analysis (PCA), and created a density distribution for each grid cell using a kernel density function for the native range environmental niche and the introduced range environmental niche. We then used the first two axes of the PCA to quantify niche overlap between the two ranges by using Schoener's *D* metric (Schoener 1970), which compares native and introduced range density distributions, calculating a number ranging between 0 and 1, where 1 indicates complete niche overlap. To test if the niche is conserved, we ran niche similarity and equivalence tests comparing the overlap between the native and North American introduced niches to 1000 randomly generated null distributions (Warren et al. 2008). We then quantified the following niche dynamics between the two ranges in analogous environmental space: niche stability, niche unfilling, and niche expansion.

Data analysis: species distribution modeling

To identify areas vulnerable to the spread of *Brassica tournefortii* within the introduced range, we used an ensemble SDM approach that combines predictions of various modeling techniques to reduce model uncertainty (Araújo et al. 2007; Thuiller et al. 2019). We used the same 12 environmental variables and study extent used to analyze niche dynamics to create our SDMs. To reduce sampling bias and redundancy in environmental space, which

Table 1 Summary of environmental variables and the rationale for including them in this study

Type	Variable	Units	Ecological rationale
Climatic	Precipitation seasonality (CV)	%	The coefficient of variation for monthly precipitation over the year can provide important information on whether a species is influenced by variability in precipitation
	Precipitation of the coldest quarter	Millimeters (mm)	The total precipitation during the three consecutive coldest months of the year; precipitation and cold temperatures may influence the species distribution
	Precipitation of the wettest quarter	Millimeters (mm)	The total precipitation during the three consecutive wettest months of the year; precipitation amount during its active growing season may influence the species distribution
	Average temperature of the driest quarter	Degrees Celsius (°C)	The mean temperature of the three driest consecutive months of the year; dry season temperature seasonal hot and arid climate may influence the species distribution
	Average temperature of the coldest quarter	Degrees Celsius (°C)	The mean temperature of the three consecutive coldest months of the year; temperature during the species active growing season may influence the species distribution
	Temperature annual range	Degrees Celsius (°C)	The range of extreme temperature conditions (Maximum temperature of the warmest month -Minimum temperature of the coldest month) can provide information on whether a species is sensitive to seasonal temperature variation
Edaphic	Clay content	g/100 g (%) Percentage of clay particles (<0.002 mm)	Clay particles contribute to the soil's ability to hold on to nutrients for plants
	Silt content	g/100 g (%) Percentage of silt particles (≥ 0.002 mm)	Silt particles provides water retention and air circulation in soil. Silty soil is considered to be one of the more fertile types of soil
	Sand content	g/100 g (%) Percentage of sand particles (>0.05 mm)	Sand particles are large, which provide fast drainage of water and do not hold nutrients well
	Bulk density	kg/m^3	Bulk density is important for infiltration and an indicator of soil health. The higher the bulk density, the more compact the soil is and higher mechanical impedance to root growth
	Available water holding capacity (AWC)	Volumetric Fraction (Field capacity = Permanent wilting point)	AWC provides information on the maximum amount of water available in the soil for plant uptake
	Soil organic carbon (SOC)	g/kg	SOC indicates the amount of organic matter in the soil, which contributes to a variety of soil properties that are useful for plants

Table 2 *Brassica tournefortii* occurrences by WWF Ecoregions for native and introduced ranges

	Native occurrences	Introduced occurrences
Ecoregion		
Temperate coniferous forest	19	0
Temperate grasslands, savannas, and shrublands	75	103
Mediterranean forests, woodlands, and scrub	308	693
Deserts and xeric shrublands	115	6824
Total	517	7620

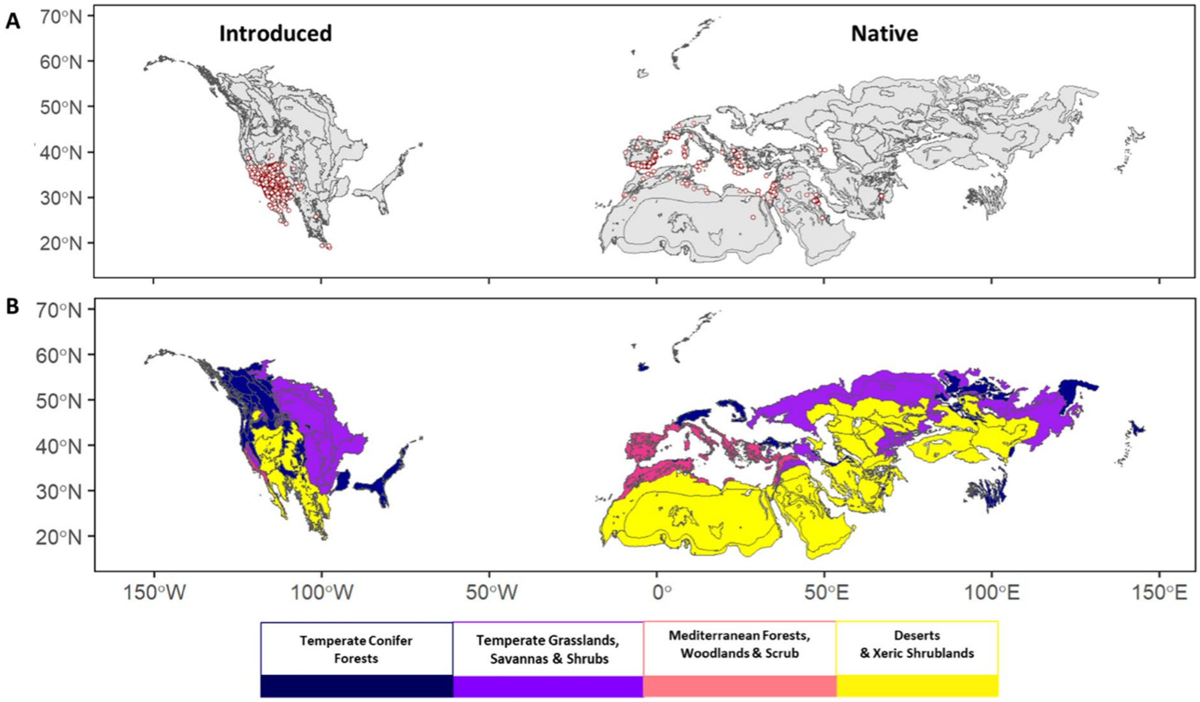

Fig. 2 Study extent, showing the native and introduced ranges of *Brassica tournefortii*. Colors represent various biomes of WWF Ecoregions (Olson et al. 2001) found within the ranges occupied by the invader

can influence model prediction, we used environmental filtering to thin the original 8138 occurrence records to 1843 records used for modeling (Varela et al. 2014; Velazco et al. 2020). We used an environmental filtering procedure in which occurrence records are filtered based on partitions or bins in environmental space, where more bins result in a greater number of filtered occurrence records. Because environmental filtering is sensitive to the number of bins (i.e., number of classes in which each environmental variable is split) used to divide environmental space, we tested 2, 3, 4, 6, 8, and 12 bins and then calculated the resulting spatial autocorrelation between variables based on the Moran's I index. The number of bins with the lowest average spatial autocorrelation between variables and the highest number of occurrences (12) was selected to filter occurrence records. Twelve bins was the optimal split. We therefore split the environmental variables into 12 groups and filtered species occurrences based on their environmental conditions, resulting in 1843 records.

To measure model transferability, models were evaluated regarding their capacity to project on geographical areas different from those used for model training (Roberts et al. 2017). We applied a spatial block partitioning method by partitioning our data into 12 spatially structured groups. To select the block cell size that best fit our species records, we tested 30 sizes (range of block size resolution). The optimum grid size was the one with the lowest spatial autocorrelation (i.e., Moran's I), maximum environmental similarity (i.e., minimum Euclidean distance), and the minimum difference of records among groups (i.e., standard deviation-SD; Velazco et al. 2019) based on our data set. Since our dataset consists of presence-only records, which is often the case for introduced species, we generated pseudo-absence records equivalent to the number of presence-only records to be able to use species distribution modeling techniques that require presence-absence data. Additionally, we created 18,000 background points (required by MAXENT) throughout the extent of our study area and extracted environmental variable data from our presence/pseudo-absence and background data before fitting our models.

We implemented five commonly used SDM algorithms: Generalized Linear Model (GLM), General Boosted Regression Model (GBM), Support Vector Machine Model (SVM), Random Forest model (RFM), and Maximum Entropy (MAXENT). For all our models, we obtained suitability values using the threshold that maximized the Sorensen similarity index, where values above the threshold were designated as suitable habitat, while values below this threshold were designated as non-suitable habitat. We fitted the GLM using a binomial distribution family and second-degree polynomials for continuous variables. For MAXENT, we used cloglog transformations as the response type. To optimize the performance of our algorithms, we performed hyperparameter tuning for GBM, SVM, RFM, and MAXENT algorithms with a range of specific values for our species (see supplemental Table 1. for model tuning and hyperparameter values), where the Sorensen metric was used for selecting the best combination of hyperparameters to tune each model (Schratz et al. 2019).

To further increase model transferability and reduce model uncertainty, we created ensemble models using the predictions of individual models with an AUC $>$ 0.95 (indicating high accuracy). GBM, SVM, RFM and MAXENT models were all retained to create an ensemble model, using the same threshold and performance metrics used for fitting and validating the individual models. We tested three types of ensemble modeling approaches—(1) using a weighted average based on model performance (meanw) (based on the Sorensen index), (2) using the average of the best models (meansup) (average of the models with above average performance according to Sorensen index), and (3) averaging cells with suitability values above the threshold that maximized the Sorensen index (meanth)—and selected the best performing ensemble model (meanw). Using the output of the ensemble model, we created a geographical prediction of habitat suitability across our focal species' study extent. All SDMs were created using the 'flexsdm' package in R (Velazco et al. 2022). We performed all analyses using R version 4.1.2. (R Core Team 2021).

Results

Niche dynamics

We found low niche overlap (*Schoener's* $D = 0.25$, where 0 indicates no overlap and 1 represents complete overlap) between the native and introduced range of *Brassica tournefortii*. When we compared the niche overlap to null distributions, we found that the niches were not identical (niche equivalence test, $p = 0.009$) between ranges, but the similarity (overlap) was greater than expected by chance (niche similarity test, $p = 0.005$), indicating evidence for niche conservatism (Fig. 3A; SI. Figure 1). We found additional support for niche conservatism when we assessed individual niche dynamics and found that 99% of the occupied niche in the introduced range is stable (i.e., falls within the native range niche; gray shading in Fig. 3A). This suggests that although niche overlap is low between ranges, this is primarily due to unfilling, not expansion; this species occupies very similar environments in both ranges. We additionally observed that this species occupied similar environmental space in both ranges, as most occurrences existed within environmental space that is relatively common between both ranges (Fig. 3B, C). Our models also detected extensive

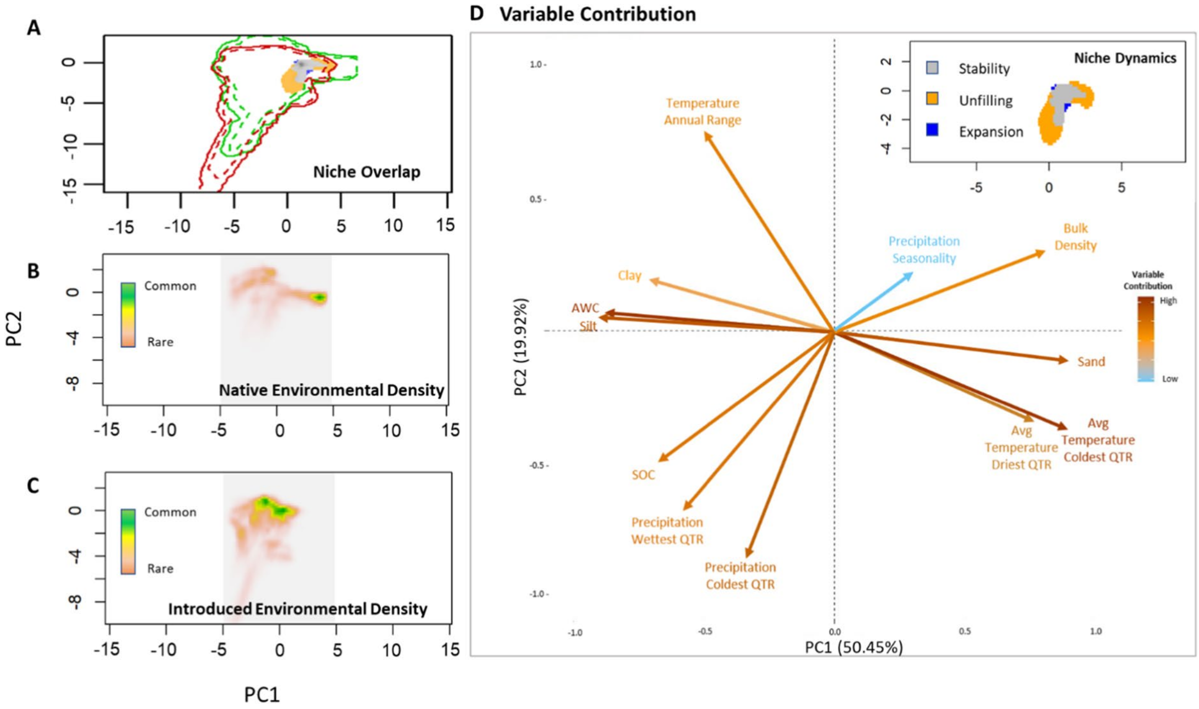

Fig. 3 **A** Niche overlap between analogous climate of the native (green outline) and introduced (red outline) range of *Brassica tournefortii*. Stable (gray) is occupied in both in native and introduced ranges; Expansion (blue) is occupied in the introduced but not native range (Stable + Expansion = occupied in introduced range); Unfilling (gold) is occupied in the native range, but not occupied in the introduced range. Environmental Density distribution in 2-dimensional available environmental space within the **B** native range and **C** introduced range. Red tones indicate an environment that is associated with lower occurrences, while yellow and green tones indicate environmental conditions that are more commonly occupied. **D** Ordination plot for the first two principal components generated in a PCA, where warmer colors indicate higher variable contribution, while cooler tones indicate lower variable contribution. The inset provides a zoomed in image of the niche dynamics plotted in A. PC scores correspond to the ordination presented in D

suitable environmental conditions available within the introduced range (Fig. 3C) that remain unoccupied, primarily within environmental conditions that are relatively rare within the native range (Fig. 3B). The differences between commonality of environmental densities (depicted by green pixels in Fig. 3B, C) between ranges explain the overall low niche overlap value. Specifically, we found that 55% of this species' environmental niche remains unfilled within the introduced range, revealing evidence for species-environment non-equilibrium. We did identify a small (1%) niche expansion within the introduced range, indicating the *B. tournefortii* is occupying some areas with environmental conditions that had not been previously occupied within the native range.

Drivers of distribution

We found that the twelve predictor variables selected for this study explained 70.37% of the variation in our data, with the first PCA axis explaining 50.45% and the second PCA axis explaining 19.92% (Fig. 3D). The first PCA axis (PC1) described a gradient of soil structure and soil water availability, where negative values were associated with greater available water holding capacity, higher percent silt, clay and low bulk density, while positive values had higher bulk density and percent sand. The second PCA axis (PC2) described a gradient of precipitation and temperature, where negative values were associated with cold-wet winters, and warm summers, while positive values had higher seasonal temperature ranges and precipitation variation. Further, our ordination revealed that soil variables along PC1 (Fig. 3D) are the main drivers of variation within the native environmental density (Fig. 3B). In contrast, within the introduced range, temperature, and precipitation variables along PC2 strongly influence environmental density (Fig. 3C) in addition to soil variables.

Within *Brassica tournefortii's* stable environmental niche, we found that species occurrence density coincided with the warmest temperatures of the coldest quarter (i.e., winter), and the driest quarter (i.e., summer), suggesting this species prefers to establish in warm conditions (Fig. 3D). We also found that this species is not strongly influenced by interannual variability in precipitation as the contribution of precipitation seasonality to the current stable range was relatively weak, indicated by the blue arrow in Fig. 3D, compared to the other predictor variables. In addition to arid climate, we also found that this species is mainly found on soils that have high bulk density and sand content, as well as low resource availability (e.g., low soil organic carbon, available water holding capacity).

Most niche unfilling occurred in environments that contained relatively cooler and wetter climate during the growing season, as well as soils with higher nutrient content compared to the stable niche (Fig. 3D). Yet, we also detected a portion of niche unfilling within environments that had even more arid climate and sandier soil than areas currently occupied within the introduced range. We also observed drivers of niche expansion and found that this species is expanding its realized niche within the introduced range into more arid environments with higher seasonal variations in temperatures compared to environments occupied within the native range.

Habitat suitability

Our SDMs performed very well across the different algorithms, with AUC values ranging from 0.97–0.98 (Table 3). Ensemble models that used a weighted average based on model performance had the highest model performance compared to the other ensemble modeling approaches and was used to create spatial predictions (AUC: 0.988 ± 0.003, TSS: 0.92 ± 0.02, Boyce Index: 0.97 ± 0.019, Sorensen: 0.963 ± 0.01, for all model performance see supplemental Table. S1.)

Table 3 Summary of Model performance values for individual and ensemble species distribution models for *Brassica tournefortii*

MODEL	AUC	TSS	JACCARD	BOYCE	IMAE
MAXENT	0.986	0.915	0.920	0.962	0.791
SVM	0.986	0.927	0.930	0.751	0.934
RAF	0.987	0.910	0.913	0.978	0.887
GBM	0.980	0.901	0.902	0.915	0.907
meanw	0.990	0.924	0.930	0.972	0.880
meanthr	0.980	0.921	0.925	0.864	0.885
meansup	0.990	0.930	0.932	0.873	0.862

Number of presences and absences for each model was 1843. Model abbreviations: SVM = support vector machine, RAF = random forest, GBM = generalized boosted regression model, meanw = Weighted average of models based on their performance; meanthr = Averaging performed only with those cells with suitability values above the threshold at which Sorensen is highest, meansup = Average of the best models

Based on our ensemble model, we found contrasting distributions of habitat suitability between native and introduced ecoregions (Fig. 4). In the native range, we observed that most of the highly suitable habitat (within the range of 0.70–1; blue to purple colors) was found in the Mediterranean ecoregion. Despite the desert and xeric shrubland ecoregion comprising a large portion of the native range, most habitat found within this ecoregion was predicted to have low suitability (0–0.50). However, our models did identify moderate (0.50–70) to high habitat suitability within countries in the middle east near the Mediterranean and Arabian sea, suggesting that this species mainly occupies coastal rather than inland habitat within the native range. As for the temperate grasslands and temperate conifer forests within the native range, our models predicted low to no habitat suitability within these ecoregions.

Like the native range, Mediterranean forests, woodlands, and scrub ecoregions also contained highly suitable habitat in the introduced range. In contrast to this species' native distribution patterns, we found that desert and xeric ecoregions within the introduced range contained the largest amount of highly suitable habitat and occurrences (Table 2). Similar to our findings of stable and expansion niche dynamic drivers, we found that high habitat suitability was primarily found in warm and dry environments with resource-limited soils. For instance, "warm" deserts such as the Chihuahuan, Sonoran

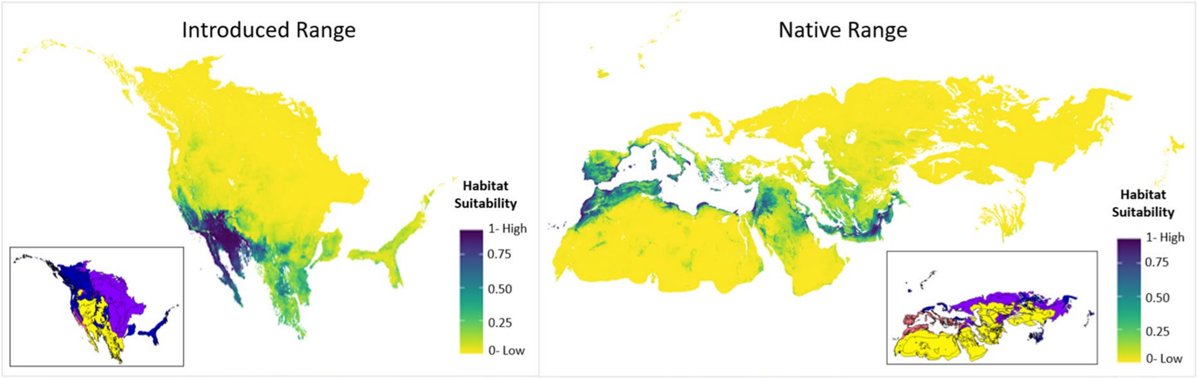

Fig. 4 Habitat suitability of *Brassica tournefortii* from ensemble model predictions constructed using a weighted average based on model performance of GBM, RAF, SVM and MAXENT models. Color scale represents suitability, where yellow indicates low habitat suitability and dark blue indicates high habitat suitability. Inset maps refer to the WWF Ecoregions from Fig. 2

and Mojave deserts contained the highest suitability, reflecting current invasion patterns for *Brassica tournefortii* within North America. The Great Basin Desert, conversely, which is considered a “cool” desert, had either no or very low habitat suitability, demonstrating that the spread of this species is likely limited by cold winter temperatures during its growing season. Our models also detected suitable habitat within North American temperate conifer forests and temperate grasslands, where this species is currently not found. However, suitability was low (<0.5) and limited in extent, likely due to these ecoregions containing more productive soils and cooler and wetter environments.

Discussion

Comparing the realized environmental niche between a species’ native and introduced range is critical to improving predictions of invader spread. Here, we build on previous modeling efforts of habitat suitability for *Brassica tournefortii* by comparing the realized environmental niches between native and introduced ranges and expanding the environmental niche dimensions to include edaphic as well as climatic factors to understand the full breadth of environmental tolerances of the species. Our study provides support for the role of edaphic variables such as soil structure and soil properties in influencing the distribution of *B. tournefortii,* in addition to the limited edaphic and topographic variables previously identified for this species (Sanchez-Flores, 2007; Berry et al. 2014). In our study, using a biogeographic approach revealed that despite having a highly conserved and stable environmental niche (very little niche expansion), *B. tournefortii* is not at equilibrium with its environment within the introduced range, as it still has substantial unfilled habitat remaining. This suggests that our focal invader is not restricted to resource-limited drylands in its introduced range and has the potential to continue to spread into both more mesic and more extreme xeric habitats within the unoccupied but suitable habitat in North America.

Evaluating niche shift dynamics is key to better estimating suitable habitat and mechanisms of spread within introduced ranges (Broenimann and Guisan, 2008; Guisan et al. 2014). Failure to account for niche conservatism can often result in inaccurate predictions of niche shifts when indeed a species is demonstrating niche unfilling (Petittpierre et al. 2012). In our study, we observed that *B. tournefortii* exhibited strong niche unfilling, and these findings are consistent with previous studies that have found that niche unfilling is more common than niche expansion among introduced species (Strubbe et al. 2013; de Andrade et al. 2019; Liu et al. 2020). However, we did observe small evidence of niche expansion where the invader was expanding into environments that were hotter and drier compared to its native range. Petittpierre et al. (2012) previously identified a similar pattern of niche expansion for species that are native to Europe and introduced to Australia and North America. However, due to the limited occurrence records of *B. tournefortii* in its native range compared to the availability of records within the introduced range in our study, there is a possibility that the 1% niche expansion we observed is an artifact of sampling bias. Moreover, with the disparity in sampling efforts across the globe, we encourage the implementation of international BioBlitz to increase data acquisition by academic and community scientists, especially in data-limited geographic regions. Community science efforts are a cost-effective way to both improve species surveillance and build stronger connections between community members, policy makers, and scientists (Cesar de Sa et al. 2019; Roy-Dufresne et al. 2019).

Considering that numerous invasive species can tolerate a broad range of environmental conditions, the accuracy of climate change and range-shifting species distribution models are likely to benefit from using data sets that use a global biogeographic approach to train models and expand beyond climatic predictor variables. For instance, climate change projection models created using regional datasets from the introduced Southwest United States predicted a 34% reduction in *Brassica tournefortii* presence under conservative climate change, and a 29% expansion under worst-case climate change scenarios (Curtis and Bradley 2015). According to our study, a large portion of the Southwestern United States is already considered suitable habitat under current climate conditions, which was not captured using the regional dataset from the introduced range. Additionally, we observed range-specific drivers of occurrence between the native and introduce ranges; within *B. tournefortii's* native range, factors related to soil structure and soil water availability were the main drivers; while precipitation played a bigger role in driving the species distribution compared to soil properties within the introduced range. Range-specificity can occur among invasive species with large niche breadths as a result of provenance-by-environment interactions, where the evolutionary history in the native range leads to pre-adapted genotypes that can respond in distinct ways depending on the interactions encountered within the new range (Zenni et al. 2014; Eyster and Wolkovich 2021). As the changing climate continues to alter ecosystems globally, it is important to use a biogeographic approach to capture as much of the environmental tolerance and range-specificity to identify drivers of invasive species spread.

Our study demonstrated that *B. tournefortii's* stable niche includes occurrences that commonly occupy arid and resource-limited environments, reflecting current patterns of invasion by this species in North American drylands, but it is important to note that biotic interactions also play an important role in determining a species' distribution. Our study revealed a large amount of highly suitable, but unoccupied habitat within California's coastal Mediterranean ecoregion. This habitat like much of California's mesic and semi-arid landscapes has a long history of disturbance and invasion, with several taxonomically related invasive mustards (i.e., *B. nigra*, *Hirshchfeldia incana, Sisymbrium irio)* already occupying this range. Competition with these other mustards may be hindering *B. tournefortii*'s ability to colonize the unfilled Mediterranean ecoregion) (Marushia et al. 2010). Moreover, native species and invaders within this region can promote plant-soil feedbacks that inhibit germination and establishment of other species including taxonomically related mustards such as *B. tournefortii* (Singh and Meyer 2020; Miller et al. 2021). In the case of temperate conifer forest and grassland ecoregions where our models predicted habitat as low-mid suitability, the combination of dispersal limitations, as well as the vegetation of the resident communities (i.e., trees and shrubs) suggest a low probability of invasion in these areas. In temperate ecoregions, limited light interception through the canopy increases competition among understory species, further influencing herbaceous annual species establishment and growth (Landuyt et al. 2019).

Another compelling facet of interpreting niche dynamics (although outside of the scope of this study) is the potential for increased evolutionary capacity through multiple introductions. In our study, we observed that *Brassica tournefortii* tolerates a broad range of environmental conditions. This may be because there have been at least three separate introductions of *B. tournefortii* in North America from different geographic locations within its native range, resulting in three genetically distinct sub-populations, with evidence of some admixture between populations (Winkler et al. 2018). The multiple introductions of this species into North America may be contributing to increased genetic diversity and phenotypic plasticity, potentially contributing to the broad environmental tolerances. Future studies should focus on testing the evolutionary and physiological differences between the subpopulations of *B. tournefortii* to provide insights into eco-evolutionary dynamics that may be facilitating the spread of this species.

Implementing knowledge about the mechanisms driving niche dynamics can improve the management of biological invasions. Prevention and eradication of invading species are highly plausible if plans for Early Detection and Rapid Response (EDRR) are put into effect in areas identified as containing environmental conditions that match a species niche unfilling or expansion. For instance, despite the high habitat suitability within the North American Mediterranean ecoregion, *B. tournefortii* has not occupied all suitable habitat, indicating niche unfilling. In these unfilled areas, *B. tournefortii* should be added to invasive species watch lists to detect early germinants and prevent the spreading of populations. In addition to monitoring detection, it is important for management plans to limit the spread of invasive species is by controlling human-mediated dispersal. Road networks are a common way for species to hitchhike to new locations, especially for *B. tournefortii,* which grows abundantly along roadsides in North American deserts (Trader et al. 2006; Sanchez-Flores 2007). Increased collaborations between scientists and stakeholders (i.e. department of transportation services) across multiple states are needed to effectively plan the maintenance (i.e. timing of mechanical or chemical removal) and surveillance of currently invaded roadsides (Davies and Sheley 2007; Otto and Brunson 2021). Additionally, raising public awareness of invasive species spread through strategies such as installing hiking trail signage to inform the public on invasive species' impacts on native communities, organizing community weed management volunteer days, and encouraging the engagement of the public to participate in BioBlitz may contribute to reducing human-mediated dispersal (Graham et al. 2019). Accordingly, minimizing the spread of invaders requires interdisciplinary collaborations and community support to detect, track and manage invaders.

Our findings highlight the importance of standardizing invasion modeling approaches to explicitly test and account for underlying assumptions of niche conservatism and species-environment equilibrium to improve the accuracy of spatial predictions for invasive species, as well as to be able to compare studies using a similar methodology (i.e. COUE Framework) to inform the niche shift debate (Catford et al. 2022; Guisan et al. 2014). As climate change models continue to forecast increased aridity in North America (Seager et al. 2007; Overpeck and Udall 2020), it is critical that we identify range-specific drivers of species distribution and identify areas that may be at risk of future invasion within North America. Modeling efforts can be paired with EDRR plans to monitor the leading edge of an invader within the introduced region to limit spread.

Author contributions CSR conceived the idea for the study. CSR led data analysis with SJEV and MBR improving the methodology. CSR wrote the first draft of the manuscript and all authors contributed to manuscript edits and approved the final manuscript version.

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Data availability Data and R code will be available upon request.

Declarations

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

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