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Original Research Article

## Assessing the habitat suitability of 10 serious weed species in global croplands

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## ABSTRACT

Weed expansion has the potential to severely affect global agriculture. Habitat suitability models (HSMs) have been widely used to assess weed expansion to enable effective prevention and control of weeds. However, few studies have focused on the habitat suitability of global croplands for these weeds. Previous studies listed the 10 serious weed species that have the largest negative impact on global agriculture. Here, we used Maxent modeling (an HSM with good performance) to quantify the habitat suitability of global croplands for these 10 weed species using occurrence records and environmental variables (i.e., climate factors, soil properties, and human footprint). We compared the habitat suitability values of these 10 serious weed species in 174 different types of cropland. The habitat suitability values for all the weed species studied was high in global croplands. Furthermore, habitat suitability may depend on the type of cropland and the spatial variation created by varying climate factors, soil properties, and human footprint. *Cynodon dactylon*, *Echinochloa crus-galli*, *Eleusine indica*, *Panicum maximum*, and *Sorghum halepense* had the highest habitat suitability values in chicory plantations. *Cyperus rotundus* and *Echinochloa colona* had the highest habitat suitability values in olive plantations. The habitat suitability values for *Imperata cylindrica* was the highest in mustard plantations, *Eichhornia crassipes* was most suited to expansion in raspberry plantations, and the habitat suitability values for *Lantana camara* was the highest in chickpea plantations. Risk prevention and control should be based on the cropland type for these 10 serious weed species, taking into account climate factors, soil properties, and human activities. Our study provides guidelines for effective management of weed risk in different croplands globally.

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## 1. Introduction

Weeds can adapt to disturbed environmental conditions and become dominant when introduced to new areas (Holm, 1969; Eue, 1986; Clements and Ditommaso, 2011). They may compete with the desired crop for the available resources (e.g., direct sunlight, soil nutrients, water, and space for growth), which potentially threatens agricultural food production (Patterson, 1995; Clements and Ditommaso, 2011; Tshewang et al., 2016). Furthermore, environmental changes have the

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potential to enhance the negative effects of weeds on agriculture on a global scale (Neve et al., 2009; Ziska, 2016). Rapid climate change could drive weed species with broad ecological niches to adapt to new environmental conditions that differ from their endemic regions (Clements and Ditommaso, 2011; Crossman et al., 2011; Roger et al., 2015). For example, there are many invasive weed species in China, Australia, South Africa, and the United States, and the range of suitable habitats may expand due to climate change (Vardien et al., 2012; Beaumont et al., 2014; Roger et al., 2015; Allen and Bradley, 2016; Wan et al., 2017a). Human-mediated processes (e.g., seed dispersal) play an important role in weed expansion at larger scales (Pickering and Mount, 2010; Wan et al., 2017b). Furthermore, variation in soil properties may lead to weed seed banks in soils, and vertical distribution of weed seeds within the soils (Benech-Arnold et al., 2000). Holm (1969) listed 10 serious weed species (i.e., purple nutsedge, bermudagrass, barnyard grass, junglerice, goosegrass, johnsongrass, guineagrass, water hyacinth, cogongrass, and lantana) that cause the largest damages to agriculture globally. These species have a strong ability to adapt to different environmental conditions, and globally have broad expansion ranges (Holm, 1969). In particular, they can be a threat to croplands, resulting in the loss of food and feed beneficial to human beings (Holm, 1969). Hence, it is necessary to explore the expansion risk of these 10 weed species worldwide.

Habitat suitability is becoming an increasingly effective indicator of weed expansion risk on a global scale (Crossman et al., 2011; Richter et al., 2013). Habitat suitability models (HSMs) are widely used to project suitable habitat distributions of weed species on large spatial scales (Ervin and Holly, 2011; Gonçalves et al., 2014; Fan et al., 2018; Wan and Wang, 2018, 2019). For example, Ervin and Holly (2011) used HSMs to project suitable habitat distribution of *Imperata cylindrica* in the United States, Gonçalves et al. (2014) generated habitat suitability maps of *Lantana camara* across continents using HSMs, and Palma-Ordaz and Delgado-Rodríguez (2014) assessed the invasion risk of *Cynodon dactylon* in Mexico based on the habitat suitability concept. However, these studies on HSMs for weed risk assessments only focused on one specific species or region, while they did not consider habitat suitability for all 10 weed species across global croplands. Croplands are typically devoted to agriculture worldwide (Ramankutty et al., 2008; West et al., 2010; Cassidy et al., 2013). Therefore, they cannot provide robust references for the prevention and control of weed expansion for global agriculture. In the present study, an HSM was used to map the habitat suitability of different global croplands for these 10 weed species to improve the prevention and control of weed expansion.

The objective of our study was to predict habitat suitability across different croplands globally for the 10 serious weed species. Here, we proposed two hypotheses: 1) there may be significant differences in the habitat suitability of croplands and non-croplands in the weeds, and 2) the habitat suitability for a weed species may differ depending on the type of cropland. If the first hypothesis was established, we could conclude that the expansion of the 10 serious weed species was propagated by croplands on a global scale. For the second hypothesis, we selected 174 key global crop regions from the study by Ramankutty et al. (2008). We expected that the distribution of the weed species would overlap with the habitat suitability of specific crop areas. Hence, the effectiveness of the indicators developed can be further tailored to improve the prevention and control of the weeds, because we would be able to recommend the necessary weed-risk preventative and management practices for these 10 species depending on the type of cropland across the entire world.

To test these hypotheses, we used MaxEnt modeling (an HSM with good performance) to quantify the habitat suitability for 10 serious weed species worldwide based on occurrence records and environmental variables (i.e., climate factors, soil properties, and human footprint). Thereafter, we used a paired *t*-test to explore the differences in habitat suitability of croplands and non-croplands for these 10 weed species. We then compared the average habitat suitability of 174 different croplands for these 10 serious weed species. Lastly, we provide suggestions on the prevention and control of these 10 serious weed species that vary depending on the type of cropland, based on the relationship between habitat suitability and cropland type.

## 2. Materials and methods

### 2.1. Data on the 10 serious weed species

Holm (1969) listed the 10 serious weed species, which are as follows: purple nutsedge (*Cyperus rotundus*), bermudagrass (*Cynodon dactylon*), barnyard grass (*Echinochloa crus-galli*), junglerice (*Echinochloa colona*), goosegrass (*Eleusine indica*), johnsongrass (*Sorghum halepense*), guineagrass (*Panicum maximum*), water hyacinth (*Eichhornia crassipes*), cogongrass (*Imperata cylindrica*), and lantana (*Lantana camara*). We obtained the occurrence records of these 10 weed species from the Global Biodiversity Information Facility (GBIF; [www.gbif.org](http://www.gbif.org); accessed in February 2019). The bias and error of the occurrence records were corrected using the following methods: (1) duplicate records were removed when within an area of 10.0-arc-minute spatial resolution to reduce the effects of the geographic autocorrelation of the data on the HSM; (2) records with both longitude and latitude = 0° were removed; (3) records with identical geographic coordinates (i.e., longitude = latitude) were removed; and (4) the records with incorrect species names were removed (García-Roselló et al., 2015; Wan and Wang, 2019). In total, between 1795 and 7931 occurrence records were found for each of 10 weed species used in our study.

### 2.2. Data on environmental variables

To run the HSM, four climatic variables [annual mean temperature (°C\*10); temperature seasonality (standard deviation\*100); annual precipitation (mm); and precipitation seasonality (coefficient of variation)] were downloaded at 10.0

arc-minutes resolution from the WorldClim database (averaged from 1950 to 2000; <https://www.worldclim.org>). Eight soil variables [bulk density (kg/cubic meter); cation exchange capacity (cmolc/kg); soil texture fraction clay (%); coarse fragments volumetric (%); soil organic carbon stock (tonnes per ha); soil organic carbon content in % (g kg<sup>-1</sup>); soil pH; soil texture fraction silt (%); and soil texture fraction sand (%)] were obtained at 0.5 arc-minutes resolution from SoilGrids (<https://www.soilgrids.org>); and the global human footprint with a resolution of 0.5 arc-minutes was from Socioeconomic Data and Applications Center (SEDAC; <https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic>). The data resolution of the soil and the human footprint variables were transformed from 0.5 arc-minutes to 10.0 arc-minutes using ArcGIS 10.6 (<https://www.esri.com/software/arcgis/arcgis-for-desktop>). These environmental variables can potentially have a large effect on habitat suitability for weed species at large spatial scales (Holm, 1969; Beaumont et al., 2014; Roger et al., 2015; Wan et al., 2017a). The Pearson's correlation coefficients of the environmental variables with other variables were lower than the absolute values of 0.75, indicating a negligible effect of multicollinearity on the adjustment of the HSM.

### 2.3. Data on croplands

All the cropland maps, including the areas of distinct crops, were downloaded from EarthStat geographic data sets (<http://www.earthstat.org/>). The details of the global cropland maps, including the locations of 174 distinct crops, were obtained from the study by Ramankutty et al. (2008). These maps were produced by combining agricultural inventory data with satellite-derived land cover data. The grid resolution of these cropland maps was 5.0 arc-minutes (ca. 10 km × 10 km at the equator). The details of the 174 distinct crops are shown on the website (<http://www.earthstat.org/harvested-area-yield-175-crops>) and Table S2).

### 2.4. Habitat suitability modeling

Maxent modeling was used to project current and future habitat suitability maps for the 10 weed species based on occurrence records and environmental variables (Phillips et al., 2017). We set the Maxent modeling parameters for each weed species as follows: 1) the regularization multiplier (beta): 2.0 to produce a smooth and general response shape, which represents biologically realistic behavior (Radosavljevic and Anderson, 2014); 2) the maximum number of background points: 10,000, while maintaining the same bias as the buffer of occurrence records on a global scale (Merow et al., 2013); and 3) the output of Maxent modeling: complementary log-log (cloglog; Phillips et al., 2017). A five-fold cross-validation approach was used with 80% of the occurrence data acting as a training set, with the remaining 20% of the occurrence data used as the test set in each run of five replicates to remove bias in recorded occurrence points, thereby improving the robustness of the HSM (Merow et al., 2013). The modeling output was the average of five replicates in a fold cross-validation approach. The cross-validation approach has one large advantage over using a single training and test division. The other sets were the same as those reported by Merow et al. (2013) and Wan and Wang (2019). The cloglog output format assigned each grid cell a value between 0 and 1, with 0 representing the lowest habitat suitability for the weed species and 1 the highest habitat suitability (Phillips et al., 2017). In the present study, we evaluated the predictive accuracy of the HSM using the area under the curve (AUC) of the receiver operating characteristic (ROC; Phillips et al., 2017) based on each HSM from the cross-validation approach. In this way, we used five AUC assessments for the HSM of each weed species, based on the cross-validation approach. Here, the modeling accuracy was high for these 10 weed species because the AUC was over 0.7 based on each run from the cross-validation approach (García-Callejas and Araújo, 2016; Jarnevich et al., 2018; Table S3).

### 2.5. Synthesis

First, we used ArcGIS 10.6 (<https://www.esri.com/software/arcgis/arcgis-for-desktop>) to overlay the occurrence records on croplands (containing 174 distinct crops) to quantify habitat suitability for the 10 weed species on a global scale. Convertino et al. (2014) used 0.6 as the optimal habitat suitability that would indicate the most areas of suitable habitats for a species based on global sensitivity and uncertainty analyses. Therefore, we used 0.6 (the result of Maxent modeling) as the threshold for high habitat suitability for weed species, as per the study by Convertino et al. (2014).

Second, climate factors and soil properties were quantified using a principal component analysis (PCA) based on environmental variables extracted from occurrence records in croplands. We set the first principal components (PCs) to represent climate factors and soil properties affecting habitat suitability for weed species in croplands. Then, we used simple linear regression modeling or binary linear regression modeling to explore the relationships between PCs (representing climate factors and soil properties) and the human footprint, and habitat suitability for the 10 serious weed species. We selected a model with a high coefficient of determination ( $R^2$ ) to explain the effects of environmental factors on the habitat suitability of croplands across the world for 10 weed species (Low-Décarie et al., 2014).

Third, we calculated the average habitat suitability value for each weed species based on both the cropland maps and the map of the areas where the 174 distinct crops grew, respectively. Finally, a paired *t*-test was used to explore the differences in habitat suitability between croplands and non-croplands for the 10 weed species. Habitat suitability for the 10 weed species in the 174 distinct crop areas was compared, checking for high habitat suitability. All analyses were performed in JMP 11.0 (<https://www.jmp.com/>).

### 3. Results

The 10 serious weed species had the highest habitat suitability (average values higher than 0.6, based on occurrence records) in global croplands (Fig. 1). Croplands had the highest habitat suitability value for *S. halepense*, while the habitat suitability value for *I. cylindrica* was highest in non-croplands globally (Fig. 1). Furthermore, there were significant differences in habitat suitability between croplands and non-croplands for *C. dactylon*, *C. rotundus*, *E. colona*, *E. crus-galli*, *E. crassipes*, *I. cylindrica*, and *S. halepense* (Fig. 1). Habitat suitability for *C. dactylon*, *E. crus-galli*, *E. crassipes*, *I. cylindrica*, and *S. halepense* was significantly higher in croplands than in non-croplands, whereas *C. rotundus* and *E. colona* showed the opposite result of these five weed species, more suited to non-croplands instead. (Fig. 1). All the serious weed species were distributed mainly in the southern regions of both North and South Americas, Southeastern Asia, and the southeastern regions of Australia (Fig. 2). *C. dactylon*, *E. crus-galli*, and *S. halepense* had the highest habitat suitability in Europe (Fig. 2). The habitat suitability of *C. rotundus*, *E. colona*, *E. indica*, and *I. cylindrica* were highest in China and India (Fig. 2).

Based on the PCA, the first three PCs potentially represented more than 60.0% of the environmental factors affecting the 10 weed species in global croplands. PC1 represented annual mean temperature, precipitation seasonality, soil organic carbon stock, and soil organic carbon content, PC2 represented annual precipitation and soil pH, and PC3 represented soil texture fraction clay, and soil texture fraction sand (Table 1). Here, we used the results of binary linear regression modeling to explain the effects of environmental factors on the habitat suitability of global croplands for weed species, because its  $R^2$  value is higher than in the simple linear regression modeling (Table S1). PC1 had the largest exploratory power on habitat suitability for *E. colona* and *E. crus-galli* (Table 1). PC2 mainly explained habitat suitability for *C. dactylon*, *C. rotundus*, *E. colona*, *E. crus-galli*, *E. indica*, *I. cylindrica*, and *P. maximum*, and PC3 had the greatest exploratory power for *I. cylindrica* (Table 1). HF explained the habitat suitability for most of the weed species, except for *C. dactylon*, *E. colona*, and *I. cylindrica* (Table 1).

Suitable habitats for the 10 serious weed species were found to be widely distributed across 172 distinct croplands globally (Tables 2 and S2). Of these different croplands, habitat suitability for weed species was high (average habitat suitability value of greater than 0.6 based on occurrence records) in 53 distinct croplands (Tables 2 and S2). *C. dactylon*, *E. crus-galli*, *E. indica*, *P. maximum*, and *S. halepense* were well-suited to chicory plantations, while *C. rotundus* and *E. colona* had the highest habitat suitability values in olive plantations (Table S2). The habitat suitability value for *I. cylindrica* was highest in mustard plantations, the habitat suitability value for *E. crassipes* was highest in raspberry plantations, and the habitat suitability value for *L. camara* were highest in chickpea plantations (Table S2).

### 4. Discussion

Our results showed that habitat suitability for the 10 serious weed species was extremely high (over 0.6) in both croplands and non-croplands worldwide, indicating that the prevention and control of weeds is a global issue. Furthermore, *C. dactylon*,

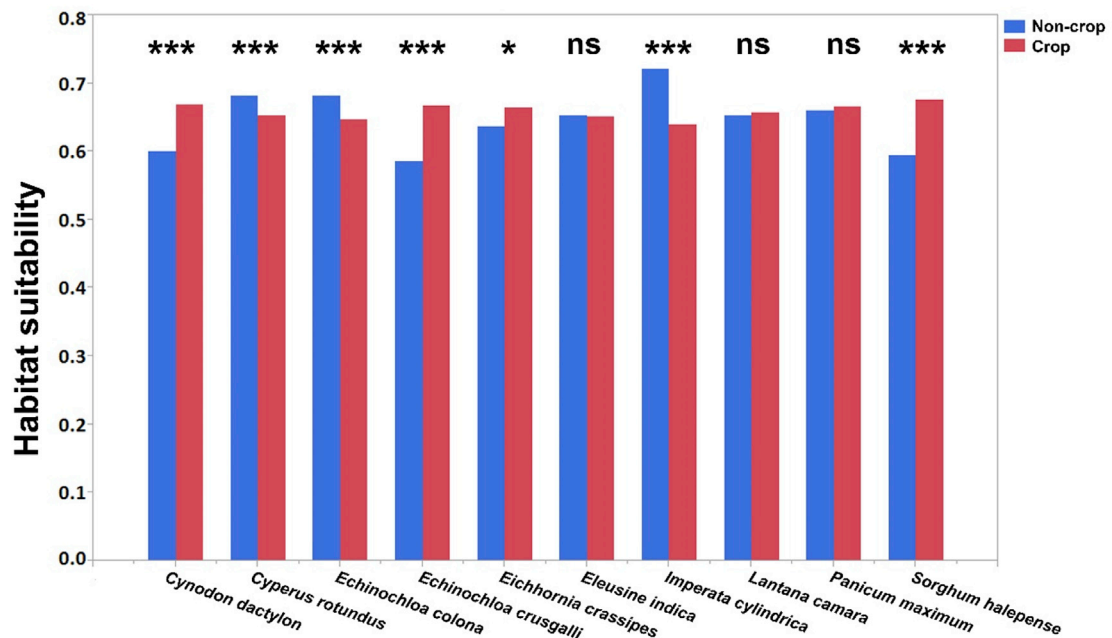


Fig. 1. Average habitat suitability for the 10 serious weed species in croplands and non-croplands. A paired *t*-test was used to explore the differences in habitat suitability between croplands and non-croplands across the 10 weed species. \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$  and ns $P < 0.05$ .

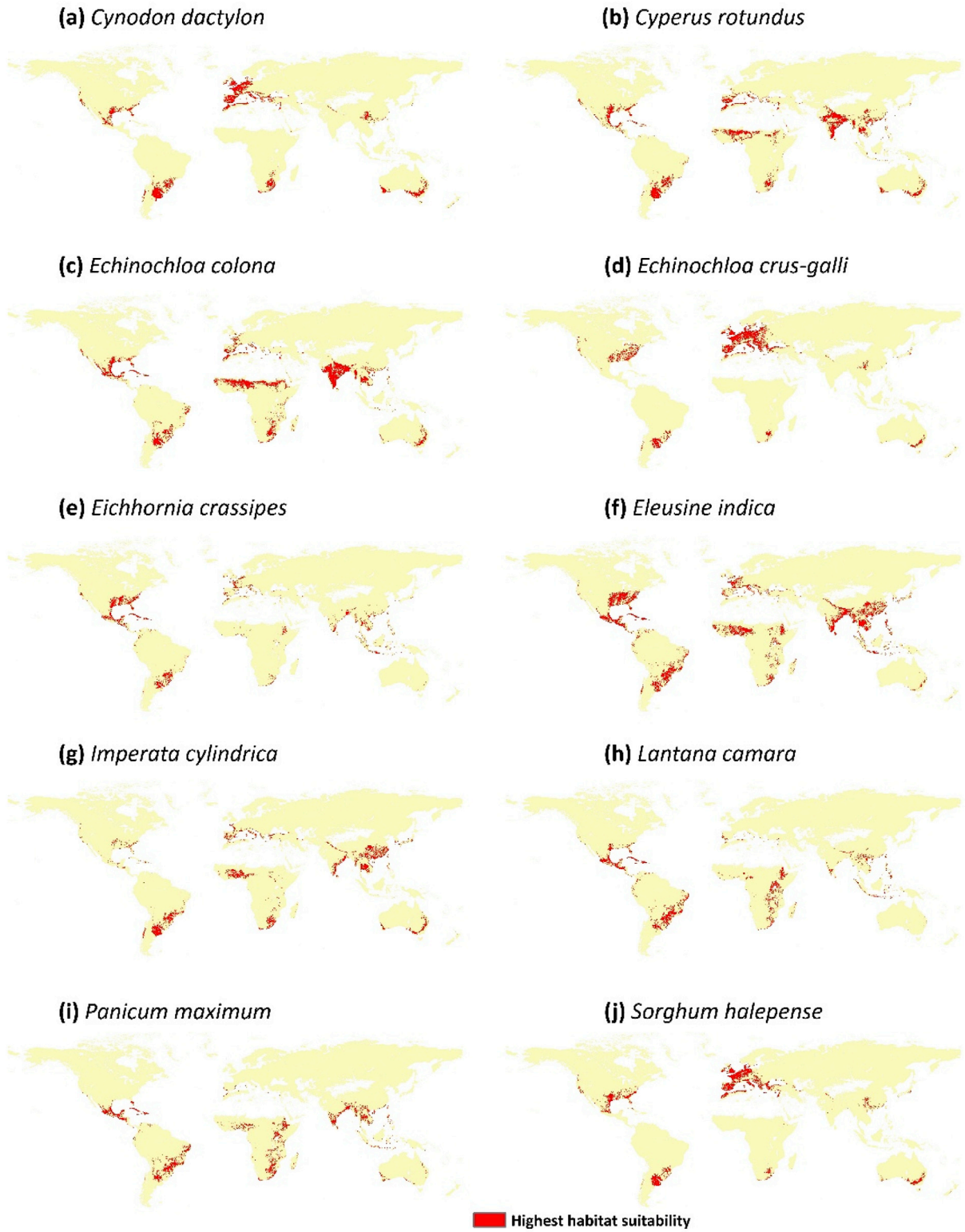


Fig. 2. Distribution maps of the highest habitat suitability of the 10 serious weed species in global croplands.

**Table 1**

Explanatory power of environmental factors on habitat suitability for 10 serious weed species in croplands based on binary linear regression modeling.

Species	PC1		PC2		PC3		HF	
	R <sup>2</sup>	P-values	R <sup>2</sup>	P-values	R <sup>2</sup>	P-values	R <sup>2</sup>	P-values
<i>Cynodon dactylon</i>	9.4%	<0.0001	14.9%	<0.0001	8.8%	<0.0001	6.7%	<0.0001
<i>Cyperus rotundus</i>	4.3%	<0.0001	21.9%	<0.0001	4.7%	<0.0001	16.1%	<0.0001
<i>Echinochloa colona</i>	16.1%	<0.0001	25.0%	<0.0001	1.5%	<0.0001	3.2%	<0.0001
<i>Echinochloa crus-galli</i>	16.8%	<0.0001	12.0%	<0.0001	3.4%	<0.0001	20.0%	<0.0001
<i>Eichhornia crassipes</i>	7.0%	<0.0001	0.7%	0.0054	1.2%	<0.0001	18.7%	<0.0001
<i>Eleusine indica</i>	4.9%	<0.0001	12.5%	<0.0001	3.2%	<0.0001	33.4%	<0.0001
<i>Imperata cylindrica</i>	5.4%	<0.0001	22.8%	<0.0001	13.9%	<0.0001	5.0%	<0.0001
<i>Lantana camara</i>	4.6%	<0.0001	5.6%	<0.0001	4.4%	<0.0001	17.7%	<0.0001
<i>Panicum maximum</i>	7.2%	<0.0001	11.3%	<0.0001	0.2%	0.2994	16.3%	<0.0001
<i>Sorghum halepense</i>	7.4%	<0.0001	7.8%	<0.0001	5.4%	<0.0001	24.8%	<0.0001

*E. crus-galli*, *E. crassipes*, *I. cylindrica*, and *S. halepense* had significantly higher habitat suitability values in croplands than in non-croplands, indicating that the development of heavy agricultural activity may be responsible for weed expansion globally. Agricultural activities were positively correlated to the footprint of human activity (Sanderson et al., 2002). The global expansion of these 10 weed species may be due to human introduction (e.g., transportation; Shimono and Konuma, 2008; Pickering and Mount, 2010; Wan et al., 2017b). Furthermore, climate factors and soil properties can affect the habitat type suitable for these weed species, but the effects may differ depending on the weed species (Table 1). *E. crassipes*, a floating plant native to the Neotropics that originated from the Amazon Basin in Brazil, spread widely across the world as an ornamental plant (Holm, 1969; Koutika and Rainey, 2015). This weed species has negative effects on its environment (Koutika and Rainey, 2015). *S. molesta* can spread rapidly by vegetative reproduction (Koutika and Rainey, 2015). The biomass of this weed species increased with a decrease in pH, which was partly consistent with our results (Koutika and Rainey, 2015, Table 1). Previous studies (e.g., Clements and Ditommaso, 2011; Ervin and Holly, 2011; Beaumont et al., 2014; Roger et al., 2015; Wan et al., 2016, 2017a) have shown that climate change increases the invasion risk of weed species (e.g., *I. cylindrica*) across different regions around the world. Phenotypic plasticity and rapid genetic change can enhance their ability to invade new areas under climate change (Clements and Ditommaso, 2011; Wan et al., 2020). Therefore, we should be mindful of the effects of climate change on weed expansion on a global scale.

Our results show that habitat suitability for the 10 serious weed species may differ depending on the type of crop, indicating that weed expansion and invasion are dependent upon the type of crop being grown, and this applies to the whole world. The competition between the weed species and the invaded crop species for growth space and access to nutrient resources determines weed expansion over large spatial scales (Holly and Ervin, 2007; Bajwa et al., 2017; Dass et al., 2017). For example, Holly and Ervin (2007) showed that seedlings growing in high-nutrient soil performed the best for *I. cylindrica* with the amount of light available (directly affected by growth space). Different types of croplands could lead to variations in growth space and available nutrient resources (Ryan et al., 2009; Bajwa et al., 2017; Dass et al., 2017). Furthermore, Ryan et al. (2009) indicated that weed–crop competition may differ between organic and conventional cropping systems. Weed–crop competition may depend on the type of cropland. Therefore, we should conduct different management systems for the 10 serious weed species depending on different types of croplands.

We also found that *C. dactylon*, *E. crus-galli*, *E. indica*, *P. maximum*, and *S. halepense* had the highest habitat suitability values in chicory plantations, while *C. rotundus* and *E. colona* had the highest habitat suitability in olive plantations. Chicory species are cultivated for their medicinal uses (Schmidt et al., 2007). However, weed invasion has the potential to affect chicory yield in plantations worldwide because the crop requires a long time to grow, which may offer weed species an advantage in growth and expansion on large scales (Sanderson et al., 2003; Li and Kemp, 2005). Thus, the annual chicory yield may be influenced by the forage persistence and the subsequent invasion of weed species (e.g., *C. dactylon*, *E. crus-galli*, *E. indica*, *P. maximum*, and *S. halepense*; Sanderson et al., 2003; Li and Kemp, 2005). Olive trees are generally cultivated worldwide for olive oil, fine-grained wood, olive leaf, and olive fruit (Şahin and Bilgin, 2018). However, olive tree plantations may be negatively affected by *C. rotundus* and *E. colona* because of the high habitat suitability values of these harmful weed species in this cropland (Table S2). These two weeds can cause substantial losses in crop yield and quality in olive plantations, which directly affect food security and safety (Holm, 1969). Furthermore, *I. cylindrica* and *L. camara* have been listed in the list of 100 of the World's Worst Invasive Alien Species (Luque et al., 2014). These two invasive weeds have a strong ability to reduce plant species diversity and reduce productivity in agricultural lands (Holly and Ervin, 2007; Ervin and Holly, 2011; Vardien et al., 2012). Climate change and certain soil properties can enhance the invasion of *I. cylindrica* and *L. camara* (Holly and Ervin, 2007; Ervin and Holly, 2011, Table 1). We found that *I. cylindrica* had high habitat suitability values in mustard plantations, and the habitat suitability values for *L. camara* was highest in chickpea plantations (Table S2). The characteristics affecting habitat suitability for these two weed species are annual precipitation, soil pH, soil texture fraction clay, and soil texture fraction sand (Table 1). Hence, we should implement better monitoring of *I. cylindrica* and *L. camara* in mustard and chickpea plantations, respectively, in sites across the world.

## 5. Limitations

Although our study extensively assessed the habitat suitability of croplands globally for 10 serious weed species, some limitations do exist. They are: 1) Our study did not consider the effects of climate change in the future on the distribution of weed species. Predicting the changes in the range of suitable habitats can be beneficial for global prevention and control of weed expansion, and so monitoring climate change and seeing its effect on weed risk may be an important contribution to weed management practices worldwide (Bradley et al., 2010; Ortega Andrade et al., 2017; Wan et al., 2018); 2) Land use and land cover were not accounted for in our study. For example, some weed species are likely to spread close to roads. Future studies on the effects of land use and land cover on weed species distribution may help inform weed management efforts (Baessler and Klotz, 2006; Armengot et al., 2011; Wan et al., 2016); 3) We did not identify whether these 10 weed species were native or invasive at the regional scale. However, these 10 weed species were identified to be the largest threats to croplands on a global scale. Hence, identifying the region the species originated from may not necessarily affect the outcome and implications of our study; 4) The HSM performance of our study may not be insufficiently robust based on AUC (Lobo et al., 2008). To decrease the uncertainty in our HSM when predicting weed species presence, we used high habitat suitability values (0.6) to assess weed risk worldwide; and 5) Feasibility of weed-risk prevention and control measures will be lower in some countries than in others owing to cost, laws, and other country-specific issues. Future studies should focus on the small-scale mechanisms underlying weed expansion (e.g., the relationship between functional traits and weed invasion) for these 10 serious weed species while focusing on different countries and taking future climate change scenarios into account.

## 6. Conclusion

The 10 serious weed species had the highest habitat suitability in global croplands. Furthermore, the suitable habitats of 10 serious weed species were widely distributed in different distinct croplands on a global scale. Different cropland systems and environmental factors could drive the expansion of these 10 weed species worldwide. The croplands of priority prevention and control included chicory for *C. dactylon*, *E. crusgalli*, *E. indica*, *P. maximum*, and *S. halepense*, olive for *C. rotundus* and *E. colona*, mustard for *I. cylindrica*, raspberry for *E. crassipes*, and chickpea for *L. camara* on a global scale. The prevention and control measures should be based on the cropland types along the spatial variation of climate factors, soil properties and human activities.

## Author contributions

Chun-Jing Wang conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper. Ji-Zhong Wan conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, approved the final draft.

## Declaration of competing interest

The authors have no interest or relationship, financial or otherwise that might be perceived as influencing the author's objectivity with this work and thus have no conflicts of interest to declare.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01142>.

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