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Original Research Article

A global invader's niche dynamics with intercontinental introduction, novel habitats, and climate change

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ABSTRACT

Species niches have been defined in different ways, variably encompassing abiotic and biotic parameters limiting an organism's spatial distribution. Climate is often the primary component of the abiotic (fundamental) niche, especially among terrestrial plants. In invasion biology, there is an ongoing debate on the prevalence of niche shifts, which may be linked to divergent traits in a species' native and invaded ranges, as well as dispersal limitations and invasion lag phases. Using a global dataset, we tested whether shifts occurred in the invader Johnsongrass (*Sorghum halepense*), which has undergone intercontinental spread as well as habitat-switching within its invaded range in North America. Climate space ordination showed that North America is, on average, colder than Afro-Eurasia, and North American Johnsongrass occupies wetter environments than in its native range. Within North America, both agricultural and non-agricultural ecotypes shifted slightly toward colder climates. Notably, while non-agricultural populations far outnumber agricultural ones, the former occupy a narrower niche ($D_M = 42.7 \pm 0.8$) than the latter ($D_M = 59.3 \pm 1.1$), implying agriculture's role in providing suitable environments in otherwise suboptimal climates. Maximum entropy models of agricultural and non-agricultural North American populations showed limited ecotypic differences in current suitability and range expansion under climate change through the rest of this century. We also predicted climatic suitability for Johnsongrass to increase most in the Upper Midwest and Great Plains by 2100. Our results help contextualize the empirical evidence for ecotypic differentiation in Johnsongrass, as well predict future range expansion and damage niches.

1. Introduction

Niche theory is of vital importance to invasion biology, whether in explaining past invasions (Fernández and Hamilton, 2015; Wan et al., 2017), predicting future invasions (Faleiro et al., 2015), projecting invasion impacts (Gidoin et al., 2015), or conceptualizing

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invasion as a phenomenon (Tilman, 2004). An abundance of empirical and model-based evidence indicates that species inhabit niches largely driven by climate parameters (Morueta-Holme et al., 2013; Bilton et al., 2016; Harrison et al., 2020). Both the abiotic and biotic niches of a species are important in characterizing its environmental suitability in a given geography (Hirzel and Le Lay, 2008; Soberon and Arroyo-Peña, 2017). Thus, geostatistical niche models have the potential to be useful tools in predicting the future range of recently arrived invaders, as well as range expansion of established invaders.

While it may be critical to model both abiotic and biotic factors of some species niches, as in the case of host-dependent invaders (e.g., Liang and Fei, 2014; Ren et al., 2020), most plants are primary producers, whose niches are quantifiable largely in abiotic terms (i.e., climatic; Kelly and Goulden, 2008; Rinnan and Lawler, 2019). Invasion suitability is often modeled from climatic occupancy in a species' home range (e.g., Beans et al., 2012). However, as invasions run their course, some models based on the native range alone can underpredict or overpredict range boundaries, often due to the invasive range not reaching an "equilibrium" (Barbet-Massin et al., 2018; Briscoe Runquist et al., 2019) or other intervening factors. Despite continuing debate surrounding the statistical and biological underpinnings of climate-based niche models in invasion biology, thermal and hydric niche breadths typically remain the most tractable proxies of distribution potential in invasive plants (Bustamante et al., 2020).

There is ongoing debate in invasion science regarding the relative prevalence of niche conservatism (i.e., no change in climatic occupancy between native and invaded ranges) and niche shift (i.e., directional and/or breadth change in climatic occupancy between ranges). Aspects of niche shifts are typically categorized as pioneering (occupying new climates not previously available), expansion (occupying new climates that were previously available but unoccupied), unfilling (retreat from previously occupied climates despite continued availability), and abandonment (retreat from climates no longer available) (e.g., Guisan et al., 2014; Atwater et al., 2018a, 2018b). To date, evidence has been presented for both conservatism and shifts (e.g., Early and Sax, 2014; Tingley et al., 2014; Atwater et al., 2018a, 2018b; Liu et al., 2020). In addition to its applied utility in determining the biological validity of invasion predictions (Fernández and Hamilton, 2015), the niche conservatism question is central to several other invasion hypotheses. For example, the Evolution of Increased Competitive Ability hypothesis (Blossey and Notzold, 1995), which attributes invasion success to augmented competitive traits that open novel niches to introduced populations over native ones, continues to be tested in a variety of study systems with mixed outcomes (e.g., Felker-Quinn et al., 2013; Joshi et al., 2014; Siemann et al., 2017). When considering early stages of invasion and genetic diversity, founder effects, particularly in the context of island biogeography, are another potentially important factor in explaining how community assembly dynamics lead to greater or lesser invasibility (Abdelkrim et al., 2005; Liao et al., 2020). In a similar vein, genetic diversity bottlenecks of founder populations are one of the challenges that invasive species overcome – seemingly paradoxically – in their introduced range (Golani et al., 2007). There are other ways in which apparent niche shifts can be attributed to progression through phases of invasion over time rather than ultimate environmental suitability. This is seen in the case of invasion lag periods that manifest as niche unfilling (Atwater et al., 2018a). In addition, niche shifts registered in two-dimensional climate space may not equate to shifts in geographic space due to structural discontinuities in the environment (Soberón and Townsend Peterson, 2011). For this and other reasons, it is important to model and assess niches both in bioclimatic and geographic space. Finally, it is worth knowing to what extent niches are conserved, as this helps parse the roles of niche availability and disturbance in making ecosystems invadable.

Invasive species are highly conducive to studying niche shifts and, particularly, multiple shifts within a species. This is due to their often multi-continental distribution, adaptability to a wide range of environments, wide availability of occurrence data of high spatial and temporal resolution (Peterson, 2003) and apparent proneness to niche shifts globally (Atwater et al., 2018a, 2018b). We chose the widespread invader Johnsongrass (*Sorghum halepense*) as our model system, as it lends itself to the investigation of two potential shifts – one intercontinental (specifically, to North America) and one intracontinental (land use-based ecotypes within North America). Johnsongrass's arrival in North America is known to be through South Carolina and later Arizona in the early 19th century (McWhorter, 1971), likely from modern-day Turkey, which is to say directly from the native range and not via spread from Central and South America. This is important, as it permits us to conceptually model North American populations independently of those on other continents. In this study, we aimed to compare Johnsongrass's native-to-North American niche shift to its potential ecotypic niche shift within North America. With regard to the latter, genetic evidence has confirmed the directional shift over time from primarily agricultural to primarily non-agricultural populations of Johnsongrass across the United States (Sezen et al., 2016).

To date, there is abundant evidence for ecotypic differences between U.S. Johnsongrass populations associated with agricultural (i.e., cropland) and non-agricultural habitats. These differences have included significant genetic segregation as well as apparent differential adaptation to competitor identity, climate origin, photosynthetic cues, and edaphic origin (Sezen et al., 2016; Atwater et al., 2017, 2018b; Kelly et al., 2020; Lakoba and Barney, 2020). It stands to reason that niche shifts can occur in response to drivers other than intercontinental transport (e.g., competition; Wiens, 2011), if these drivers present sufficiently novel niche availability. With ample and precise occurrence data, we can test whether niche shifts have occurred at the intercontinental and/or ecotypic scales of Johnsongrass's distribution. Given empirical confirmation of differences between agricultural and non-agricultural ecotypes at a population level, we were also interested in whether these differences will be conserved or amplified in the future under climate change, which is likely to facilitate invasion in general (Bradley et al., 2010b). Atwater et al. (2016) found greater niche breadth across the non-agricultural ecotype, using 70 field-validated agricultural and non-agricultural populations. The present study aims to expound on this effort by extrapolating ecotype attribution from digitally available species occurrence and land cover data, which affords us much greater geographic coverage and resolution.

Specifically, we had three questions. The first was whether a niche shift occurred in Johnsongrass's North American range, as compared to its native range. The second was whether a niche shift occurred within North America between agricultural and non-agricultural ecotypes. The third was to what extent we can expect range expansion of Johnsongrass or either of its ecotypes given climate change through the remainder of the 21st century.

Answers to these questions will help us understand the mechanisms shaping invasion, as well as the niche trajectory of this model invader in the future. This, in turn, will allow us to begin comparing the relative contributions of three major factors in species distributions: transport by humans, disturbance as part of land use change, and climate change. All three are known anthropogenic facilitators of invasion (Meyerson and Mooney, 2007) and the Johnsongrass study system allows us to form specific hypotheses about their relation to niche dynamics. It should be noted that niches can not only shift, but also change in size (expand and contract). An expanding or contracting niche can suggest more or less future range change, respectively. (Scheele et al., 2017). Thus, comparing ecotypic niches under current and future climates also allows us to speculate on damage niches or geographies where policymakers and managers may focus prevention efforts (e.g., Kumar et al., 2015; Ancillotto et al., 2016).

2. Methods

2.1. Species occurrence data

We retrieved Johnsongrass occurrence records from the Global Biodiversity Information Facility (GBIF) with no limits to geographic extent, under the entry '*Sorghum halepense* Pers.' At the time of extraction (February 2021), this yielded 28,731 occurrences. As a preliminary measure of data quality control, we removed 8363 duplicated, non-georeferenced, and geographically misreferenced points from the dataset, whose associated coordinates placed them in nonsensical (e.g., ocean) locations.

Spatial autocorrelation (SAC) is often present in ecological data and can bias variables' relative contributions to species distribution models (SDM). To quantify SAC in our georeferenced occurrence dataset we calculated Moran's *I* (Global Moran's *I* function in ArcMap 10.7.1; Environmental Systems Research Institute, Redlands CA). We then optimized this dataset's spatial resolution for minimal Moran's *I*, as discussed by Dormann et al. (2007) and Zhang et al. (2019). We compared the SAC of 100,000 random points distributed across all continents of interest to the SAC of versions of our dataset aggregated to 1, 10, 25, 50, and 100 km resolutions. As a result of this analysis, we proceeded with the dataset aggregated to 50 km, as it reduced SAC to a level below that of the 100,000 random points (random points Moran's $I = 0.92$; $p < 0.0001$; dataset Moran's $I = 0.78$; $p < 0.0001$), resulting in 14,077 occurrence points worldwide. Likewise, we generated up to 100,000 randomly distributed background points (Random Points function in ArcMap 10.7.1) throughout our study areas to be no closer than 50 km together.

While Johnsongrass is considered to be native to parts of the Middle East and North Africa, an exact delineation of its origin in the eastern Mediterranean basin is difficult to draw (McWhorter, 1971). Furthermore, the palimpsest of agricultural land uses spanning millennia in this part of the world makes it difficult to tease apart a "natural" range and one facilitated by crop husbandry (Snir et al., 2015). Nonetheless, several sources list largely-overlapping native range extents (USFS-PIER 2008, USDA-ARS 2008, ISSG, 2012). We chose the USDA-ARS definition for this work, as collated by the CABI Invasive Species Compendium (CABI 2021), due to its greater inclusivity and reference specificity than the PIER or ISSG counterparts individually. Thus, we designated as native those populations

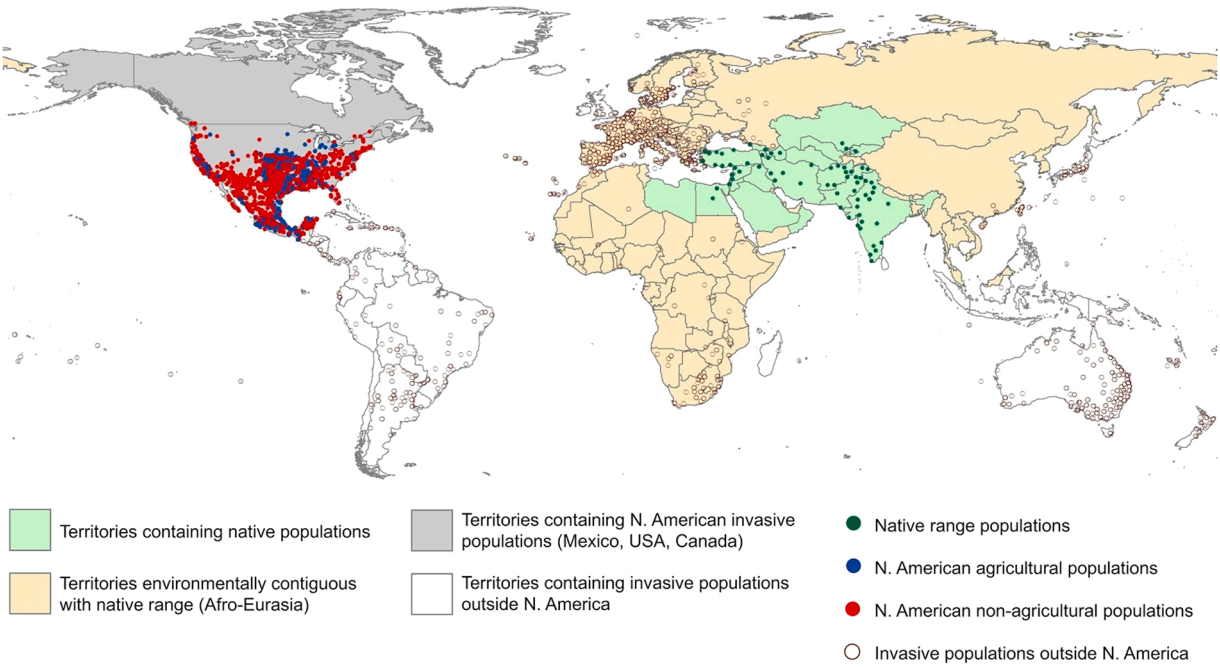

Fig. 1. Map of Johnsongrass occurrences, designated by symbol color as native, North American invasive (agricultural), North American invasive (on-agricultural), and non-North American invasive. Outlines of the native and invasive range available environments are designated by color. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

which occurred within a contiguous territory bounded by the modern (2021) states of Libya to the west, Kazakhstan to the north, India to the east, and Saudi Arabia and Oman to the south. The general location of Johnsongrass's native range is also supported by its genetically-inferred evolutionary history as a hybrid of a northwest African and an east Asian species – *S. bicolor* and *S. propinquum*, respectively (Paterson et al., 2020). While portions of this native range are bounded by coastlines (i.e., Indian Ocean, Mediterranean Sea) and major mountain ranges (i.e., Caucasus, Himalayan, Arakan), its western and northern edges are largely environmentally continuous with the continent. Therefore, we chose to define the available environmental space of the "native range" as the contiguous Afro-Eurasian landmass, excluding major islands (i.e., Madagascar, Sri Lanka, Iceland, the British Isles, Cyprus, Japan, etc.) (Fig. 1). We generated background points for the native range throughout contiguous Afro-Eurasia and throughout Mexico, the United States, and Canada for the invaded North American range.

2.2. Comparison of North American niche to that in the native range

We compared the climatic niche of Johnsongrass's native range in the Middle East and Central/South Asia to that of its invaded range in Mexico, the United States, and Canada. To generate environmental background points for this niche comparison, we used contiguous Afro-Eurasia as available geographic space for native populations and Mexico, the U.S. and Canada for the invasive populations of interest. The territories of other North American countries were excluded due to a combination of their being islands and the need for boundary consistency with our intra-continental niche comparison, which was shaped by land cover data quality, as described below.

For the climate data, we retrieved a suite of 19 bioclimatic variables from WorldClim (Fick and Hijmans, 2017) with complete global spatial extent serving as means from 1970 to 2000. Using the 'Spatial Analyst' toolbox in ArcMap 10.7.1, we associated all of these climatic variables with each occurrence point in our refined dataset, as well as with each generated background point. Prior to modeling niche dynamics, we performed principal components analysis (PCA) on the global occurrence dataset in order to interpret factor loadings for the first two principal components (PCs). PCA of Johnsongrass distributions across North America alone, as well as in conjunction with Africa, Europe, and Asia, revealed the two leading PCs to correlate with measures of temperature and precipitation, respectively. In both sets of niche analyses, increase in PC 1 is interpretable as colder and more thermally variable climate, while increase in PC 2 means drier and more hydrically variable climate. The 'ecospat' package in R (Di Cola et al., 2016) was used to model niche dynamics and generate niche shift ordination plots and vectors using occurrence and background points. As part of this analysis, we also performed niche similarity and niche equivalency tests (Di Cola et al., 2016), as well as quantifying niche overlap with Schoener's D (Schoener, 1968).

2.3. Comparison of agricultural and non-agricultural ecotypic niches in North America

To differentiate between agricultural and non-agricultural Johnsongrass populations in North America, we used the Global Land Cover Characterization (GLCC) dataset developed by USGS EROS (Loveland et al., 2000). This 1 km resolution dataset was generated through unsupervised classification of hyperspectral data, including Advanced Very High Resolution Radiometer (AVHRR) and Normalized Difference Vegetation Index (NDVI) values from 1992 to 1993. Country-by-country ancillary data, including elevation, vegetation, and land cover variables also contributed to GLCC. For this modeling effort, we chose to limit our coverage of North America to Canada, the United States, and Mexico, as there was a marked decrease in the range of land use values coinciding with Mexico's southern border, which we interpreted as a loss of classification certainty.

The GLCC definition of 'agricultural' land cover corresponds to cropland (i.e., excluding pasture) and varies on a scale of 0–100, with the value representing the percentage of the 1 km pixel occupied by this land cover type. In order to classify both occurrence and background points, it was necessary to determine the threshold for binning this continuous measure into discrete types – agricultural and non-agricultural. With regard to background points, we chose 50% as the threshold because it was unbiased toward either land cover and most inclusive of all available environments. To determine the effect of GLCC threshold value on model performance, we generated six iterations of our North American occurrence dataset. Each iteration designated *n*% of occurrences as 'agricultural' and 'non-agricultural', with *n* equivalent to the percentage removed from 100 and 0, respectively, in corresponding GLCC value. For example, the '5% dataset' included occurrences with GLCC values of 0–5 as non-agricultural, those of 96–100 as agricultural, and those of 6–95 were excluded as 'uncertain'. The other iteration thresholds were 10%, 20%, 30%, 40%, and 50%, with the last iteration excluding no occurrences. Each iteration was input into a Maxent model (Phillips et al., 2017) with all 19 WorldClim bioclimatic variables and a bias layer generated in R using the packages 'dismo', 'raster', 'MASS', 'magrittr', and 'maptools' (Hijmans et al., 2017; Hijmans, 2020; Venables and Ripley, 2002; Bache and Wickham, 2014; Bivand and Lewin-Koh, 2020). Model outputs were used to generate the area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS), a common prevalence-dependent measure of SDM performance (Allouche et al., 2006). As there was no major reduction in model performance between the iterations – with each performing at the lower end of 'good to excellent' AUC and TSS – we chose to use the 50% iteration of the occurrence dataset as it was most inclusive.

Niche comparison and shift analyses of agricultural and non-agricultural ecotypes were performed similarly to those of North American and World distributions. Using 'ecospat' in R, we performed PCA and two-PC niche ordination on agricultural and non-agricultural ecotypes, as well as their respective available environments. Both occurrence and background points were binned by ecotype with a 50% GLCC 'agricultural' threshold. We also quantified niche overlap with Schoener's *D*, as well as niche similarity and equivalency tests. In addition, we quantified agricultural and non-agricultural niche breadth both in composite variable space (PCA 95% confidence interval ellipsoids) and in multi-dimensional simple variable space (Mahalanobis distance). Mahalanobis *D* was

calculated using R version 4.0.2 (R Core Team, 2020).

2.4. Current and future suitability of Johnsongrass and its ecotypes in North America

We ran three separate Maxent SDMs in current (2021) and future (2100) climate scenarios for (1) all Johnsongrass, (2) the agricultural ecotype, and (3) the non-agricultural ecotype, all constrained to North America. To project suitability into future climates, we used the 'fossil-fuel development' scenario (SSP585) and the 'sustainable' scenario (SSP126). Each model incorporated the SAC bias layer previously generated for North America. In order to visualize discrete suitable ranges, a threshold of 0.5 suitability (on a scale of 0–1) was applied to all suitability score projections. Areas of highest increase in suitability between 2021 and 2100 were visualized as the 95th percentile of suitability increase (difference between 2100 and 2021 raw values).

3. Results

3.1. Johnsongrass niche shift from native range to North America

Our comparison of Johnsongrass's native and North American ranges showed the majority of their climate niches not overlapping, with a limited amount of niche abandonment following invasion, minimal unfilling, considerable niche expansion, and no pioneering (Fig. 2). Niche overlap between the two ranges was characterized by a Schoener's D value of 0.239 and niche similarity p-value of 0.048, suggesting that these ranges predict one another's occurrences significantly better than would a random process. Niche abandonment is illustrated in Fig. 2 as native niche area within the Afro-Eurasian environment but outside the North American environment in the warmest climates. Three small areas of niche unfilling are visible in Fig. 2 as native range occupancy within both Afro-Eurasian and North American climate space not occupied by Johnsongrass in North America, largely in the coldest climates. Niche expansion, or North American populations' novel occupancy of climates available in both Afro-Eurasia and North America, is more prevalent than areas of both abandonment and unfilling and occurred primarily in the wettest climates. Notably, North American Johnsongrass expanded into these wetter climates in a similar hydric range as the abandoned niche areas, but at colder temperatures. Overall, the niche shift from the native range to North America consisted of abandonment of Afro-Eurasia's warmest climates, which are not available in North America, and expansion into wetter climates, which are available both in Afro-Eurasia and North America.

3.2. Niche shift within North America between ecotypes and differences in niche breadth

The switch from agricultural to non-agricultural habitats within North America since initial introduction in the late 19th century corresponded to an overall niche breadth reduction (Fig. 3), small, localized areas of niche abandonment, unfilling, expansion, and pioneering, but almost no directional shift (Fig. 4). The agricultural ecotype occupies both colder and warmer extremes, while the non-agricultural ecotype is represented by both a greater number and a greater density of populations in climate space (Fig. 3A). Note that this density in climate space persists despite thinning to comparable density in geographic space to account for sampling bias and SAC. This reduction in niche breadth is also apparent in 19-dimensional simple variable space, as characterized by Mahalanobis distance (agricultural $D_M = 59.3 \pm 1.1$; non-agricultural $D_M = 42.7 \pm 0.8$; $p < 0.0001$, Fig. 3B). Niche overlap between North American agricultural and non-agricultural ecotypes (Schoener's $D = 0.479$) is greater than between native and North American niches, while niche similarity is also significant ($p = 0.004$). While non-agricultural environmental space in North America represents novel availability of wetter and colder climates, Johnsongrass populations shifted very little toward colder temperatures (Fig. 4). Overall, the

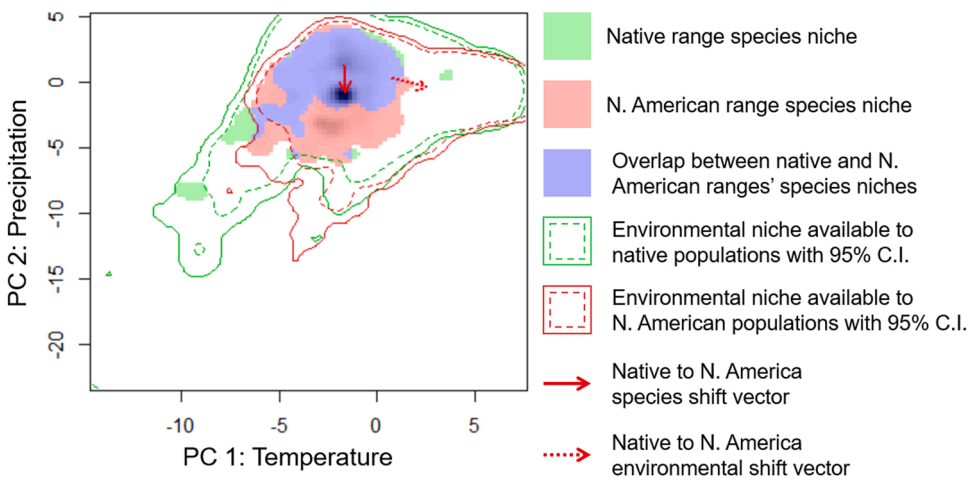

Fig. 2. Niche shift ordinations and vectors comparing the native and North American invaded ranges, given environmental availability of Afro-Eurasia for the native range and Mexico, the U.S., and Canada for the invaded range. Schoener's $D = 0.239$, Niche similarity $p = 0.048$.

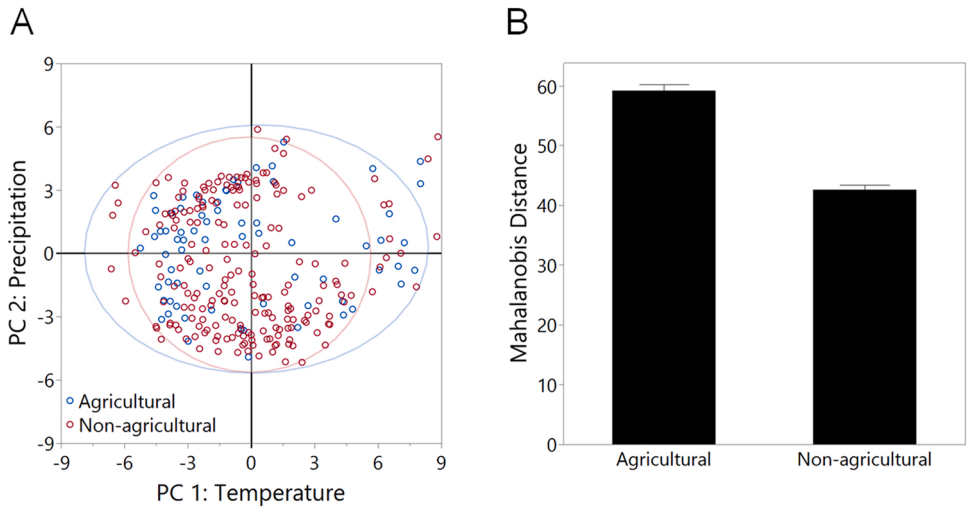

Fig. 3. Niche breadth comparison of North American agricultural and non-agricultural niches in (A) Principal Component (PC) space with 95% confidence interval ellipsoids, and (B) 19-dimensional bioclimatic variable space via Mahalanobis D ($p < 0.0001$).

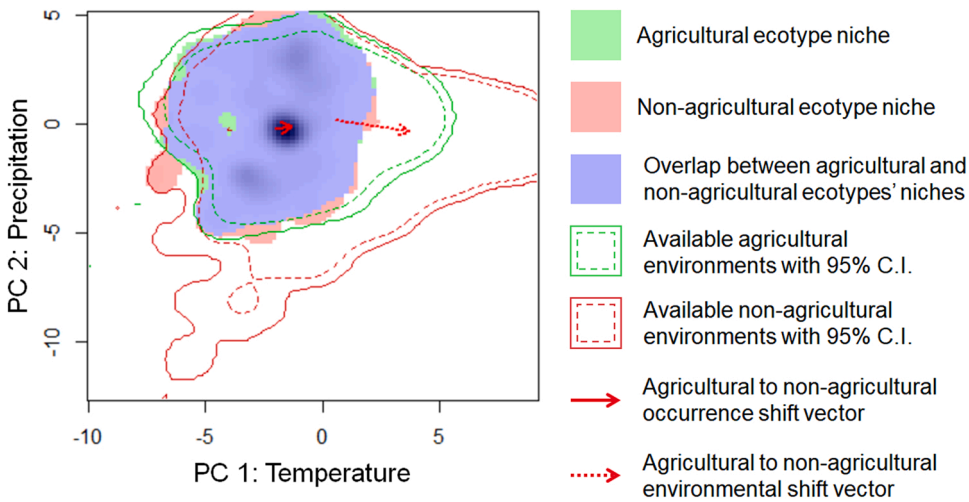

Fig. 4. Niche shift ordinations and vectors comparing the North American agricultural and non-agricultural invaded ranges, given environmental availability as split between 51% and 100% and 0–50% agricultural land cover, respectively. Schoener's $D = 0.479$, Niche similarity $p = 0.004$.

habitat switch from an agricultural to a non-agricultural ecotype was associated primarily with niche narrowing more so than any directional shift.

3.3. Projected range change under future climate scenarios in North America

Maxent models of Johnsongrass range dynamics under future climate scenarios showed northward movement in North America associated with the fossil fuel development scenario (SSP585) but not under the sustainable development scenario (SSP126). This was true for each ecotype individually (Fig. 5), as well as considering the species as a whole, with both ecotypes combined (Fig. 6A). While we found agricultural populations to exhibit greater climatic niche breadth, this did not correspond to greater geographic breadth (Fig. 5A vs. B). However, the greater thermal niche breadth (Fig. 3A) is evident in the agricultural, and not the non-agricultural, ecotype's greater suitability in northern Nebraska, south Florida, and the Yucatan. We saw that this breadth relationship is conserved in the agricultural ecotype's year 2100 suitability in Minnesota, Ontario, and Oaxaca. The model projected 50% or higher suitability for North American Johnsongrass as limited around the 39th parallel in 2040 and around the 43rd parallel by 2100, with southward deviation in the West. The whole species' range expansion with fossil fuel development-associated climate change was also projected to include the Yucatan peninsula. Our estimation of greatest (i.e., 95th percentile) increased in Johnsongrass suitability in North America highlighted large portions of the upper Midwest as areas of highest risk. Lower elevation portions of the Mountain West

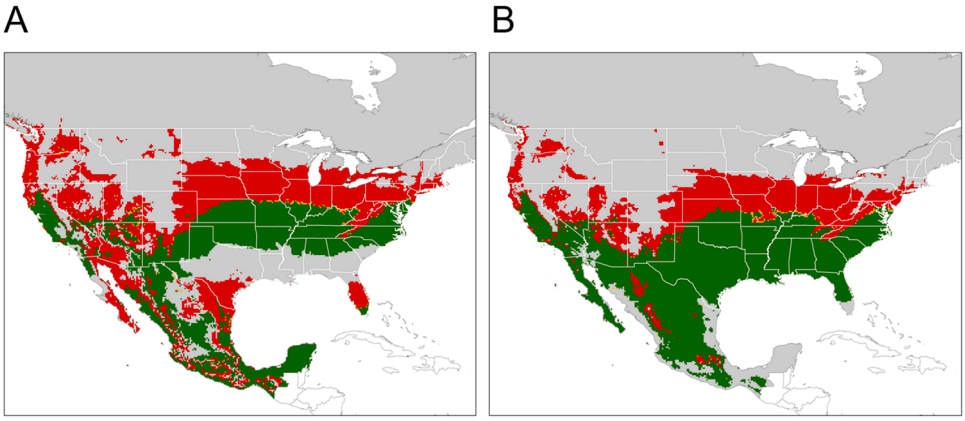

Fig. 5. Maxent environmental suitability maps of North American (A) agricultural and (B) non-agricultural ecotypes in 2021 (green) and 2100 based on sustainable development (SSP126; gold) and fossil fuel development (SSP585; red) climate scenarios. Suitability is visualized as a monotonal band of > 0.5 suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

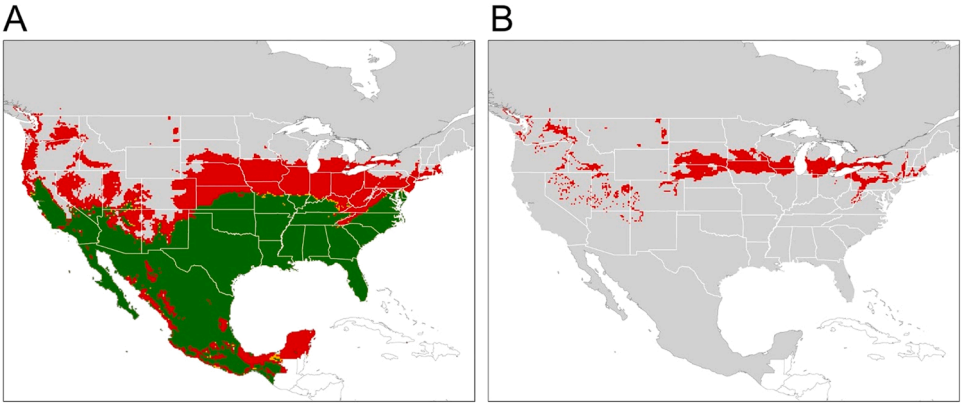

Fig. 6. Whole species (i.e., both ecotypes) Maxent projections of (A) environmental suitability in 2100 based on SSP126 (sustainable scenario; gold) and SSP585 (fossil fuel scenario; red) compared to suitability in 2040 (green). Suitability is visualized as a monotonal band of 0.5 + suitability. (B) Whole species increase in Johnsongrass environmental suitability between 2040 and 2100, under the SSP585 scenario (red). The shaded region represents the 95th percentile of increase in suitability. Suitability increase under SSP126 was not visualized as its magnitude was negligible. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(eastern Washington through northern Utah), upland and lake coast portions of western New York and Pennsylvania, and parts of southern New England are also in the path of likely expansion.

TSS values for all Maxent models showed them to have 'good' performance, with values between 0.7 and 0.9 (Allouche et al., 2006).

Table 1
Maxent model validation measures: area under the receiver operating characteristic curve (AUC), True Skill Statistic (TSS), and false negative rate (FNR), by ecotype and climate scenario.

Ecotype	Climate scenario		train AUC	test AUC	TSS	FNR
agric.	sustainable	[ssp126]	0.905	0.914	0.772	1.87
agric.	fossil fuel	[ssp585]	0.904	0.912	0.770	1.87
non-agric.	sustainable	[ssp126]	0.881	0.881	0.770	3.16
non-agric.	fossil fuel	[ssp585]	0.880	0.881	0.770	3.16
both	sustainable	[ssp126]	0.863	0.859	0.770	3.32
both	fossil fuel	[ssp585]	0.863	0.859	0.769	3.32

AUC values (possible range 0–1; 0.5 represents random guessing) of training and testing subsets were calculated with 1000 iterations of an 80:20 random split of occurrence data. TSS values (possible range −1 to 1; 0 represents random guessing) and FNR (range 0–100) used predictions from the same 80:20 split and prevalence and threshold values of the Maxent model. FNR (i.e., underprediction of suitable habitats) is defined as [false negative/(false negative + true positive) x 100].

AUC values of training and testing subsets of the Maxent models ranged between 'excellent' and 'outstanding' performance (Mandrekar, 2010), see Table 1.

4. Discussion

Since its introduction into North America from the Middle East in the early 1800s, Johnsongrass has expanded into wetter environments, then into non-agricultural habitats, where its thermal niche narrowed, all the while maintaining a consistent cold temperature niche boundary. Once in North America, Johnsongrass abandoned some of the hottest climates it occupied (available in Africa and South Asia), while expanding into many wetter climates that had already been available to it in Afro-Eurasia, with only localized partial barriers to dispersal. In moving from agricultural to non-agricultural habitats in North America (Sezen et al., 2016), the latter ecotype has since narrowed its climate niche, particularly in terms of temperature. The non-agricultural climate niche has shifted very slightly overall toward colder temperatures but is associated with very little unfilling or expansion and virtually no abandonment or pioneering of climates. Thus, Johnsongrass has not yet exploited the abundance of colder and wetter non-agricultural environments in North America despite their availability. Assuming niche stability of North American populations in the 21st century, both ecotypes and Johnsongrass as a whole will see large increases to suitable climates across the continent, likely leading to northward range expansion, particularly in the upper Midwestern United States.

Johnsongrass's intercontinental shift was toward wetter environments, maintaining the native range's limit on cold temperatures and abandoning the hottest climates it occupied in the eastern hemisphere (e.g., Africa and India), which were no longer available in North America. The expansion to wetter climates was a major broadening of the climate niche, with no abandonment or unfilling of the driest environments. While the climate niche occupied in the eastern hemisphere today includes much of western Europe, as well as East Asia and southern Africa as aided by human introduction, these environments were unoccupied prior to human introduction despite climatic contiguity and no major limits to dispersal in northern Africa and the Eurasian steppe. In expanding to wetter climates in the invaded range, there may have been a selection for greater soil moisture (i.e., waterlogging) tolerance or plasticity in this trait. Examples of greater moisture tolerance plasticity in invaded ranges have been observed in a number of species (e.g., Chen et al., 2013), as well as being an important advantage of some invaders over native congeners (e.g., Chen et al., 2013; Javed et al., 2020). Atwater et al. (2016) found Johnsongrass's non-agricultural ecotype to have more local specialization and the agricultural ecotype to be a more 'general purpose genotype'. This earlier study found greater climatic niche breadth in the non-agricultural ecotype, but this result was based on only 70 populations sampled in the U.S, and is not expected to represent the density or breadth of distributions of each ecotype. However, we do not interpret the intercontinental niche shift to be merely plasticity due to its magnitude and that a similar degree of plasticity would be expected, but is not apparent, in the native range. We also note that in both Afro-Eurasian and North American climate space, Johnsongrass's niche clusters toward the driest and thermally moderate climates, avoiding extreme cold, as well as extreme soil moisture. The latter two conditions have been applied as empirical assessments of the rhizomes' stress response (Hull, 1970; McWhorter, 1972, Lakoba unpublished data) and found to be unequivocally lethal in modest dosage.

While there was relatively little intracontinental shift between Johnsongrass ecotypes compared to the intercontinental shift, there are two notable ecotypic niche differences. The niche narrowing of non-agricultural populations implies a trend toward niche and range stasis rather than further habitat switching or niche shift (e.g., Botts et al., 2013). However, it should be noted that niche breadth implications are not well understood at this time and have important interactions with genetic diversity and reproductive strategies that affect range extents (Park et al., 2017; Sexton et al., 2017; Carscadden et al., 2020).

The geographic projection of the two ecotypes' climatic suitabilities shows that the non-agricultural ecotype is more closely associated with what we consider to be the North American core range (South Carolina through Texas and Arizona) (McWhorter, 1971). This difference between ecotypes' suitability in the core versus peripheral ranges brings up three questions. First, could the habitat switch from agricultural to non-agricultural habitats be a spatially non-uniform phenomenon (i.e., more pronounced in the Southeast and Southwest and less so in other regions)? This would be surprising, given that these regions do not represent pioneered climates for North American Johnsongrass, nor do they represent the high-density agricultural activity of the Midwest. In fact, it abandoned sizable portions of the hottest climates occupied in the native range, meaning heat is unlikely to be limiting in North America. Second, there could be under-sampling bias in the regions where Johnsongrass has been found in agricultural habitats the longest (i.e., least novelty and interest). This seems possible, although the great majority (4900 of 6248; or 78%) of our North American occurrence records are from the last 4 decades, by which time the species had been long established throughout its current range, not just the "core". Some authors suggest accounting for such suspected bias by comparing the temporal discovery curve of the species of interest to those of other contemporaneous invaders (Delisle et al., 2003). However, the initial invasion was approximately 200 years ago and the earliest herbarium-based records we accessed do not accumulate to even 10% of the current total until 1965. Therefore, the discovery curve comparison approach addresses an important potential source of bias but cannot be reliably applied to our system and area of interest. Third, could lower occurrence in Southern agricultural habitats be a product of more intensive management in areas of heaviest and most impactful infestation? There could also be an interaction between high management and low novelty in the core range, per the previous point. While these are important questions, we have no evidence to assess these biases, nor do we find studies identifying these specific biases in similar systems. Therefore, we interpret the ecotypic differences in suitable range projection to be true to the ecology of the species. Specifically, the core North American range (Southeast and Southwest) is more suitable for the non-agricultural ecotype, while more peripheral portions of the range are similarly suitable for both ecotypes. This underscores the importance of considering the interactions of ecotype identity and climate (as well as other local factors) and understanding ecotype as a loose association of trait differences rather than a simple bifurcation of the species.

We saw significant climatic niche narrowing following Johnsongrass's transition from agricultural to non-agricultural habitats.

Greater breadth of the agricultural niche (i.e., populations in agricultural lands occupying a larger variety of climates) suggests cropland's role in providing suitable environments. Agriculture across the ages has been regarded as a form of niche construction that humans persistently and intentionally engage in (Boivin et al., 2016). In addition to intentional assembly of biotic communities, it can also lead to unintended introductions, some of which are detrimental (Saul et al., 2017). A history of agricultural land use can, in some cases, even affect the invasibility of sites following abandonment (Mattingly and Orrock, 2013). Both agriculture and urbanization have been associated with microhabitat creation, facilitating invasive plant establishment (e.g., Hierro et al., 2006; David and Menges, 2011; Guo et al., 2018; Salinitro et al., 2018). However, while there is a body of empirical evidence showing ecotypic differences in Johnsongrass (Atwater et al., 2016, 2018b; Fletcher et al., 2020; Kelly et al., 2020; Lakoba and Barney, 2020), there is no reason to think that they are so specialized as to be unable to establish in one another's habitats. Indeed, neither the 'general purpose' nor the 'jack of all trades' characterization that Atwater et al. (2016) gave the agricultural and non-agricultural ecotypes, respectively, suggest that they should be seen as non-overlapping divisions within the species, despite the genetic divergence found by Sezen et al. (2016).

Johnsongrass's northward range expansion appears imminent given climate change; however, its magnitude could vary widely, depending on the global climate trajectory in this century. Overall, ecotypic differences in projected climate change-driven range potential mirror current suitability differences (i.e., somewhat broader suitability for the agricultural ecotype). This primarily latitudinal change northward is linked with temperature (i.e., temperature minima and variability) being the most explanatory bioclimatic variables of Johnsongrass's niche globally and in North America. We predict that, in North America, the species will track rising temperatures northward, due in part to an apparently stable rhizome cold tolerance limit (Lakoba unpublished data; manuscript in review).

In predicting Johnsongrass's range expansion, it is most useful to model the whole species, rather than the ecotypes individually. This is due both to our finding few ecotypic climate niche differences and to the fact that there is no evidence that agricultural and non-agricultural populations are reproductively disjunct or habitat-exclusive. The greatest increase in climatic suitability, and therefore the greatest risk of new establishment, will be in the Upper Midwest and Great Plains. This includes cropland, rangeland, and developed landscapes, all of which Johnsongrass readily occupies (Sezen et al., 2016; Ohadi et al., 2018). The Midwest is an unsurprising invasion front due to its smooth latitudinal transition in climate, topography, and soils, compared to the coastal regions and Appalachian and Rocky Mountains (Sayre et al., 2009). The crop damage niche in these new areas will likely be in corn (McDonald et al., 2009) and soybean (McWhorter and Anderson, 1981), which are associated with a robust body of knowledge on Johnsongrass management (e.g., Dale, 1981; Winton-Daniels et al., 1990; Ghosheh and Chandler, 1998). However, issues of herbicide resistance and other factors in a changing climate mean that this will not necessarily be a linear process (Johnson et al., 2014; Matzrafi et al., 2016; Vazquez-Garcia et al., 2020). In the southern Great Plains, Johnsongrass is already seen as a problem in native prairie (Rout et al., 2013), so land managers and conservationists working in Midwestern prairies should take note of the forecasted northward expansion.

Using this model invader system, we were able to compare range changes associated with three anthropogenic drivers: species transport; land use change; and climate change. Species intercontinental transport was most consequential, followed by climate change (i.e., 2100 projection), with land use change (i.e., habitat switch after management in cropland) as a distant third. This ranking can help us prioritize how we conceptualize and respond to invasions in the arenas of land management and policy. Focus on prevention, as well as early detection and rapid response (EDRR), will yield the most return on investment, because it targets transport. This includes precautionary screening, risk assessment, and quarantine in case of arrival (Reaser et al., 2020). We know that climate change will continue to be a major invasion driver and need to take it into account when anticipating new and continuing invasion (Bradley et al., 2010a). Specifically, we need to project future distributions under climate change to gauge potential impacts and limiting variables (e.g., Adhikari et al., 2019; Briscoe Runquist et al., 2019). While land use change plays an important role in producing invadable sites, it was least associated with Johnsongrass niche shift or differences in range. However, what is true for Johnsongrass may not be true for other species, particularly if there are other biotic interactions at play (e.g., Green et al., 2011; Jackson, 2015). Therefore, best management practices in agriculture, forestry, fisheries, shipping, and plant and animal trade can contribute to preventing and slowing the spread of invasions (Chornesky et al., 2005; Buck, 2013; Donaldson and Cooke, 2016; Paini et al., 2016; Lockwood et al., 2019).

Future research should include multi-taxa studies comparing range change based on these three anthropogenic drivers (transport, land use, and climate change). We recognize invasive species as a socio-biological problem of human origin and need to advance our knowledge in how it interacts with other types of global change and society at large (Vaz et al., 2017). Further exploration of damage niche shifts will also be important, as it helps prioritize different invasion responses based on impacts (McDonald et al., 2009; Vanderhoeven et al., 2017). Understanding future harm is also central to how researchers communicate about invasions to the public (Mattingly et al., 2020). Projections of future invasive species distributions and impacts contain useful information for the science, management, and policy of invasive species and will allow us to determine the best allocation of resources in confronting the invasion crisis in an increasingly connected world.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01848.

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