Modeling impacts of human footprint and soil variability on the potential distribution of invasive plant species in different biomes

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ARTICLE INFO

ABSTRACT

Human footprint and soil variability may be important in shaping the spread of invasive plant species (IPS). However, until now, there is little knowledge on how human footprint and soil variability affect the potential distribution of IPS in different biomes. We used Maxent modeling to project the potential distribution of 29 IPS with wide distributions and long introduction histories in China based on various combinations of climatic correlates, soil characteristics and human footprint. Then, we evaluated the relative importance of each type of environmental variables (climate, soil and human footprint) as well as the difference in range and similarity of the potential distribution of IPS between different biomes. Human footprint and soil variables contributed to the prediction of the potential distribution of IPS, and different types of biomes had varying responses and degrees of impacts from the tested variables. Human footprint and soil variability had the highest tendency to increase the potential distribution of IPS in Montane Grasslands and Shrublands. We propose to integrate the assessment in impacts of human footprint and soil variability on the potential distribution of IPS in different biomes into the prevention and control of plant invasion.

1. Introduction

Plant invasion is a large threat to global biodiversity (Gurevitch and Padilla, 2004; Hejda et al., 2009; Vilà et al., 2011; Bellard et al., 2013). Invasive plant species (IPS) can invade their non-native ranges, and decrease the habitable space of native plant species (Hejda et al., 2009; Vilà et al., 2011; Pyšek et al., 2012). Invasion biologists have conventionally developed some risk assessment tools such as species distribution models (SDMs) to evaluate the invasion risk of IPS based on significant abiotic and biotic factors influencing the potential distribution of IPS (Thuiller et al., 2005; Foxcroft et al., 2010; Xu and Qiang, 2011; Spear et al., 2013; Donoghue and Edwards, 2014; Ray et al., 2016). Human footprint is the combination of human activities that affect the nature directly or indirectly (Gallardo et al., 2014). It is an environmental variable that may contribute to the distribution of IPS by increasing reproductive opportunities through gardening, forestry and transportation in new areas (Beans et al., 2012; Donaldson et al., 2014; Gallardo et al., 2014). Furthermore, soil factors may also play an important role in the spread of IPS. For instance, the spread of IPS occurs more frequently than expected and causes greater damage in the soil conditions of high resource biomes such as tropical and sub-tropical grasslands and forests (Foxcroft et al., 2010; Donoghue and Edwards,

2014; Joshi et al., 2015; Ray et al., 2016).

A biome is a large community of plant and faunal species that have common characteristics due to similar conditions (i.e. climate), and usually found at a large geographical scale (Olson et al., 2001). Different biomes may provide habitats that favor the expansion of IPS at varying degrees (Thuiller et al., 2005; Petitpierre et al., 2012; Faulkner et al., 2014; Wan et al., 2016; Wang et al., 2017). Some studies have developed the model-based methods to evaluate the potential distribution of IPS in the invaded regions based on different biomes worldwide (e.g. Thuiller et al., 2005; Bellard et al., 2013; Donoghue and Edwards, 2014; Wan et al., 2017). For instance, biological conservationists have developed valuable biosecurity tools for the invasion of IPS based on the potential distributions and biomes using SDMs (Donaldson et al., 2014; Faulkner et al., 2014). However, these studies may misestimate the potential distribution of IPS in the invaded ranges by using only climatic variables. This is because climate alone cannot thoroughly explain the potential distribution of IPS in the invaded ranges (Beans et al., 2012; Bellard et al., 2013; Merow et al., 2013; Radosavljevic and Anderson, 2014), and other environmental variables such as human footprint and soil characteristics may also play an important role (Beans et al., 2012; Zhang et al., 2014). Furthermore, strategies for preventing and controlling IPS may be derived from the

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relationships between human footprint, soil characteristics and the distribution of IPS in different biomes (Thuiller et al., 2005; Keeley, 2006; Faulkner et al., 2014). Hence, an understanding of effects of such variables on the potential distribution of IPS in different biomes is important, but still poorly explored. We hypothesize that human footprint and soil variability have varying degrees of impacts on the potential distribution of IPS among different biomes.

To explore the relationships among human footprint, soil variability, biomes and the distribution of IPS, we modeled the distribution of different IPS that are widely distributed and also have long introduction histories in China. Specifically, we addressed the following questions: 1) Can combined human footprint and soil variables have large contribution to the potential distribution of IPS? 2) Are there any differences in the impacts of human footprint and soil variables on the potential distribution of IPS among various biomes?

2. Materials and methods

2.1. Study area

The study region was the mainland China, which has a total land area of 9.6×10^6 km^2 with higher altitudes in the west compared to the eastern regions. Mountains, plateaus and hills cover about 67% of the land area, while basins and plains make up around 33%. Climatic conditions in the mainland are mainly continental monsoons, and vary considerably (Domrös and Peng, 2012). There are seven main biomes, including grasslands, shrublands and forests (Fig. 1; Olson et al., 2001). The maps of the biomes used were downloaded from www.worldwildlife.org.

2.2. Species data

A total of 29 IPS with wide distributions in China were used based on Xu and Qiang (2011). We chose these species based on the following criteria: 1) the species should have had severely invaded mainland China; 2) there were more than 50 occurrence records in invaded regions (i.e. China) to ensure the reliability of logistic SDM, and 3) they

should have been introduced to China for more than 100 years (Xu and Qiang, 2011). Thus, the IPS could reach the full invaded ranges (i.e. China) as far as possible. Some IPS have no enough occurrence records in native ranges (the detailed information in Table S1). The occurrence records, especially specimens or recorded sightings, of the 29 IPS were compiled in both native and invaded ranges from a variety of online databases, including Global Biodiversity Information Facility (GBIF; www.gbif.org) and Chinese Virtual Herbarium (CVH; www.cvh.org.cn). We minimized the sample bias of the species occurrence data as follow: all occurrence localities were checked using ArcGlobe 10.2 and ArcGIS 10.2 (Esri; Redlands, CA, USA) to determine whether they were distributed in reasonable ranges based on Xu and Qiang (2011) and the ISSG (Invasive Species Specialist Group; www.issg.org) and obvious errors were removed.

2.3. Environmental variables

Environmental variables such as climate, elevation, soil and human footprint were included as input of SDM (Table S2). Data on the 19 bioclimatic variables and elevation at a 2.5-arc-minute spatial resolution (4.3 km at the equator) were downloaded from the WorldClim database (Hijmans et al., 2005; Table S2). A collinearity test was done among the 19 bio-climatic variables based on Pearson's correlation coefficient to eliminate highly correlated variables from the final modeling procedure (Dormann et al., 2013). We excluded the variables with a cross-correlation coefficient value of > 0.75 or < −0.75 (Zhang et al., 2014; Park and Potter, 2015; Table S3). In this way, we selected finally only six out of the 19 bio-climatic variables. These six bio-climatic variables were related to the potential distribution of Chinese plant species (Zhang et al., 2016). Elevation data were also used because elevation was suggested as an important predictor variable in SDM (Hof et al., 2012). Data on nine soil variables at the 0.5-arc-minute spatial resolution were downloaded from SoilGrids1km (http://soilgrids.org/; detailed information in Table S2). Data of human footprint at the 0.5-arc-minute spatial resolution (1 km at the equator) were obtained from The Global Human Footprint Dataset of the Last of the Wild Project, Version 2, 2005 (LWP-2; HFD; http://sedac.ciesin.columbia.edu/
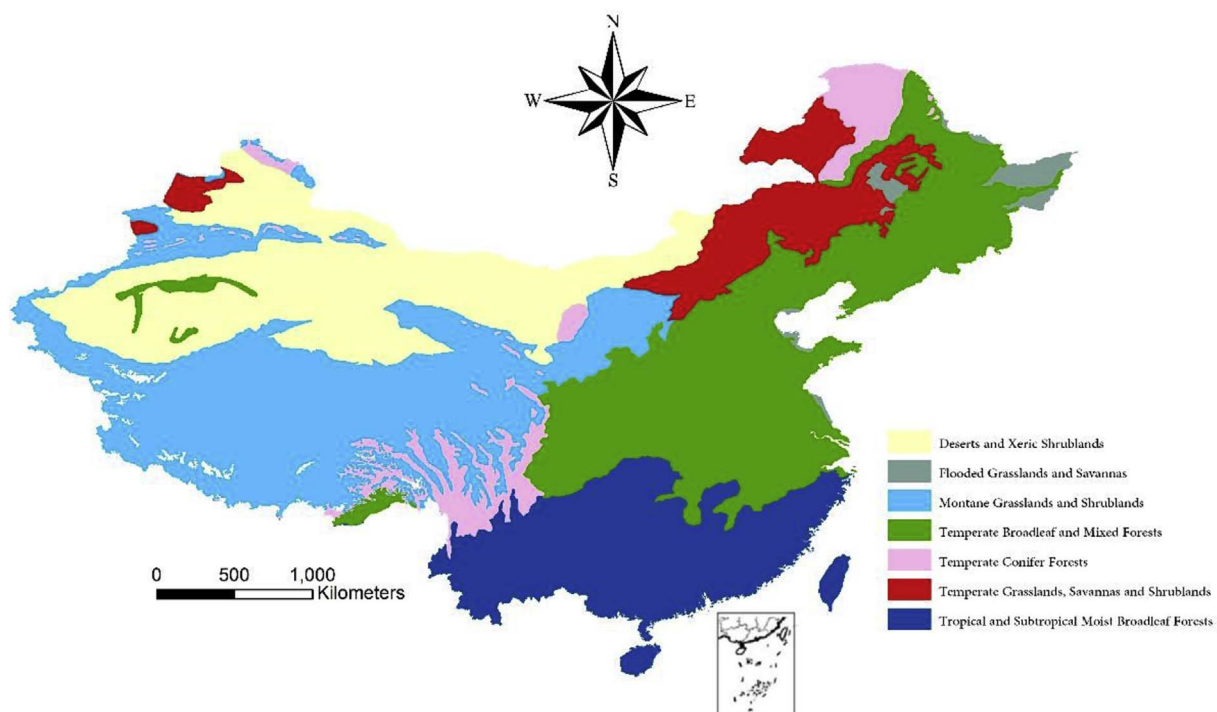

Fig. 1. The study biomes in China (Olson et al., 2001).

wildareas/). This dataset was created from nine global data layers covering human population pressure (population density), land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers). Re-sampled analyses in ArcGIS 10.2 (Esri; Redlands, CA, USA) were used to translate the 0.5-arc-minute into 2.5-arc-minute for human footprint and soil variables, as summarized in Table S2. These environmental variables, including climate, soil and human footprint variables, were related to the expansion and physiological performance of plant species. Here, elevation was combined with climatic variables as one dataset (namely, climatic variables). To evaluate the impact of human footprint and soil variability on the potential distribution of IPS, we used the following four datasets as input to SDM: 1) climatic variables, 2) climatic and human footprint variables, 3) climatic and soil variables, and 4) climatic, soil and human footprint variables.

2.4. Modeling the potential distribution of IPS

Maxent (Version 3.4.0; http://biodiversityinformatics.amnh.org/open_source/maxent/) is currently one of the most frequently applied SDMs (Phillips et al., 2006; Baldwin, 2009). In this study, it was used to estimate the function of the potential distribution of the 29 IPS based on the occurrence records including both native and invaded ranges (Shabani and Kumar, 2015; Mainali et al., 2015). Then, we modeled the geographic locations of these distributions based on the four variable datasets described above. Thus, we built four different Maxent models: 1) model C (based on climatic variables only), 2) model H (based on climatic and human footprint variables), 3) model S (based on climatic and soil variables) and 4) model H + S (based on climatic, soil and human footprint variables). Then, based on these four models, we ran the models based on the occurrence records of either native or invaded ranges. For the maps that were predicted using Maxent, cells with a value of 1 indicated the highest potential distribution probability, and those with a value of 0 corresponded to the lowest (Merow et al., 2013).

To improve the accuracy of Maxent, a 4-fold cross-validation approach was used to divide the presence dataset into approximately four equal partitions, three of which were used to train the model and one to generate the SDM estimate (Van Breugel et al., 2016). We set the regularization multiplier (*beta*) to 2.0 to produce a smooth and general response (Radosavljevic and Anderson, 2014). The maximum number of background points was 10,000, which closely matched the empirical average distribution and thus the training data of each IPS (Phillips et al., 2009; Merow et al., 2013). Auto features were used while other values were kept as Elith et al. (2011) and Mainali et al. (2015).

The receiver operating characteristic (ROC) curves regarded each value of the prediction as a possible judging threshold (Elith et al., 2011; Merow et al., 2013; Banag et al., 2015). We assessed the Maxent model performance using the area under the ROC curve (AUC). To ensure a high precision, only SDMs with AUC values greater than 0.7 were used (Elith et al., 2011; Merow et al., 2013). However, using the traditional AUC may not be sufficient to evaluate the performance of SDMs (Fielding and Bell, 1997; Anderson et al., 2002; Lobo et al., 2008) as AUC may also show good fit for poor models (Lobo et al., 2008; Smith, 2013). Hence, we also used 25% of the occurrence localities to test whether predictions from Maxent (training data) were better than random predictions (Anderson et al., 2002, 2003). We used the binomial test based on the omission rate to evaluate the performance of Maxent modeling for the 29 IPS (Anderson et al., 2002). The training omission rate is the proportion of the training occurrence localities laid in pixels of predicted absence (Anderson et al., 2002; Phillips et al., 2006). These are 1-sided tests for the null hypothesis that training points are predicted no better than those by a random prediction. The binomial probabilities were based on the 11 common thresholds defaulted by Maxent (Phillips et al., 2006; Hu and Jiang, 2010; Anderson and Gonzalez, 2011). Although the training omission rate may also not be sufficient, a low omission rate (i.e. lower than 17%) is a necessary

condition for a good model (Phillips et al., 2006).

2.5. Evaluating impacts of human footprint and soil variability on the potential distribution of IPS

We averaged and overlapped the SDM results of all 29 IPS to produce the potential distribution map of the 29 IPS based on the four models (C, H, S and H + S), respectively (Dubuis et al., 2011). Here, we computed the change in the potential distribution probabilities for each IPS between the model C and the other three models (i.e. H, S and H + S) as CPD = $(A\text{-}B)/A$, where CPD is the change in the potential distribution probabilities of IPS in a grid, A is the potential distribution probabilities of IPS in that grid based on the model C, B is the potential distribution probabilities of IPS in that grid based on the models H, S, and H + S, respectively.

We determined the impacts of human footprint and soil variability on the potential distribution of each IPS in the biomes based on the difference of contribution of environmental variables, the difference of potential distribution ranges and their similarities between the different Maxent models. First, the jackknife method was adapted to evaluate effects of each environmental variable on the potential distribution of IPS using the percentage contribution (PC) for H, S and H + S. PC represents the contribution degree of the environmental variable to the final model (sum up of all the variables to 100%). We assessed the PC of soil variability based on the sum of all soil variables (Table S2). Also, we evaluated the PC of climate using the sum of all the bio-climatic variables (Table S2). Here, we considered the variable to be important if its PC was at least 15% of the models for each IPS, and used analysis of variance to compare the differences in importance of environmental variables except for the climatic ones (Oke and Thompson, 2015). Then, we used a non-parametric test to explore the difference between the models C, H, S and H + S based on the potential distribution probabilities of the occurrence records of each IPS to evaluate the effects of human footprint and soil variability on the potential distribution of IPS.

Second, ENMTools 1.4.4 was used to evaluate niche breadth of each IPS in the biomes (Warren et al., 2010; Oke and Thompson, 2015). Niche breadth, a metric with values from 1 to 0, represents the environment range strongly correlated with the potential distribution probability of IPS (Treier et al., 2009; Oke and Thompson, 2015; Gallagher et al., 2015). In other words, niche breadth equates to the level of the potential distribution of IPS (Warren et al., 2008; Thuiller et al., 2012; Slatyer et al., 2013; Oke and Thompson, 2015). The ratio between niche breadth of C and the other three models were computed for each biome and each IPS. We used T-test to examine differences in the ratio of niche breadth among the four models.

Third, ENMTools 1.4.4 was used to measure the similarity of predictions of the potential distribution probabilities for each IPS in the biomes between C and the other three models by using Schoener's D [see Warren et al. (2008, 2010) for detailed information]. Also, we evaluated the similarity between predictions of the potential distribution probabilities based on occurrence records at native ranges and those based on occurrence records at invaded ranges. Schoener's D ranges from 0 (species having completely discordant potential distribution) to 1 (species having an identical potential distribution). We used T-test to analyze the similarity of predictions of the potential distributions between C and the other three models.

3. Results

All modeling approaches resulted in good fits. All AUC values of the models were bigger than 0.7 (Table 1 and Table S4), and the training omission rates of the four models were very low (mean values ranging from 0.036 in H to 0.148 in C; Table 2; binomial probabilities: $P < 0.0001$). Furthermore, the AUC values of the models H, S and H + S were slightly larger than those of C (Table S4), and the mean omission rates of H, S and H + S were lower than that of C (Table 2). We
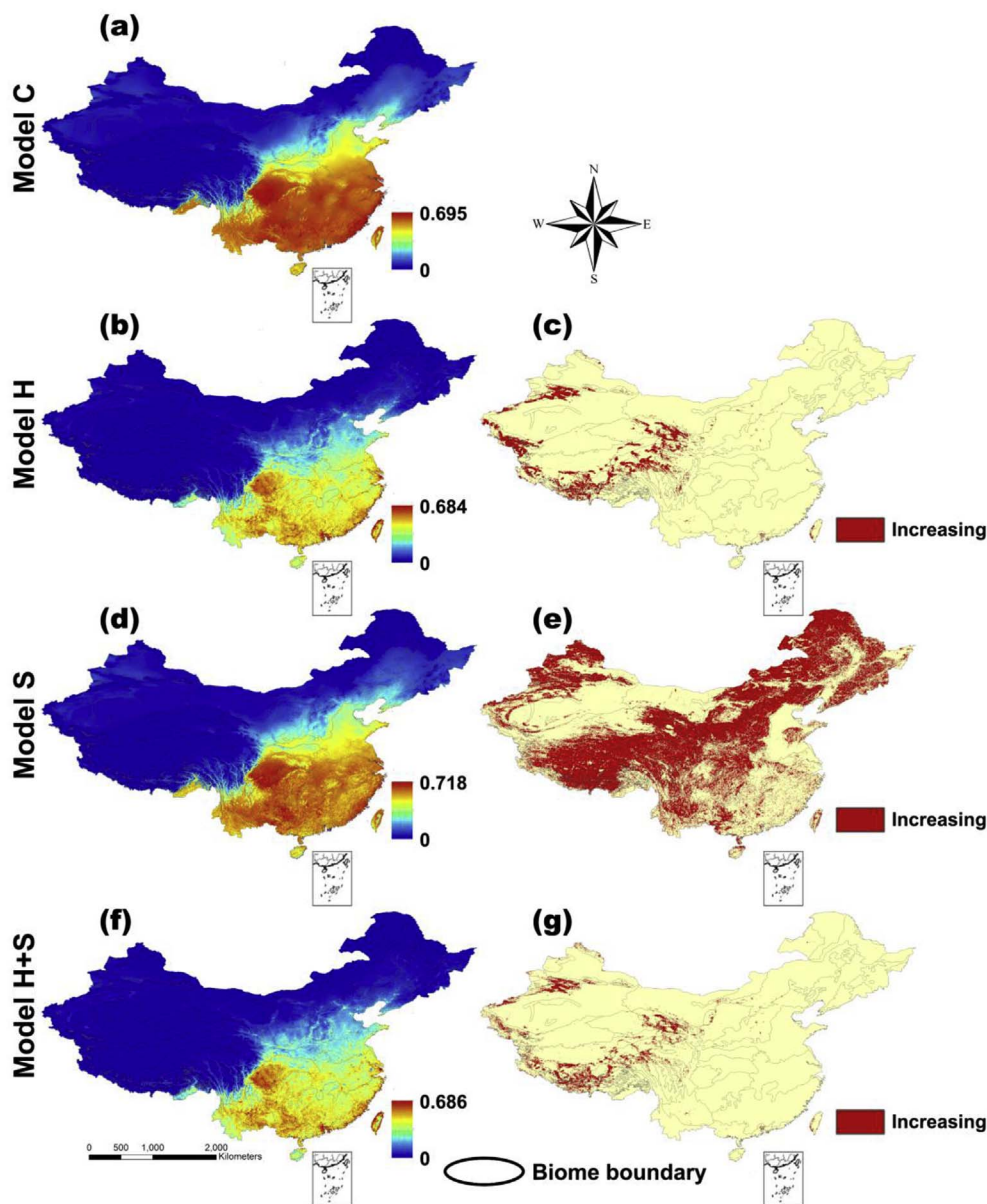
found that the model C had the largest overlap between predictions of the potential distribution probabilities based on occurrence records at native ranges and those based on occurrence records at invaded ranges across all the 29 IPS (Table S1).

The suitable habitat areas of IPS were mainly distributed in southern China (Fig. 2a, b, d and f). Specifically, the potential distribution of IPS was the highest in Tropical and Subtropical Moist Broadleaf Forests (Fig. 1 and Table S5). The potential distribution probabilities differed significantly between the model C and the other three models based on the occurrence records (non-parametric test for each IPS: $P < 0.05$). Compared to the model C, model H increased the potential distribution probability of IPS in southwestern China (Fig. 2c). Compared to the model H (Fig. 2c), the model S increased the potential distribution probability of IPS in larger areas in northern China, and even promoted the potential distributions of IPS in many regions of southern China (Fig. 2e). The potential distributions of IPS based on the model H + S (including both human footprint and soil variability; Fig. 2g) were consistent with those based on the model H (Fig. 2c).

Soil variability had a large effect on the potential distribution of IPS because the average percentage contribution (PC) across the 29 IPS was 34.09% in the model S (Table 1). The contribution of soil variability to

the model ranged from 14.85% in *Eucalyptus robusta* to 60.36% in *Hibiscus trionum* (Table 1). However, there was little effect of each soil variable on the potential distribution of IPS (PC of each soil variable was lower than 15%; data not shown). Comparing with soil variability, human footprint did not have so large effect on the potential distribution of IPS (mean PC = 27.24% in the model H; Table 1). The contribution of human footprint to the potential distributions of IPS ranged from 1.18% (*Conyza bonariensis*) to 67.96% (*Tagetes patula*). Coupling human footprint with soil variability had the large contribution to the potential distribution of IPS (mean PC = 32.43% in the model H + S; Table 1). It had the least contribution to the potential distribution of *Bidens pilosa* (10.92%) and the largest to that of *T. patula* (68.76%; Table 1).

Significant differences were also observed in terms of niche breadth among the four models ($P < 0.001$). The ratio of niche breadth between S and C was the largest, indicating that soil variability did not severely alter the level of the potential distribution of IPS (Table 3; Figs. 1 and 2). The ratio between H + S and C was the smallest, especially in Deserts and Xeric Shrublands, and Flooded Grasslands and Savannas (Table 3; Figs. 1 and 2). We found that soil variability coupled with human footprint could increase the potential distribution

Table 1

Information of the 29 IPS and percentage contributions of human footprint and soil variability to Maxent modeling.

Species	Family	Occu.	Train.	Test	PC$_C$	PC$_H$	PC$_S$	PC$_{H+S}$
			AUC	AUC	(%)	(%)	(%)	(%)
Abutilon theophrasti	Malvaceae	1603	0.92	0.92	89.84	53.45(42.42)	37.62(59.33)	56.20(40.47)
Amaranthus lividus	Amaranthaceae	372	0.97	0.96	95.25	43.83(56.07)	40.19(59.38)	44.69(55.20)
Amaranthus paniculatus	Amaranthaceae	112	0.98	0.95	94.84	39.40(57.55)	52.56(46.65)	51.51(47.51)
Amaranthus retroflexus	Amaranthaceae	8700	0.80	0.79	91.31	34.11(65.52)	36.64(63.32)	35.66(63.98)
Amaranthus spinosus	Amaranthaceae	1149	0.92	0.91	93.52	33.97(65.89)	55.39(43.66)	37.44(62.32)
Amaranthus tricolor	Amaranthaceae	124	0.95	0.89	97.86	40.36(57.05)	57.63(41.00)	57.67(40.02)
Amaranthus viridis	Amaranthaceae	1519	0.91	0.91	91.96	40.24(57.47)	29.35(66.91)	44.80(53.58)
Asclepias curassavica	Asclepiadaceae	2863	0.89	0.89	95.06	13.87(85.69)	28.66(69.96)	21.02(78.65)
Avena fatua	Gramineae	13018	0.75	0.74	93.94	32.39(67.41)	37.86(61.48)	33.61(66.23)
Bidens pilosa	Compositae	4561	0.84	0.84	95.96	5.13(94.70)	28.60(71.35)	10.92(88.97)
Cannabis sativa	Cannabinaceae	2493	0.90	0.90	95.97	54.37(45.51)	37.16(62.75)	58.21(41.70)
Cassia mimosoides	Leguminosae	648	0.94	0.93	97.34	27.76(71.28)	31.26(68.18)	37.44(62.16)
Conyza bonariensis	Compositae	5021	0.85	0.85	96.83	1.18(98.76)	41.24(58.70)	11.92(88.04)
Eryngium foetidum	Umbelliferae	410	0.97	0.96	98.04	9.38(90.47)	23.74(75.04)	18.09(81.85)
Eucalyptus robusta	Myrtaceae	743	0.97	0.97	84.43	10.61(82.08)	14.85(78.09)	11.36(81.29)
Euphorbia hirta	Euphorbiaceae	2421	0.88	0.87	96.20	8.23(91.06)	27.38(71.10)	12.51(86.86)
Galinsoga parviflora	Compositae	7052	0.82	0.82	98.88	34.21(65.66)	27.40(72.55)	34.48(65.47)
Hibiscus trionum	Malvaceae	1937	0.90	0.89	97.86	7.33(92.27)	60.36(38.30)	21.90(77.95)
Indigofera suffruticosa	Leguminosae	1131	0.93	0.93	96.91	18.27(81.36)	22.50(77.34)	19.64(80.09)
Jatropha curcas	Euphorbiaceae	582	0.94	0.94	97.37	18.88(80.90)	23.51(75.28)	23.78(76.04)
Mirabilis jalapa	Nyctaginaceae	1104	0.94	0.92	98.35	51.15(48.26)	32.65(67.15)	52.8(46.99)
Oxalis corymbosa	Oxalidaceae	293	0.98	0.97	99.74	32.85(66.95)	19.72(79.61)	34.76(65.07)
Physalis angulata	Solanaceae	1676	0.88	0.88	89.86	4.67(85.10)	44.90(51.83)	13.34(76.88)
Ricinus communis	Euphorbiaceae	2359	0.87	0.88	94.10	28.34(71.48)	20.48(77.67)	31.09(68.69)
Robinia pseudoacacia	Leguminosae	13397	0.74	0.75	99.39	26.99(72.90)	21.09(78.90)	26.94(72.95)
Setaria palmifolia	Gramineae	590	0.96	0.97	98.62	15.77(83.92)	25.35(73.38)	17.66(81.92)
Solanum aculeatissimum	Solanaceae	335	0.96	0.96	97.62	9.46(86.18)	27.79(67.92)	12.44(84.05)
Tagetes patula	Compositae	384	0.96	0.93	94.29	67.96(31.42)	32.39(66.49)	68.76(30.75)
Talinum paniculatum	Portulacaceae	510	0.94	0.94	90.50	25.79(72.80)	50.36(49.31)	39.80(58.34)
Mean		2658.9	0.91	0.90	95.24	27.24(71.31)	34.09(64.57)	32.43(66.35)
SD		3518.7	0.06	0.06	3.45	17.05(16.77)	11.94(11.71)	16.42(16.09)

Occu. stands for number of occurrence records; PC$_C$, PC$_S$, PC$_H$ and PC$_{S+H}$ represent the percentage contribution of climatic variables, soil variability, human footprint and both soil variability and human footprint to Maxent modeling, respectively. The values in the bracket represent the contribution of climatic variables to Maxent modeling in the presence of soil variability and/or human footprint. *I. suffruticosa* and *J. curcas* are shrubs and all other species are herbs. Train. AUC represents training AUC.

probabilities of some IPS, for example, *Euphorbia hirta* in Deserts and Xeric Shrublands, *Amaranthus spinosus* in Flooded Grasslands and Savannas, *Amaranthus tricolor* in Montane Grasslands and Shrublands, *Indigofera suffruticosa* in Temperate Conifer Forests, and *Solanum aculeatissimum* in Temperate Grasslands, Savannas and Shrublands (Table 4).

There were also significant differences in the similarity of predictions of potential distribution probabilities between C and the other three models in each biome based on the 29 IPS ($P < 0.001$). The potential distribution probability was most similar between S and C (0.930 ± 0.025) and least similar between H + S and C (0.745 ± 0.079; Table 3; Figs. 1 and 2). The largest gap between C and the other three models was found in both Deserts and Xeric Shrublands and Montane Grasslands and Shrublands, and the smallest gap was in Tropical and Subtropical Moist Broadleaf Forests (Table 3; Figs. 1 and 2). Specifically, the species with the largest gap between C and H + S include *Oxalis corymbosa* in Deserts and Xeric Shrublands, *T. patula* in both Flooded Grasslands and Savannas and Temperate Grasslands, Savannas and Shrublands, *I. suffruticosa* in Montane Grasslands and Shrublands, *Jatropha curcas* in Temperate Broadleaf and Mixed Forests, *Abutilon theophrasti* in Temperate Conifer Forests, and *Eryngium foetidum* in Tropical and Subtropical Moist Broadleaf Forests (Table 4).

4. Discussion

We observed significant differences in the impacts of human footprint and soil variability on the potential distribution of IPS between various biomes. Furthermore, our results indicated that the contribution extents of human footprint and soil factors to the potential

distribution could vary across different IPS and biomes (Table 1) because the eco-physiological and abiotic environmental requirements of IPS are different (Foxcroft et al., 2010; Xu and Qiang, 2011; Beans et al., 2012; Donoghue and Edwards, 2014; Gallardo et al., 2014). Specifically, the potential distribution of many IPS were better predicted by climatic variables coupling with human footprint and soil factors than climatic factors only (Table 2). Human footprint and soil variability increased the potential distribution probabilities of some IPS in the biomes, particularly in Montane Grasslands and Shrublands (Tables 3 and 4).

Although overall human footprint was important to the potential distribution of IPS, it had a large impact on some IPS, including *T. patula*, *A. theophrasti* and *Cannabis sativa* (Table 1). Furthermore, including human footprint as the SDM variable improved the performance of modeling for some IPS such as *Amaranthus viridis*, *E. robusta* and *I. suffruticosa* (Table 2). The regions with increasing potential distribution due to human footprint included southwestern China. In these regions, economic conditions is not underdeveloped, but economic growth rate is very fast (Naughton, 2006; www.stats.gov.cn). Economic growth related human activities such as the trade, transportation and agriculture may increase the invasion of IPS in southwestern China (Liu et al., 2005; Xu and Qiang, 2011; Lotz and Allen, 2013; Donaldson et al., 2014). Furthermore, human footprint is the main driving force for the introduction of IPS into their non-native ranges (Xu and Qiang, 2011; Donaldson et al., 2014; Gallardo et al., 2014), and the original purpose to introduce IPS are for ornamental use, forestry and dune stabilization (Beans et al., 2012; Donaldson et al., 2014). We found that human footprint may have a significant effect on the potential distribution of *T. patula* (Xu and Qiang, 2011; Beans et al., 2012). This

Table 2
The training omission rate of the four models (C, H, S and H + S) for the 29 IPS based on the 11 common thresholds defaulted by Maxent.

Species	Model C	Model H	Model S	Model H + S
Abutilon theophrasti	0.088 ± 0.029	0.065 ± 0.048	0.087 ± 0.032	0.066 ± 0.047
Amaranthus lividus	0.072 ± 0.064	0.057 ± 0.029	0.070 ± 0.060	0.060 ± 0.032
Amaranthus paniculatus	0.057 ± 0.038	0.046 ± 0.043	0.069 ± 0.010	0.026 ± 0.030
Amaranthus retroflexus	0.101 ± 0.098	0.089 ± 0.099	0.101 ± 0.097	0.089 ± 0.098
Amaranthus spinosus	0.045 ± 0.054	0.065 ± 0.052	0.044 ± 0.052	0.068 ± 0.051
Amaranthus tricolor	0.051 ± 0.063	0.066 ± 0.052	0.104 ± 0.013	0.044 ± 0.037
Amaranthus viridis	0.148 ± 0.073	0.078 ± 0.063	0.153 ± 0.077	0.079 ± 0.068
Asclepias curassavica	0.095 ± 0.039	0.074 ± 0.062	0.093 ± 0.035	0.072 ± 0.056
Avena fatua	0.121 ± 0.113	0.107 ± 0.116	0.119 ± 0.113	0.104 ± 0.116
Bidens pilosa	0.123 ± 0.057	0.101 ± 0.077	0.066 ± 0.089	0.096 ± 0.075
Cannabis sativa	0.074 ± 0.058	0.075 ± 0.055	0.071 ± 0.056	0.077 ± 0.055
Cassia mimosoides	0.097 ± 0.007	0.061 ± 0.050	0.096 ± 0.006	0.053 ± 0.043
Conyza bonariensis	0.067 ± 0.093	0.090 ± 0.076	0.067 ± 0.092	0.087 ± 0.075
Eryngium foetidum	0.073 ± 0.011	0.042 ± 0.035	0.038 ± 0.039	0.041 ± 0.030
Eucalyptus robusta	0.126 ± 0.065	0.056 ± 0.030	0.125 ± 0.064	0.052 ± 0.027
Euphorbia hirta	0.131 ± 0.066	0.087 ± 0.067	0.132 ± 0.067	0.086 ± 0.070
Galinsoga parviflora	0.097 ± 0.084	0.091 ± 0.088	0.097 ± 0.084	0.091 ± 0.088
Hibiscus trionum	0.069 ± 0.048	0.073 ± 0.061	0.064 ± 0.048	0.066 ± 0.058
Indigofera suffruticosa	0.104 ± 0.010	0.059 ± 0.048	0.033 ± 0.050	0.055 ± 0.047
Jatropha curcas	0.096 ± 0.033	0.065 ± 0.043	0.021 ± 0.043	0.068 ± 0.046
Mirabilis jalapa	0.036 ± 0.054	0.066 ± 0.046	0.025 ± 0.046	0.060 ± 0.042
Oxalis corymbosa	0.051 ± 0.071	0.034 ± 0.027	0.127 ± 0.064	0.033 ± 0.026
Physalis angulata	0.105 ± 0.056	0.079 ± 0.073	0.033 ± 0.064	0.077 ± 0.068
Ricinus communis	0.119 ± 0.065	0.103 ± 0.078	0.119 ± 0.064	0.099 ± 0.074
Robinia pseudoacacia	0.106 ± 0.118	0.108 ± 0.118	0.098 ± 0.121	0.107 ± 0.119
Setaria palmifolia	0.091 ± 0.025	0.059 ± 0.037	0.062 ± 0.053	0.058 ± 0.038
Solanum aculeatissimum	0.056 ± 0.034	0.061 ± 0.046	0.053 ± 0.031	0.058 ± 0.039
Tagetes patula	0.081 ± 0.013	0.064 ± 0.037	0.052 ± 0.043	0.053 ± 0.034
Talinum paniculatum	0.058 ± 0.048	0.073 ± 0.042	0.088 ± 0.015	0.061 ± 0.037
Mean ± SD	0.088 ± 0.028	0.072 ± 0.019	0.069 ± 0.020	0.080 ± 0.034

Values are mean ± SD across the 11 common thresholds defaulted by Maxent.

species was introduced to China from Mexico as an ornamental plant, and is now distributed around the tropical and subtropical regions of China (Xu and Qiang, 2011). The introduction method is related to human social activities (Xu and Qiang, 2011). Hence, we could establish the ecological relationship between the social factors and the distributions of *T. patula* (Beans et al., 2012; Lotz and Allen, 2013). Here, we suggested to integrate human footprint into SDM may represent the effect of human activities on the potential distributions of IPS.

Each soil variable could not contribute greatly to the potential distribution of IPS, and soil variability could not severely change the level of the potential distribution of IPS. However, the sum of all soil variables could affect the potential distribution of IPS at a large geographical scale (Table 1). Based on AUC and the jackknife method, soil factors had a large contribution to the modeling of the potential distribution of IPS, and including soil variables improved the model prediction for some IPS (Table 2). Previous studies have shown that IPS are likely to expand more frequently in biomes with higher resources such

as tropical and sub-tropical grasslands and forests than in those with limited resources such as deserts and rocks (Foxcroft et al., 2010; Donoghue and Edwards, 2014; Joshi et al., 2015), and that IPS (e.g. *E. hirta* in this study; Table 4) can adapt to neutral or alkaline soil pH but not to prolonged drought and saturated soils (Ehrenfeld et al., 2001; Jordan et al., 2008; Martin et al., 2009). In forests, there is evidence of positive associations between IPS invasions and soil fertility (Martin et al., 2009). Hence, soil variables coupling with human footprint were important predictors for the potential distribution of IPS (Van der Putten et al., 2013; Zhang et al., 2014; Thalmann et al., 2015).

Impacts of human footprint and soil variability on the potential distribution of IPS differed between biomes. We found that human footprint and soil variability combined could improve the potential distribution of some IPS such as *T. patula* both in Flooded Grasslands and Savannas and in Temperate Grasslands, Savannas (Figs. 1 and 2; Table 4). Furthermore, combining human footprint and soil variability could also promote the discordant potential distribution of IPS to

Table 3
Ratio of niche breadth and similarity of predictions of potential distribution probabilities between the model C and the other three models (i.e. H, S and H + S) for all 29 IPS in the seven biomes.

Biome	Ratio of niche breadth			Similarity of potential distribution probabilities		
	Model H	Model S	Model H + S	Model H	Model S	Model H + S
Deserts and Xeric Shrublands	0.609 ± 0.274	0.853 ± 0.169	0.455 ± 0.243	0.705 ± 0.098	0.883 ± 0.086	0.624 ± 0.140
Flooded Grasslands and Savannas	0.539 ± 0.223	0.983 ± 0.065	0.514 ± 0.213	0.718 ± 0.110	0.929 ± 0.032	0.695 ± 0.098
Montane Grasslands and Shrublands	0.767 ± 0.275	0.988 ± 0.199	0.729 ± 0.356	0.679 ± 0.088	0.919 ± 0.040	0.670 ± 0.087
Temperate Broadleaf and Mixed Forests	0.728 ± 0.159	0.995 ± 0.019	0.712 ± 0.156	0.815 ± 0.065	0.953 ± 0.024	0.800 ± 0.065
Temperate Conifer Forests	0.799 ± 0.185	0.998 ± 0.043	0.780 ± 0.171	0.799 ± 0.056	0.955 ± 0.024	0.790 ± 0.058
Temperate Grasslands, Savannas and Shrublands	0.767 ± 0.224	0.975 ± 0.051	0.732 ± 0.218	0.789 ± 0.103	0.913 ± 0.035	0.770 ± 0.090
Tropical and Subtropical Moist Broadleaf Forests	0.893 ± 0.082	0.989 ± 0.009	0.871 ± 0.085	0.888 ± 0.059	0.958 ± 0.017	0.868 ± 0.059
Mean ± SD	0.729 ± 0.110	0.969 ± 0.048	0.685 ± 0.137	0.770 ± 0.068	0.930 ± 0.025	0.745 ± 0.079

For each biome, values are mean ± SD across the 29 IPS.

Table 4
Ratio of niche breadth and similarity of predictions of potential distribution probabilities between the models C and H+S for each IPS in the seven biomes.

Species	Ratio of niche breadth							Similarity of potential distribution probabilities						
	DXS	FGS	MGS	TBMF	TCF	TGSS	TSMBF	DXS	FGS	MGS	TBMF	TCF	TGSS	TSMBF
Abutilon theophrasti	0.467	0.443	0.380	0.796	0.417	0.670	0.827	0.656	0.706	0.623	0.838	0.649	0.763	0.841
Amaranthus lividus	0.272	0.772	0.850	0.916	0.694	0.910	0.878	0.490	0.773	0.676	0.843	0.756	0.738	0.867
Amaranthus paniculatus	0.241	0.600	0.890	0.865	0.766	0.862	0.847	0.475	0.753	0.648	0.866	0.746	0.731	0.832
Amaranthus retroflexus	0.710	0.914	0.643	0.909	0.734	0.816	0.833	0.760	0.905	0.788	0.902	0.791	0.874	0.868
Amaranthus spinosus	0.342	1.101	0.646	0.763	0.527	0.871	0.903	0.623	0.769	0.703	0.814	0.726	0.756	0.880
Amaranthus tricolor	0.197	0.659	1.230	0.942	1.247	0.459	0.964	0.347	0.695	0.699	0.844	0.768	0.684	0.929
Amaranthus viridis	0.595	0.391	0.673	0.674	0.611	0.840	0.865	0.683	0.658	0.509	0.785	0.766	0.807	0.865
Asclepias curassavica	0.438	0.418	0.746	0.522	0.741	0.940	0.808	0.652	0.767	0.615	0.762	0.806	0.844	0.843
Avena fatua	0.697	0.758	0.807	0.870	0.829	0.700	0.939	0.750	0.812	0.839	0.871	0.853	0.791	0.926
Bidens pilosa	0.921	0.385	0.741	0.698	0.855	0.963	0.975	0.888	0.613	0.641	0.806	0.892	0.813	0.934
Cannabis sativa	0.465	0.673	0.559	0.833	0.652	0.649	0.885	0.650	0.805	0.719	0.852	0.748	0.780	0.862
Cassia mimosoides	0.247	0.531	0.813	0.571	0.892	0.666	0.967	0.459	0.617	0.639	0.703	0.826	0.678	0.926
Conyza bonariensis	0.776	0.303	0.494	0.664	0.779	0.602	0.955	0.827	0.539	0.633	0.773	0.862	0.811	0.916
Eryngium foetidum	0.331	0.525	0.217	0.363	0.769	0.708	0.665	0.559	0.719	0.632	0.709	0.709	0.826	0.673
Eucalyptus robusta	0.279	0.590	0.549	0.661	0.566	0.385	0.808	0.558	0.744	0.553	0.745	0.679	0.660	0.824
Euphorbia hirta	1.156	0.368	0.448	0.731	0.808	0.888	0.930	0.737	0.559	0.685	0.792	0.836	0.886	0.905
Galinsoga parviflora	0.363	0.278	0.635	0.690	0.764	0.897	0.925	0.747	0.643	0.737	0.798	0.817	0.847	0.905
Hibiscus trionum	0.717	0.884	0.750	0.916	0.774	0.874	0.682	0.784	0.844	0.828	0.892	0.815	0.840	0.778
Indigofera suffruticosa	0.355	0.211	0.886	0.541	1.147	0.803	0.800	0.576	0.557	0.489	0.738	0.739	0.817	0.856
Jatropha curcas	0.449	0.455	0.456	0.334	0.884	0.673	0.737	0.647	0.736	0.702	0.668	0.814	0.791	0.806
Mirabilis jalapa	0.201	0.333	0.765	0.674	0.824	0.634	0.932	0.520	0.568	0.646	0.772	0.822	0.600	0.888
Oxalis corymbosa	0.153	0.323	0.334	0.556	0.610	0.180	0.817	0.329	0.571	0.537	0.681	0.716	0.570	0.829
Physalis angulata	0.308	0.555	0.943	0.819	0.742	1.079	0.922	0.629	0.756	0.733	0.876	0.839	0.868	0.906
Ricinus communis	0.706	0.419	0.720	0.747	0.715	0.785	0.942	0.799	0.702	0.782	0.839	0.833	0.826	0.906
Robinia pseudoacacia	0.635	0.478	0.633	0.871	0.764	0.743	0.916	0.745	0.720	0.766	0.894	0.836	0.825	0.918
Setaria palmifolia	0.376	0.525	0.376	0.736	0.708	0.716	0.961	0.590	0.748	0.704	0.828	0.831	0.775	0.925
Solanum aculeatissimum	0.426	0.509	2.220	0.653	0.939	1.127	0.934	0.696	0.736	0.554	0.799	0.872	0.852	0.909
Tagetes patula	0.171	0.188	0.692	0.557	0.772	0.224	0.736	0.423	0.492	0.673	0.702	0.790	0.527	0.758
Talinum paniculatum	0.212	0.325	1.049	0.786	1.094	0.564	0.919	0.484	0.646	0.681	0.819	0.765	0.739	0.888
Mean	0.455	0.514	0.729	0.712	0.780	0.732	0.871	0.624	0.695	0.670	0.800	0.790	0.770	0.868
SD	0.243	0.213	0.356	0.156	0.171	0.218	0.085	0.140	0.098	0.087	0.065	0.058	0.090	0.059

DXS: Deserts and Xeric Shrublands; FGS: Flooded Grasslands and Savannas; MGS: Montane Grasslands and Shrublands; TBMF: Temperate Broadleaf and Mixed Forests; TCF: Temperate Conifer Forests; TGSS: Temperate Grasslands, Savannas and Shrublands; TSMBF: Tropical and Subtropical Moist Broadleaf Forests.

climatic conditions, but such an effect was limited only to some biomes such as Deserts and Xeric Shrublands, Flooded Grasslands and Savannas and Montane Grasslands and Shrublands. These impacts may be mainly due to the role of human footprint and soil variability in modifying habitat conditions and seed propagation strategies of IPS (Beans et al., 2012; Gallardo et al., 2014).

Human footprint is associated with human activities (e.g. transport services and land use) and human population density (Beans et al., 2012; Gallardo et al., 2014), and high population density commonly results in intensive human activities (Cincotta et al., 2000; Gallardo et al., 2014). Intensive human activities can provide enough agents (Xu and Qiang, 2011; Donaldson et al., 2014; Ray et al., 2016) and create suitable microclimatic and soil conditions for IPS to invade (Donoghue and Edwards, 2014). For example, *T. patula* is an alien plant with the capacity to adapt to wide environmental conditions in China (Xu and Qiang, 2011). With the introduction pathways by human activities, *T. patula* has a large potential to grow and survive in suitable microclimatic conditions of Flooded Grasslands and Savannas in China (Table 4). Studies have shown that some IPS are difficult to expand in Montane Grasslands and Shrublands due to poor climatic and soil conditions (Le Maitre et al., 2002; Donoghue and Edwards, 2014). However, our results suggest that human footprint could result in an increase in the potential distribution of IPS in this biome in China likely due to human activity mediated increases in IPS agents and improvement in microclimatic and soil conditions. On the other hand, the potential distribution of IPS decreased in Deserts and Xeric Shrublands in China. This may be due to little human activities and poor soil conditions in this biome. Thus, human footprint plays little role in promoting the expansion of IPS in these unsuitable soil habitats (Harris, 2014).

Our results suggest that there is a need to integrate human footprint

and soil variability into the assessment of the potential distribution of IPS in different biomes. Such an integration will be more helpful in coming up with strategies to prevent and control risks of plant invasion. We also suggest to use human footprint and soil factors as the predictor variables for improving the performance of SDM (Tables 1 and 2). SDM using climatic variables may over-estimate the potential distributions of IPS (Table 3). To address the practical issues, we need to control the introduction of IPS and design long-term management plans to monitor the potential distribution of IPS based on human footprint, particularly in more vulnerable biomes in China. However, since our study was limited by the amount of data for ecological validation, more studies are needed for verification, including field investigations, ecological monitoring and the precision trainings and validations of SDMs. For example, further evaluation metrics are required to show the robustness of the models because it has been demonstrated that the issue of high AUC value is not addressed in SDMs. With the accelerating process of economic globalization and rapid climate change, the risk evaluation of universal coverage for IPS also is urgently required.

Author contributions

Ji-Zhong Wan conceived and designed the experiments, analyzed the data, wrote the paper. Chun-Jing Wang analyzed the data, contributed reagents/materials/analysis tools, prepared figures and tables. Fei-Hai Yu conceived and designed the experiments, contributed reagents/materials/analysis tools, reviewed drafts of the paper.

Acknowledgements

Development Program of China (2016YFC1201100) and NSFC (31570413).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2017.10.008.

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