Global cultivation of wheat crops induces considerable shifts in the range and niche of species relative to their wild progenitors

Yang Rujing, Gong Xiang, Hu Xiaokang, Hu Yawen and Feng Jianmeng

Department of Life Science and Agronomy, Dali University, Dali 671003, People’s Republic of China

* Author to whom any correspondence should be addressed.

E-mail: fjm@dali.edu.cn

Keywords: cultivation, global niche dynamic, niche conservatism, range size, wheat, wild progenitors

Abstract

Species’ range and niche play key roles in understanding ecological and biogeographical patterns, especially in projecting global biotic homogenization and potential distribution patterns of species under global change scenarios. However, few studies have investigated the ability of crop cultivation to influence potential range sizes and niche shifts of species. Wheat and its wild progenitors share the same origin and evolutionary history, and thus provide an excellent system to explore this topic. Using ensembled ecological niche models and niche dynamic models, we studied the potential range sizes of wheat and its wild progenitors, as well as their niche dynamics. Our results showed that wheat had larger range size and niche breadth than its wild progenitors, suggesting that wheat cultivation is a more powerful driver of range and niche expansion than natural niche evolution. Additionally, wheat and its wild progenitors occupied different niche positions, and the former did not conserve the niches inherited from the latter, implying that wheat cultivation considerably induces niche shifts. The niche dynamics between wheat and its wild progenitors were not only closely associated with cultivation but were also modified by the niche conservatism of its wild progenitors. In contrast to most invasive plants, wheat, as a global staple crop species, did not conserve the niche space inherited from its wild progenitors, suggesting that compared with most plant invasions, cultivation may have a stronger effect on niche shifts. Therefore, global niche shifts induced by crop cultivation need much more attention, though the underlying mechanisms require further study.

1. Introduction

Biodiversity provides many benefits to human ecosystems; however, human activities are strongly affecting biodiversity patterns and thus altering ecosystem function and stability (Isbell et al 2017). The ranges of many species have contracted because of intensifying land use and habitat loss (Ceballos and Ehrlich 2002, Laanisto et al 2015, Marco and Santini 2015), which has increased their likelihood of extinction (Pimm et al 2014, Humphreys et al 2019). By contrast, many species have expanded their ranges because of anthropogenic activities, such as through human-mediated dispersal (e.g., global transport) (van Kleunen et al 2015), and have thrived in anthropogenic landscapes (Lobo et al 2011). These opposing processes—human-mediated range contraction and expansion—can lead to global biotic homogenization (Lobo et al 2011, Gossner et al 2016). However, as far as we have known few studies have estimated the influences of crop cultivation on species range dynamics (contraction and expansion).

As a key concept bridging ecology and biogeography, ecological niche is playing an essential role in understanding mechanisms underlying species distribution patterns across time and space (MacArthur 1968, Rolland et al 2018). Therefore, species’ niche spaces and their dynamics have attracted much attention in recent decades, especially in projecting potential distribution patterns of species under global change scenarios through ecological niche models (ENMs). Niche theory defined niches spaces into two categories, i.e., realized niche and fundamental niche (Hutchinson 1957). The former was restricted by abiotic and biotic factors, while the latter...
was delimited by abiotic ones, suggesting that the latter generally is greater or wider than the former (Whittaker et al 1973, Colwell and Rangel 2009). In the Anthropocene, human activities have had and continue to exert substantial influences on species distributions (Smith et al 2018, Xu et al 2019), generally due to human activities that alter constraints of niches. For example, human activities can take species to regions outside their original ranges; consequently, the species have opportunities to adapt to novel environment, shifting its niche spaces and colonizing in new regions. Therefore, studies on the influences of human activities on niche shifts should be prioritized.

Niche conservatism is the tendency for a species to retain ancestral niche characteristics; it is an important hypothesis in ecology and biogeography because it helps us understand historical biogeography and patterns of species diversity, as well as future ecological and biogeographical patterns (Wiens and Graham 2005, Wiens et al 2010). In recent decades, ENMs have been widely used to predict species’ range shifts under climate change (Wiens et al 2009, Guisan et al 2014, Burns et al 2020, Polaina et al 2021), and their underlying assumption is that species show niche conservatism (i.e., that species will occupy similar niche spaces in new geographical ranges or time periods) (Pearman et al 2008, Petitpierre et al 2012). However, there has been much recent controversy over the niche conservatism of species across time and space (Peterson 2011, Guisan et al 2014, Sexton et al 2017). Guisan et al (2014) argued that the inconsistencies among studies may stem from differences in the three different techniques used to test the niche conservatism hypothesis: the ordination approach, ENM approach, and univariate approach. Recently, Liu et al (2020) used COUE scheme (Centroid shift, Overlap, Unfilling, and Expansion), a golden method in exploring niche dynamics, to investigate the niche dynamics of alien invasive species whose niche spaces could be modified by human activities, and found that most invasive species conserved their niche spaces. However, could cultivated crop species whose niche spaces can be more strongly modified by human activities conserve the niche spaces inherited from their wild progenitors? However, as far as we have known, studies on it were rarely reported.

Wheat is one of the most important crops in the world and plays an irreplaceable role in maintaining global food security (Yue et al 2019). According to the Food and Agriculture Organization of the United Nations (FAO), there is large area of world wheat cultivation, i.e., ca. 224 M km² (an average of the cultivated areas between the year 1970 and 2000). Wheat cultivation measures (e.g., fertilization, irrigation and breeding, et al) could help wheat adapt to harsh environmental conditions, resulting in its niche expansions and colonizing out of its original ranges (Ventrella et al 2012, Boudjabi et al 2019). Moreover, wheat introduction could provide wheat much more opportunities to encounter and adapt to diverse and novel environmental conditions, which also could result in its range and niche shifts and colonizing in new regions. Additionally, wheat cultivation could also exclude competition and predation from other species. Therefore, wheat, as a global–cultivated crop species, doesn’t distribute in its realized niche spaces, but in niche spaces beyond its fundamental niche spaces, and therefore considerable cultivation-induced range and niche shifts relative to its wild progenitors can be assumed.

According to a checklist edited by Milla (2020), the wild progenitors of cultivated wheat (Triticum aestivum) are Aegilops tauschii and Triticum dicoccoides. The germplasm resources of the wild progenitors now preserved in the wild are mainly distributed in areas such as the Fertile Crescent, Syria, and Israel (Ozkan et al 2011, Dvorak and Dehghani 2012). Of note, wheat and its wild progenitors shared the same evolutionary origins and history, as well as same range and niche spaces before wheat cultivation, whereas after wheat cultivation, the former evolved under crop cultivation, and the latter, in contrast to their cultivated counterpart, continued its evolution under natural conditions. Therefore, wheat and its wild progenitors provide an excellent system for characterizing the influences of human activities on range and niche dynamics. We can reasonably assume that there are considerably range and niche dynamics between wheat and its wild progenitors, and studies on this topic need much attention.

In a word, wheat and its wild progenitors provide an excellent system for characterizing the effects of human activities on range and niche dynamics. Here, we examined range and niche dynamics between wheat and its wild progenitors, and tested whether wheat has retained the niche inherited from its wild progenitors. Generally, this study enhances our understanding of the roles of human activities in shaping ranges and niches of species and provides new insight into the niche conservatism hypothesis.

2. Material and methods

2.1. Occurrence records of wheat and its wild progenitors
To obtain global occurrence records of wheat and its wild progenitors (A. tauschii and T. dicoccoides), we conducted an extensive search in the following online databases: Global Biodiversity Information Facility (GBIF), Centre Agriculture Bioscience International (CABI), LIFEMAPPER, Web of Science, and Chinese Virtual Herbarium (CVH). All duplicate records were removed. After checking the nomenclature and
taxonomic identity according to the plant list (www.theplantlist.org) and time records (between 1970 and 2000), we obtained occurrence records with distinct geographic coordinate information with an uncertainty less than 10 km (ca. 5 arc-minutes), in which the time records were set to meet the time stamp of bioclimatic data near current conditions (between 1970 and 2000) from Worldclim (Fick and Hijmans 2017). Spatial bias caused by the spatial autocorrelation of occurrence records may affect the performance of ENMs (Warren and Seifert 2011). We spatially rarefied occurrence data (SROD) with a resolution of 10 km (ca. 5 arc-minutes) through SDM toolboxes developed by Brown (2014) and Brown et al (2017) to reduce the effect of spatial bias associated with having one record per grid cell as suggested by Warren and Seifert (2011).

2.2. Environmental parameters
As our primary goal was investigating climatic niche dynamics between wheat and its wild progenitors and their ranges, we therefore only used the climatic predictors. This also made our study comparable to past studies (Gallagher et al 2010, Petitpierre et al 2012, Broennimann et al 2014, Liu et al 2020). The 19 bioclimatic parameters with a spatial resolution of 5 arc-minutes (ca. 10km) were downloaded from Worldclim (Fick and Hijmans 2017). Of note, Worldclim data is a 30-year climatology, which may make it difficult to capture lethal extremes. It could necessarily over-detect niches that are marginal, and therefore we must acknowledge that our approach is not a conservative estimate.

As the target of ecological niche models (ENMs) is to fit the realm of niches (Peterson and Soberón 2012), biomod2, an integrated platform of ENMs (Thuiller et al 2009), was used to identify the determinants that are responsible for the niche spaces of wheat and its wild progenitors, as well as to account for the collinearity among those factors. To account for overprediction caused by strong collinearity among factors, we performed factor selection based on the Akaike information criterion (AIC). We used the stepAIC function in MASS R package (Ripley et al 2013), and obtained factor combination with the least AIC (S1). The retained factors were used in the investigations of niche dynamics.

2.3. ENMs for species’ range sizes
Considering the variability between different ENMs, the biomod2 package, an ensemble ENMs platform, was used to obtain the central trends for different models (Thuiller et al 2009). We used seven different algorithms—generalized boosting model (GBM), generalized additive model (GAM), classification tree analysis (CTA), artificial neural network (ANN), flexible discriminant analysis (FDA), maximum entropy models (MaxEnt) and random forest (RF)—to develop the ENMs for each species (Thuiller et al 2009). In the ENMs for each species, a five-times repeated split sampling approach was used to evaluate the predictive performance of each model, wherein a 70% random sample of initial data was used for model development, and the remaining 30% was used for evaluation, which was repeated five times. The evaluation indices included true skill statistics (TSS) (Allouche et al 2006), area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997), and the Kappa coefficient (Cohen 1960). The thresholds of the models for inclusion in the ensemble models were TSS > 0.6 and AUC > 0.8 (Bellard et al 2014). As required by all ENMs, we generated pseudo-absences (PAs or background) by selecting random points across the globe. As suggested by Barbet-Massin et al (2012), if the number of presence records ≤1000, 1000 PAs were selected, or equal weights were assigned to presences and PAs. Weights proportional to the TSS evaluation were used to build an ensemble model for each species. From these ensemble ENMs, we obtained importance values of each factor. To distinguish between suitable and unsuitable regions in the model results, we used the thresholds of the sensitivity-specificity sum maximization approach to classify the suitable and unsuitable land for each species (Liu et al 2016). Of note, range sizes of each species were represented by the areas of suitable land. To compare the spatial patterns of the ranges of between wheat and its wild progenitors, we used Mapcurves, a quantitative goodness-of-fit (GOF) method proposed by Hargrove et al (2006) that reliably shows the degree of spatial concordance between two categorical maps.

2.4. Divergence time estimation
Following the methods of Duan et al (2020) and Mehmood et al (2020), we estimated the divergence time of the wild progenitors using the nucleic acid sequences downloaded from the NCBI site (https://www.ncbi.nlm.nih.gov/). We conducted progressive multiple amino acid sequence alignments through Clustal X 2.0 (Larkin et al 2007), which were also corrected manually using BioEdit (Hall 1990) (http://www.mbio.ncsu.edu/bioedit/bioedit). We used the Bayesian Markov chain Monte Carlo (MCMC) algorithm implemented in BEAST package v.2.5.2 (Bouckaert et al 2019) to estimate divergence times within the family or subfamily. In this estimation, the ITS sequences were used, and the fossil time and the outgroup were obtained from an extensive literature survey. We used a relaxed lognormal molecular clock for all partitions. Additionally, we performed the Yule process for the tree prior with a constant speciation rate for each lineage (Drummond et al 2006), and we used random tree as the starting tree. The Bayesian MCMC 100 million generations were run with parameters sampled at every
1000 generations at three independent time points (Mehmood et al, 2020). We used Tracer v1.7.1 to evaluate convergence and the correct mixing of all parameters by visually checking log traces and estimate the effective sample size (ESS) of each parameter (Drummond and Rambaut 2007). After discarding the first 10% of each analysis as burn-in, we combined results from the runs at three independent times using LogCombiner v2.6.3 (Drummond et al, 2012). In TreeAnnotator v2.3.6 (Drummond et al, 2012), we used a Maximum Clade Credibility target tree to summarize the remaining trees, as well as Bayesian posterior probability (PP), MEDIAN/MEAN height, and the 95% highest posterior density heights interval (95% HPD) of each node (Duan et al, 2020, Mehmood et al, 2020). We examined the MCMC output for convergence to guarantee that all ESS values were greater than 200.

2.5. Niche dynamics between wheat and its wild progenitors

We explored niche dynamics (i.e., overall changes in breadth and position between the niches of wheat and its wild progenitors) through the COUE scheme (Broennimann et al, 2012, Petitpierre et al, 2012), which is considered the gold standard method for studying niche dynamics (Guisan et al, 2014, Atwater et al, 2018). In this analysis, we assumed that wheat inherited its wild progenitors’ potential niche space before cultivation, which was generally associated with evolution under natural conditions; thus, they shared the same potential niche space before cultivation (figure 1). From the date of wheat cultivation to the present, the potential niche spaces of the wild progenitors were continually controlled by evolution under natural conditions, whereas those of wheat were generally associated with its evolution under crop cultivation (figure 1). We first used principal component analysis (PCA) to build a two-dimensional niche space composed of two PC axes representing major variation in all of the environmental variables. We divided the total environmental space defined by the two PC axes into a 100 × 100 grid. We then used a kernel density function to calculate the smoothed density of occurrences in environmental space for ecological niche comparison, which is independent of sampling effort and of the spatial resolution of the environmental grid (Broennimann et al, 2012, Fraimout et al, 2018). The niche space occupied by species was divided into expansion (E), stability (S), and unfilling (U) (Guisan et al, 2014) (figure 2). E is the niche space (represented by the proportion of densities, same as follows) corresponding to the climatic conditions that only wheat can tolerate (i.e., not observed in the wild progenitors) and thus reflects the magnitude of the niche shift. By contrast, niche unfilling is the niche space corresponding to the climatic conditions that are tolerated by the wild progenitors of wheat, and thus reflect the potential environmental conditions that wheat could tolerate in the future (Guisan et al, 2014). Finally, S is the niche space corresponding to the climatic conditions that can be tolerated by both wheat and its wild progenitors (Guisan et al, 2014). The niche conservatism hypothesis was rejected if the niche expanded rapidly (i.e., the niche breadth of wheat were larger than those of its wild progenitors) (Pearman et al, 2008) or if the niche position changed rapidly (i.e., wheat and its wild progenitors occupied different niche positions measured by Sørensen’s similarity index) (Broennimann et al, 2007). The breadth of wild progenitors was estimated as the sum of U and S, and that of wheat was estimated as the sum of S and E. We used the ln-transformed ratio of niche breadth of the wild progenitors to that of wheat to measure the changes in niche breadth:

\[ B_R = \ln \left( \frac{B_N}{B_Y} \right) \]
where $BR$, $BN$, and $BI$ were the breadth ratio, the niche breadth of the wild progenitors, and the niche breadth of wheat, respectively. Following Pearman et al (2008) and Liu et al (2020), the niche conservatism hypothesis was rejected if $BR < 0$ ($BN < BI$).

The Sørensen’s similarity index was used to measure the changes in niche position (Baselga 2017):

$$Sim = \frac{2S}{BN + BI}$$

where $Sim$ and $S$ were the Sørensen’s similarity index and the niche space under climatic conditions occupied by both wheat and its wild progenitors, respectively. Following Broennimann et al (2007) and Liu et al (2020), the niche conservatism hypothesis was rejected if $Sim < 0.5$. All analyses were carried out using the 'ecospat' package (Di Cola et al 2017).

### 3. Results

Totally, we obtained 790, 275, and 43 occurrence records for wheat ($T. aestivum$), $A. tauschii$ and $T. dicoccoides$ (figure 3 and S2). The ENMs used to identify major factors shaping the niche spaces showed high predicting reliability. The TSS, AUC, and Kappa of the integrated ENMs for wheat were 0.90, 0.99, and 0.78, respectively; those for $A. tauschii$ were 0.94, 0.99, and 0.73, respectively; and those for $T. dicoccoides$ were 0.99, 0.99, and 0.92, respectively. The most important predictor for the niche spaces of wheat ($T. aestivum$) was bio1, followed by bio11 and bio4, which had importance values of 0.36, 0.33, and 0.29, respectively (S1). The least important predictors were bio17 (0.06), bio9 (0.06), and bio15 (0.06) (S1). The most important predictor for the niche spaces of $A. tauschii$ was Precipitation of bio11 (0.40), bio18 (0.35), and bio4 (0.34) (S1). The least important predictors were bio8 (0.10), bio2 (0.09), and bio15 (0.08) (S1). The most important predictor for the niche spaces of $T. dicoccoides$ was bio19 (0.65), followed by bio14 (0.42) and bio17 (0.26) (S1). The least important predictors were bio8 (0.06), bio2 (0.05), and bio5 (0.04) (S1). Thus, climatic factors made larger contributions to shaping the niche spaces of the three species compared with other factors (S1).

The potential range size (suitable habitats) of wheat was determined to cover an area of ca. $1.00 \times 10^7$ km$^2$, and was mostly observed in middle latitudinal regions, such as Europe, the west coast regions of the United States and southern part of South America, the southern coast regions of Australia and the southernmost tip of Africa (figure 4). Additionally, the range spanned ca. 126.56° and 344.44° in latitude and longitude, respectively. The potential range of $T. tauschi$ covered ca. $4.00 \times 10^6$ km$^2$, and was concentrated in East Europe, West Asia,
Central Asia and scattered parts of the western United States, and spanned 24.66° and 202.34° in latitude and longitude, respectively (figure 4). The potential range for *T. dicoccoides* covered ca. $2.42 \times 10^5$ km$^2$, and was mostly concentrated in West Asia, and spanned 9.05° and 74.33° in latitude and longitude, respectively (figure 4). The overlap between wheat and *T. tauschi* was mostly concentrated in the range of the latter; the percentage of the overlap area was 14.81% (figure 5), covering $8.88 \times 10^5$ km$^2$. The overlap between wheat and *T. dicoccoides* was $6.83 \times 10^4$ km$^2$ and was also mostly concentrated in the range of the latter; the percentage of the overlap area was 0.70. GOF analysis showed that the degree of spatial concordance between wheat and *Aegilops tauschi* was 0.012, and that between wheat and *Triticum dicoccoides* was 0.0015, suggesting low spatial concordance between wheat and its wild progenitors.

Figure 3. Global occurrence records of wheat and its wild progenitors. a, *T. aestivum* (wheat) (790 records); b, *A. tauschi* (275 records); c, *T. dicoccoides* (43 records). All of the occurrence records have a time stamp between 1970–2000.

Figure 4. The range sizes (suitable habitats) of wheat and its wild progenitors. a, *Triticum aestivum* (wheat); b, *Aegilops tauschi*; c, *Triticum dicoccoides*. The threshold of the suitable and unsuitable habitats was made on the basis of sensitivity-specificity sum maximization approach. Area: the area of range sizes; Rlat: the latitudinal ranges; Rlong: longitudinal ranges.
The minimum time of cultivation of wheat (i.e., 10,000 years) was retrieved from a checklist by Milla (2020). Our study on divergence time estimation showed that the divergence time of the wild progenitors was 3.33 Myr and 0.61 Myr for *A. tauschii* and *T. dicoccoides*, respectively.

The investigation of the niche dynamics showed high reliability; the first two axes of the PCA were responsible for most of the variation in the datasets for the investigation of niche dynamics: 76.2% of the variation in the environmental variables for wheat and *A. tauschii*, and 76.1% for wheat and *T. dicoccoides*. The niche dynamics between wheat and *A. tauschii* showed that E, S, and U were 0.60, 0.40, and 0.00, respectively (figure 6). For the niche dynamics between wheat and *T. dicoccoides*, E, S, and U were 0.90, 0.10, and 0.00, respectively (figure 6). The breadth ratios between wheat and *A. tauschii* and between wheat and *T. dicoccoides* were −0.91 and −2.30, respectively; thus, the niche breadth of wheat was much wider than that of its wild progenitors. Additionally, the similarity indices between wheat and *A. tauschii* and between wheat and *T. dicoccoides* were 0.57 and 0.18, respectively, suggesting that wheat and its wild progenitors occupied different niche positions. Overall, the breadth ratios and similarity indices between wheat and its wild progenitors showed that wheat did not conform to niche spaces inherited from their wild progenitors, i.e., these results were not consistent with the niche conservatism hypothesis.
4. Discussion

Wheat and its wild progenitors shared the same evolutionary origin, evolutionary history, as well as potential ranges and niche spaces prior to wheat cultivation; however, the degree of human intervention differed after wheat cultivation. Using biomod2 (an ensemble platform for ENMs) (Thuiller et al 2010) and the COUE scheme (Broennimann et al 2012, Petitpierre et al 2012), we investigated the potential range sizes of wheat and its wild progenitors, as well as the niche dynamics between them. Our results showed that wheat had larger range size and niche breadth than its wild progenitors, which may suggest that wheat cultivation is a more powerful driver of range and niche expansion than niche evolution under natural conditions. Additionally, we observed that wheat and its wild progenitors occupied different niche positions, and wheat did not conserve the niches inherited from its wild progenitors, implying that wheat cultivation considerably induces niche shifts. Overall, the findings of this study could enhance our understanding of the roles of crop cultivation in determining the range and niche dynamics of species.

The size of a species’ range and niche space is closely associated with evolution history, i.e., longer evolution history generally suggests larger range sizes and niche spaces (Liu et al 2020). Our results showed that in the ca. 10,000 years of cultivation history, the range and niche breadth of wheat were larger compared with its wild progenitors (i.e., A. tauschii and T. dicoccoides) which have evolved their niche breadths over the course of 3.33 Myr and 0.61 Myr, respectively. Thus, wheat cultivation has a much stronger effect on range and niche expansion compared with niche evolution under natural conditions. We also observed that wheat’s ca. 10,000 years of cultivation history had resulted in the evolution of a niche position that differs from its two wild progenitors (i.e., A. tauschii and T. dicoccoides), both of which have undergone a much longer period of evolution (ca. 333 and 61 times of the time length, respectively), suggesting that crop cultivation could considerably modify the niche position of species and result in considerable niche shifts over relatively short periods of time, which could be supported by Stanhill (1986) and Yan et al (2018) that irrigation and trait selection of wheat could facilitate wheat production in arid regions. These observations were partially consistent to a finding that niche shifts in introduced species can be far faster than those in native species (Wiens et al 2019). Thus, the effect of crop (wheat) cultivation on niche shifts requires increased attention.

The strong effect of wheat cultivation on the niche dynamics between wheat and its wild progenitors may be closely associated with cultivation activities. To meet the human demand for wheat, wheat has often been introduced to and cultivated in regions beyond its original range, which has exposed wheat to higher probability to adapt to novel environments, resulting in niche expansions (Long et al 2018, Zhou et al 2018). Moreover, wheat cultivation measures (e.g., fertilization, irrigation and genetic modification breeding) could enhance wheat’s adaptation to harsh environmental conditions (Ventrella et al 2012, Lopes et al 2015), in which it would fail without cultivation measures. This may also result in wheat’s niche shifting, colonizing outside the range of climate conditions that it can naturally tolerate. However, for its wild progenitors, the probability of having these opportunities is low; and so too were the probabilities of their niche expansions. Wheat cultivation thus plays an important role in inducing the niche dynamics between wheat and its wild progenitors, resulting in wheat’s non-conservation of niche spaces inherited from its wild progenitors.

Niche shifts in plant invasions have attracted much attention and have led to much controversy in recent decades. Using the COUE scheme, Liu et al (2020) found that only a small portion of invasive plant species (0.7%) did not show conserved niches. Using a similar methodology, we found that wheat did not conserve the niche species inherited from its wild progenitors, suggesting that the ability of wheat cultivation in shaping niche dynamics is much stronger compared with most plant invasions. First, this might be related to the differences in their cultivation or introduction history. Wheat has been cultivated for ca. 10,000 years, and the introduction history of most invasive plants is generally shorter than 500 years (Liu et al 2020). Second, compared with wheat, most invasive plants generally do not have a cultivation history that permits adaptation to different climatic conditions, which would aid their ability to expand their niche. Therefore, with the aid of cultivation, cultivated crop species can more easily expand the niche space compared with invasive plants. Therefore, compared with the niche shifts induced by plant invasions, those induced by crop cultivation need much more attention.

Our study showed that the niche dynamics between wheat and A. tauschii were weaker than those between wheat and T. dicoccoides (breadth ratio, −0.91 versus −2.30; similarity index, 0.57 versus 0.18, respectively), and the potential range size of A. tauschii was larger than that of T. dicoccoides (figure 4). These observations indicate that although we found that wheat cultivation may result in considerable niche shifts and even lead to the evolution of a niche space that differs from its wild progenitors, variation in the niche shift caused by wheat cultivation may depend on the ranges of the wild progenitors. In other words, wheat of the generalist wild progenitor species showed weaker niche shifts than that of the specialist wild progenitor species, possibly because generalist progenitor species with a larger range size may show stronger niche conservatism (Li et al 2014, Rosenblad et al 2019). Therefore, although wheat cultivation may result in significant niche shifts, its ability may be modified by the niche conservatism of the wild progenitors.
shifts, and highlights opportunities for future studies to address the underlying mechanisms.

5. Conclusions

Using biomod2 and the COUE scheme, this study examined the potential ranges of wheat and its wild progenitors, as well as the niche dynamics between them. Our results demonstrated considerable range and niche expansions wheat relative to its wild progenitors. We also found that the niche dynamics between wheat and its wild progenitors were not only closely associated with cultivation but were also modified by the niche conservatism of its wild progenitors. Moreover, in contrast to most invasive plants, wheat, as a worldwide staple crop species, did not conserve the niche space inherited from its wild progenitors, suggesting that cultivation may have a stronger effect on niche shifts compared with most plant invasions. Compared with plant invasions, range and niche shifts induced by crop cultivation have been understudied. Considering the role of wheat crop cultivation in addition to that of wild progenitors broadens understanding of factors controlling species niche shifts, and highlights opportunities for future studies to address the underlying mechanisms.

Acknowledgments

This study is supported by the National Natural Science Foundation of China (Grant ID: 31901102; 41963007), Innovative team of Plant Ecology and Climate change in Hengduan Mountains, Dali University, China (Grant ID: ZKLX2019217) and Scientific Research Fund of Department of Education of Yunnan Province (Grant ID: 2021Y391).

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/https://github.com/fengjiammenglab/R-code-for-niche-and-range-shifts-of-wheat.git.

ORCID iDs

Feng Jianmeng @ https://orcid.org/0000-0002-2373-2031

References

Allouche O, Tsoar A and Kadmon R 2006 Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS) J. Appl. Ecol. 43 1223–32
Atwater D Z, Ervine C and Barney J N 2018 Climatic niche shifts are common in introduced plants Nat. Ecol. Evol. 2 34–43
Barbet-Massin M, Jiguet F, Albert C H and Thuiller W 2012 Selecting pseudo-absences for species distribution models: how, where and how many? Methods. Ecol. Evol. 3 327–38
Baselga A 2017 Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients Methods. Ecol. Evol. 8 799–808
Bouckaert R et al 2019 BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis PLoS Comput. Biol. 15 e1006650
Boudjabi S, Kribaa M and Chenchouni H 2019 Sewage sludge fertilization alleviates drought stress and improves physiological adaptation and yield performances in Durum Wheat (Triticum durum): A double-edged sword J. King. Saud. Univ. Sci. 31 336–44
Broennimann O, Treier U A, Muller-Scharer H, Thuiller W, Peterson A T and Guisan A 2007 Evidence of climatic niche shift during biological invasion Ecol. Lett. 10 701–9
Broennimann O et al 2012 Measuring ecological niche overlap from occurrence and spatial environmental data Glob. Ecol. Biogeogr. 21 481–97
Broennimann O, Mráz P, Petitpierre B, Guisan A and Müller-Scharer H 2014 Contrasting spatio-temporal climatic niche dynamics during the eastern and western invasions of spotted knapweed in North America J. Biogeogr. 41 1126–36
Brown J L 2014 SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses Methods. Ecol. Evol. 5 694–700
Brown J L, Bennett J R and French C M 2017 SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses PeerJ 5 e4095
Burns P, Clark M, Salas L, Hancock S, Leland D, Jantz P, Dubayah R and Goetz S J 2020 Incorporating canopy structure from simulated GEDI lidar into bird species distribution models Environ. Res. Lett. 15 095002
Ceballos G and Ehrlich P R 2002 Mammal population losses and the extinction crisis Science 296 904–7
Cohen J 1960 A coefficient of agreement for nominal scales Educ. Psychol. Meas. 20 37–46
Colwell R K and Rangel T F 2009 Hutchinson’s duality: The once and future niche Proc. Natl Acad. Sci. 106 19651–8
Di Cota V et al 2017 ecospat: an R package to support spatial analyses and modeling of species niches and distributions Ecolography 40 774–87
Drummond A J, Ho S Y W, Phillips M J and Rambaut A 2006 Relaxed phylogenetics and dating with confidence PLoS Biol. 4 e88
Drummond A J and Rambaut A 2007 BEAST: bayesian evolutionary analysis by sampling trees BMC Evol. Biol. 7 214
Drummond A J, Suchard M A, Xie D and Rambaut A 2012 Bayesian phylogenetics with BEAUti and the BEAST 1.7 Mol. Biol. Evol. 29 1969–73
Duan L, Harris A J, Su C, Ye W, Deng S W, Fu L, Wen J and Chen H F 2020 A fossil–calibrated phylogeny reveals the biogeographic history of the Cladrastis clade, an amphi-Paciﬁc early-branching group in papilionoid legumes Mol. Phylogeen. Evol. 143 106673
Dvorak J, Deel K R, Luo M C, You F M, von Borslet K and Dehghani H 2012 The Origin of Spelt and Free-Threshing Hexaploid Wheat J. Hered. 103 426–41
Fick S E and Hijmans R J 2017 World Clim 2: new 1–km spatial resolution climate surfaces for global land areas Int. J. Climatol. 37 4302–15
Fielding A H and Bell J F 1997 A review of the methods for assessment of prediction errors in conservation presence/absence models Environ. Conserv. 24 38–49
Framout A and Monnet A C 2018 Accounting for intraspecific variation to quantify niche dynamics along the invasion routes of Drosophila suzukii Biol. Invasions. 20 2963–79
Gallagher R V, Beumont I J, H Hughes, Land Leishman M R 2010 Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia J. Ecol. 98 790–9
Gosner M M et al 2016 Land-use intensification causes multivariate homogenization of grassland communities Nature 540 266–9
Guisan A, Petitpierre B, Broennimann O, Daehler C and Kueffer C 2014 Unifying niche shift studies: Insights from biological invasions Trends Ecol. Evol. 29 260–9
Hargrove W W, Huffman F M and Henssberg P F 2006 Mapcurses: a quantitative method for comparing categorical maps J. Geogr. Syst. 8 187–208
Humphreys A M, Govaerts R, Ficinski S Z, Lughadha E N and Vorontsova M S 2019 Global dataset shows geography and life form predict modern plant extinction and rediscovery Nat. Ecol. Evol. 3 1043–7
Hutchinson G E 1957 Concluding remarks, Coldspring Harbor Symp. Quant. Biol. 22 415–27
Ibella F et al 2017 Linking the influence and dependence of people on biodiversity across scales Nature 546 65–72
Laanisto L, Sammul M, Kull T, Macek P and Hutchings M J 2015 Trait-based analysis of decline in plant species ranges during the 20th century: a regional comparison between the UK and Estonia Glob. Chang. Biol. 21 2726–38
Larkin M A et al 2007 Clustal W and Clustal X version 2.0 Bioinformatics. 23 2947–8
Li Y M, Liu X, Li X P, Abdullah, Ubaid Z, Shahzadi I, Ahmed I, Waheed M T, Poczai P and Mirza B 2020 Plastid genomics of Nicotiana Environ. Res. Commun. 3 115012 Y Rujing et al
Liu C L, Wolter C, Xian W W and Jeschke J M 2020 Most invasive species largely conserve their climatic niche Proc. Natl Acad. Sci. 117 23643–51
Lobo D, Leao T, Melo F P L, Santos A M M and Tabarelli M 2011 Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization Divers. Distrib. 17 287–96
Long T W, Leipe C, Jin G Y, Wagner M, Guo R Z, Schroder O and Tarasov P E 2018 The early history of wheat in China from C-14 dating and Bayesian chronological modelling Nat. Plants 4 272–9
Lopes M S et al 2015 Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change J. Exp. Bot. 66 3477–86
MacArthur R H 1968 The theory of the niche Population biology and evolution ed R Lewontin (New York: Academic) pp 139–79
Marco M and Santini L 2015 Human pressures predict species’ geographic range size better than biological traits Glob. Chang. Biol. 21 2169–78
Meemood F, Abdullah, Ubad Z, Shahzadi I, Ahmed I, Waheed M T, Poczai P and Mirza B 2020 Plastid genomics of Nicotiana (Solanaceae): insights into molecular evolution, positive selection and the origin of the maternal genome of Aztec tobacco (Nicotiana rustica) PeerJ 8 e9552
Milla R 2020 Crop Origins and Phylo Food: A database and a phylogenetic tree to stimulate comparative analyses on the origins of food crops Glob. Ecol. Biogeogr. 29 606–14
Ozkhan H, Wilkons G, Granner A, Salamini F and Killian B 2011 Geographic distribution and domestication of wild emmer wheat (Triticum dicoccoides) Genet. Resour. Crop. Evol. 58 11–53
Pearman B P, Guisan A, Broennimann O and Randin C F 2008 Niche dynamics in space and time Trends Ecol. Evol. 23 149–58
Peterson A T 2011 Ecological niche conservatism: a structured approach of evidence J. Biogeogr. 38 817–27
Peterson A T and Soberon J 2012 Species distribution modeling and ecological niche modeling: getting the concepts right Nat. Conserv. 10 102–7
Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C and Guisan A 2012 Climatic niche shifts are rare among terrestrial plant invaders Science 335 1344–8
Pimm S L, Jenkins C N, Abell R, Brooks T M, Gittleman J L, Joppa L N, Raven P H, Roberts C M and Sexton J O 2014 The biodiversity of species and their rates of extinction, distribution, and protection Science 344 987
Polaina E, Soustlan A, Part T and Recio M R 2021 The future of invasive terrestrial vertebrates in Europe under climate and land-use change Biol. Lett. 16 044004
Ripple W, Yenables B, Bates D M, Hornik K, Gebhardt A and Firth D 2013 Package ‘mass’. Cran R
Rosenblad K C, Perret D L and Sax D F 2019 Niche syndromes reveal climate-driven extinction threat to island endemic conifers Nat. Clim. Chang. 9 627–31
Rolland J, Silvestro D, Schluter D, Guisan A, Broennimann O and Salamin N 2018 The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity Nat. Ecol. Evol. 2 459–64
Sexton J P, Montiel I, Shay J E, Stephens M R and Slattery R A 2017 Evolution of Ecological Niche Breadth Annu. Rev. Ecol. Evol. Syst. 48 183–206
Smith J A, Thomas A C, Levi T, Wang Y W and Wilmers C C 2018 Human activity reduces niche partitioning among three widespread mezocarnivores Othus. 127 890–901
Stanhill G 1986 Irrigation in arid lands Philos. T. R. Soc. A 316 261–74
Thullier W, Lafoucade B, Engler R and Araujo M B 2009 BIOMOD—a platform for ensemble forecasting of species distributions Ecol. Lett. 12 369–73
van Kleunen M et al 2015 Global exchange and accumulation of non-native plants Trends Ecol. Evol. 30 475–80
Ventrella D, Charfeddine M, Moriondo M, Rinaldi M and Bindi M 2012 Agronomic adaptation strategies under climate change for winter durum wheat and tomato in southern Italy: Irrigation and nitrogen fertilization Reg. Environ. Change 12 407–19
Warren D L and Seifert S N 2011 Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria Ecol. Appl. 21 335–42
Whittaker R H, Levin S A and Root R B 1973 Niche, Habitat, and Ecotope Ann. Nat. 107 321–8
Wiens J A, Stralberg D, Longsomjit D, Howell C A and Snyder M A 2009 Niches, models, and climate change: Assessing the assumptions and uncertainties Proc. Natl Acad. Sci. 106 18729–35
Wiens J J et al 2010 Niche conservatism as an emerging principle in ecology and conservation biology Ecol. Lett. 13 1310–24
Wiens J J and Graham C H 2005 Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology Annu. Rev. Ecol. Evol. Syst. 36 519–39
Wiens J J, Litvinenko Y, Harris L and Jezkova T 2019 Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change J. Biogeogr. 46 2115–25
Xu W B, Svenning J C, Chen G K, Zhang M G, Huang J H, Chen B, Ordonez A and Ma K P 2019 Human activities have opposing effects on distributions of narrow-ranged and widespread plant species in China Proc. Natl Acad. Sci. 116 26674–81
Yan J K, Zhang N N, Wang X L and Zhang S Q 2018 Selection of Yield-Related Traits for Wheat Breeding in Semi-Arid Region Int. J. Agric Biod. 316 569–74
Yue Y J, Zhang P Y and Shang Y R 2019 The potential global distribution and dynamics of wheat under multiple climate change scenarios Sci. Total Environ. 688 1308–18
Zhou Y et al 2018 Uncovering the dispersion history, adaptive evolution and selection of wheat in China Plant Biotechnol. J. 16 280–91