






Implications of climate change for environmental niche overlap between five *Cuscuta* pest species and their two main Leguminosae host crop species

Research Article

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Abstract

Some parasitic plants are major pests in agriculture, but how this might be affected by climate change remains largely unknown. In this study, we assessed this question for five generalist holoparasitic *Cuscuta* species (smoothseed alfalfa dodder [*Cuscuta approximata* Bab.], alfalfa dodder [*Cuscuta europaea* L.], soybean dodder [*Cuscuta chinensis* C. Wright], Peruvian dodder [*Cuscuta australis* R. Br.], and Japanese dodder [*Cuscuta japonica* Choisy]) and two of their main Leguminosae host crop species (soybean [*Glycine max* (L.) Merr.] and alfalfa [*Medicago sativa* L.]). For each of the five *Cuscuta* species and the two crop species, we ran MaxEnt models, using climatic and soil variables to predict their potential current distributions and potential future distributions for 2070. We ran species distribution models for all seven species for multiple climate change scenarios, and tested for changes in the overlap of suitable ranges of each crop with the five parasites. We found that annual mean temperature and isothermality are the main bioclimatic factors determining the suitable habitats of the *Cuscuta* species and their hosts. For both host species, the marginally to optimally suitable area will increase by 2070 for all four representative concentration pathway scenarios. For most of the *Cuscuta* species, the marginally to optimally suitable area will also increase. While the suitable areas for both the hosts and the parasites will increase overall, Schoener's *D*, indicating the relative overlap in suitable area, will change only marginally. However, the absolute area of potential niche overlap may increase up to 6-fold by 2070. Overall, our results indicate that larger parts of the globe will become suitable for both host species, but that they could also suffer from *Cuscuta* parasitism in larger parts of their suitable ranges.

Introduction

Climatic and edaphic factors are the main determinants of plant species' distributions (Cain 1944). It has been suggested that if global temperatures increase 1 °C, the ecological zones on Earth will move 160 km poleward (Thuiller 2007). As the climate is currently rapidly changing, there has been an increasing interest in predicting species' potential future distributions (Chen et al. 2011; Ren et al. 2020; Speed et al. 2011; Walther et al. 2002). Indeed, many studies have shown that climate change will directly or indirectly affect species distribution patterns. Such information is vital to develop long-term conservation strategies and to manage weeds and other pests in agriculture (Gomes et al. 2020; Jayasinghe and Kumar 2019; Ma and Sun 2018; Oteros et al. 2013; Qin et al. 2017; Wan and Wang 2019; Wang and Wan 2020; Yi et al. 2016). Of the approximately 4,750 parasitic plant species, many are major pests in agricultural crops (Hershey 1999; Marvier 1996; Nickrent 2020; Press and Phoenix 2010). How the distributions of parasitic plants and their host crops might change with ongoing climate change remains largely unknown.

Previous studies on parasitic plants have mainly focused on their physiology, species conservation, and weed control (Bouwmeester et al. 2021; Liu et al. 2019; Ren et al. 2020; Wang et al.

2019; Zhang et al. 2016). In recent years, there has also been an increase in research on the relationships between the distributions of parasites and those of their hosts (Lira-Noriega and Peterson 2014; Liu et al. 2019; Yun et al. 2020). Understanding these relationships can provide important insights and enable forecasting of potential future distributions, which can guide conservation management, as well as pest control (Liu et al. 2019; Ren et al. 2020).

Dodder (*Cuscuta* spp.) is a unique genus of approximately 200 mostly holoparasitic species in the Convolvulaceae family. At germination, *Cuscuta* species form a rudimentary and short-lived (approximately 4 to 5 d) root system before they connect to the host plant (Teixeira-Costa and Davis 2021; Truscott 1966). *Cuscuta* can cause serious crop yield losses (Dawson et al. 1994; Li et al. 2007; Tepe et al. 2017). It is considered to be the third most detrimental genus of parasitic plants worldwide, after *Striga* and *Orobanche*, as it can infect nearly all dicotyledonous species and occurs in a wide variety of climates and ecosystems on all continents except Antarctica (Albert et al. 2008; Costea et al. 2011). Two legume crops that can be highly infected by *Cuscuta* are soybean [*Glycine max* (L.) Merr.] and alfalfa (*Medicago sativa* L.), both of which are cultivated on many continents for various economic uses, primarily because of their high protein content (Johnson et al. 2008; Wang et al. 2014). Recently, a species distribution modeling study by Ren et al. (2020) showed that the suitable range size of soybean dodder (*Cuscuta chinensis* C. Wright) may decline in response to climate change. However, it remains unknown how the distribution of some of its major host crop species as well as the distribution of other *Cuscuta* pest species might change.

Cuscuta species are usually generalists; they can use multiple species from different families as host plants (Kelly et al. 1988). Many *Cuscuta* species have strong preferences for legumes, likely because these hosts have high nitrogen content (Kelly et al. 1988; Pennings and Callaway 2002). Therefore, the legumes soybean and alfalfa are important hosts for the *Cuscuta* species that co-occur with them. Cultivated soybean, with its main distribution in eastern Asia, is an important host for *C. chinensis* (Flora of China Editorial Committee 1995) and for Peruvian dodder [*Cuscuta australis* R. Br.]. Alfalfa, with its main distribution in Europe, is an important host for alfalfa dodder (*Cuscuta europaea* L.) (Flora of China Editorial Committee 1995) and for smoothseed alfalfa dodder (*Cuscuta approximata* Bab.) (Yergin-Ozkan and Tepe 2018). However, it is likely that soybean and alfalfa can both be infected by all four of these *Cuscuta* species, as well as by others. For example, although Japanese dodder (*Cuscuta japonica* Choisy) is frequently found on shrubs, experiments have shown it can also grow on soybean and alfalfa.

In this study, we modeled the potential current and future environmentally suitable ranges of five *Cuscuta* species and two of their major host crops (soybean and alfalfa). For future suitable ranges, we used the year 2070 to make our study more comparable to other studies (Carlson et al. 2022; Gwendolyn 2022; Tang et al. 2017, 2020; Velazco et al. 2021). We used species distribution models (SDMs) to assess the potential distributional range under current and future climate scenarios (Liu et al. 2019). We then explored the potential current and future overlap in suitable areas between the parasites and hosts. This study addresses the following specific questions: (1) Does climate change affect the environmental suitability of the parasites and their host species? (2) Does climate change affect the overlap of suitable environments between the parasites and their host species?

Materials and Methods

Species Occurrence Data

The occurrence points for the five parasitic species (*C. approximata*, *C. australis*, *C. chinensis*, *C. europaea*, and *C. japonica*) and the two crop species (soybean and alfalfa) were obtained from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>). In addition, because some important distribution data from China are not included in GBIF, occurrence data from the National Specimen Information Infrastructure (<http://www.nsii.org.cn>, accessed on September 20, 2018), the Chinese Virtual Herbarium (<http://www.cvh.org.cn>, accessed on September 20, 2018), and the Plant Photo Bank of China (<http://ppbc.iplant.cn>, accessed on September 20, 2018) were obtained. Each record was assigned to a 2.5' grid cell (approximately 4.3 km × 4.3 km) (Ren et al. 2020). Duplicate records within the same grid cells and potentially invalid records were excluded. Records for which both longitude and latitude were zero or longitude and latitude values were identical were deemed potentially invalid, as they probably represent erroneous repetitive data entries (Wang and Wan 2020; Warren et al. 2010). The final distribution records of *C. approximata* (204 occurrences), *C. australis* (251), *C. chinensis* (377), *C. europaea* (5,748), *C. japonica* (621), soybean (1,285), and alfalfa (11,070) were used in combination with environmental variables (see next section) to model the potential distributions of the seven species (Supplementary Table S1). The Kernel density tool from the spatial analysis toolbox of ArcGIS v. 10.2 (ESRI, Redlands, CA, USA) was used to estimate the current distribution areas for the seven target species (Supplementary Figure S1).

Environmental Variables

To model the currently suitable areas of the species, all 19 bioclimatic variables (Table 1) were extracted for the period 1960 to 1990 from the WorldClim database (<http://www.worldclim.org>) at a 5' resolution. This period was used because it covers the period in which many of the species occurrence data were collected. As edaphic factors may also codetermine species' distributions, 15 soil variables (Table 1) were extracted at 0.5' resolution from the SoilGrids database (<http://soilgrids.org>). Little is known about the important edaphic factors for *Cuscuta*. Although *Cuscuta* has only a very short soil-bound phase (Truscott 1966), edaphic factors could indirectly determine *Cuscuta* distributions by affecting the distribution of their hosts. To make the resolutions of the climatic and soil variables match, the soil variable data were aggregated at a resolution of 5' using ArcGIS.

To avoid severe multicollinearity among the bioclimatic variables in the SDMs, calculated Pearson correlation coefficients were calculated for all pairs of bioclimatic and soil variables. Then, for each pair of variables with a Pearson correlation coefficient $|r| > 0.75$, the variable with the lowest contribution was removed from the final SDMs (Dormann et al. 2013; Du and Chen 2010; Sun et al. 2014; Yi et al. 2016).

To model the potential future suitable ranges of the species in 2070, forecast values of the 19 bioclimatic variables were extracted from WorldClim for the period 2061 to 2080. These forecast values are based on four different representative concentration pathways (RCPs), which are different scenarios of greenhouse gas concentration trajectories developed by the Intergovernmental Panel on Climate Change (IPCC) (Ma and Sun 2018). Here, climate change forecasts based on RCPs 2.6, 4.5, 6.0, and 8.5, which represent net radiative forcings of 2.6, 4.5, 6.0, and 8.5 W m⁻² by the end of the

Table 1. Environmental variables used for predicting the potential distributions of the five parasitic and two host plants.

Type of environmental variable	Variable name	Variable code	<i>Cuscuta chinensis</i>	<i>Cuscuta australis</i>	<i>Cuscuta japonica</i>	<i>Cuscuta europaea</i>	<i>Cuscuta approximata</i>	Soybean	Alfalfa
Bioclimatic variables	Annual mean temp.	Bio1	✓	✓	✓	✓	✓	✓	✓
	Mean diurnal range (mean of monthly [max. temp. – min. temp.])	Bio2	✓	✓	✓	✓	✓	✓	✓
	Isothermality (Bio2/Bio7) (*100)	Bio3	✓	✓	✓	✓	✓	✓	✓
	Temp. seasonality (SD *100)	Bio4	✓	✓		✓			✓
	Max. temp. of warmest month	Bio5			✓	✓	✓	✓	✓
	Min. temp. of coldest month	Bio6							
	Temperature annual range (Bio5 – Bio6)	Bio7					✓	✓	
	Mean temp. of wettest quarter	Bio8		✓	✓	✓	✓	✓	✓
	Mean temp. of driest quarter	Bio9		✓			✓		✓
	Mean temp. of warmest quarter	Bio10		✓					
	Mean temp. of coldest quarter	Bio11							
	Annual precipitation	Bio12		✓	✓	✓	✓		✓
	Precipitation of wettest month	Bio13				✓			
	Precipitation of driest month	Bio14		✓			✓	✓	
	Precipitation seasonality (coefficient of variation)	Bio15	✓	✓	✓	✓	✓	✓	✓
	Precipitation of wettest quarter	Bio16							
	Precipitation of driest quarter	Bio17							
	Precipitation of warmest quarter	Bio18	✓				✓	✓	✓
	Precipitation of coldest quarter	Bio19	✓		✓				✓
Soil variables	Topsoil organic carbon (% weight)	T_OC	✓	✓	✓	✓	✓	✓	✓
	Topsoil calcium carbonate (% wt.)	T_CACO ₃	✓	✓	✓	✓	✓	✓	✓
	Topsoil gypsum (% weight)	T_CASO ₄		✓		✓	✓	✓	✓
	Topsoil USDA texture classification (name)	T_USDA		✓	✓				
	Topsoil pH (H ₂ O) [–log(H ⁺)]	T_PH_H ₂ O	✓	✓	✓	✓	✓	✓	✓
	Topsoil gravel content (% vol.)	T_GRAVEL	✓	✓	✓	✓	✓	✓	✓
	Topsoil sand fraction (% wt.)	T_SAND	✓	✓	✓	✓	✓	✓	✓
	Topsoil silt fraction (% wt.)	T_SILT	✓	✓	✓		✓	✓	✓
	Topsoil clay fraction (% wt.)	T_CLAY	✓	✓	✓		✓	✓	✓
	Topsoil cation exchange capacity (clay) (cmol kg ⁻¹)	T_CEC_CLAY	✓	✓	✓	✓	✓	✓	✓
	Topsoil cation exchange capacity (soil) (cmol kg ⁻¹)	T_CEC_SOIL	✓	✓	✓		✓	✓	
	Topsoil base saturation (%)	T_BS							✓
	Topsoil top exchange base (cmol kg ⁻¹)	T_TEB	✓	✓	✓	✓	✓	✓	✓
	Topsoil sodicity (ESP) (%)	T_ESP	✓	✓	✓	✓	✓	✓	✓
	Topsoil salinity (Elco) (dS m ⁻¹)	T_ECE	✓		✓	✓	✓	✓	✓

Abbreviations: ESP, Exchangeable sodium percentage; Elco, Electric conductivity.

year 2100 (John et al. 2009; Moss et al. 2008) and the CCSM4 global climate model (IPCC 2013) were used.

Environmental Suitability Modeling

MaxEnt v. 3.4.1 (https://biodiversityinformatics.amnh.org/open_source/maxent) was used to model environmentally suitable ranges of the five parasitic plant species and the two host crop species under current and potential future (2070) climates by relating the occurrence records to the climatic and soil variables (Evangelista et al. 2011; Phillips et al. 2006, 2017). For each species, the occurrence and environmental variables were used to run the MaxEnt models with 30 replicates using the bootstrap method (Efron 1979). The MaxEnt models were run with a convergence threshold of 10^{-5} , a maximum number of iterations of 500, a

maximum number of 10,000 background points (Phillips and Dudik 2008), and a regularization parameter value of 1 (Radosavljevic and Anderson 2013). The auto-feature option and the logistic output format were used. Other settings were the same as described in Merow et al. (2013). In each of the 30 replicates per species, 10% of the total database was randomly selected as test data, with the remaining data (90%) used as training data to evaluate the accuracy and quality of the model predictions. Then, model accuracy was tested using the area under the curve (AUC) of the receiver operating characteristic as implemented in MaxEnt (Phillips et al. 2006). The AUC can vary from 0.5 to 1, and a larger AUC value indicates a higher discrimination (Yi et al. 2016). Based on the AUC values, model performance is categorized as insufficient (0.5 to 0.6), poor (0.6 to 0.7), average (0.7 to 0.8), good (0.8 to 0.9), or excellent (0.9 to 1) (Swets 1988).

Predicting the Suitable Area of Species under Global Climate Change

Among the available tools for SDMs, the maximum entropy (MaxEnt) approach is one of the most widely used, as it does not require absence data points (Brambilla et al. 2017; Liu et al. 2019; Ren et al. 2020). Based on the MaxEnt output results, ArcGIS was used to map the predicted suitable areas for the five parasitic and two crop species at the global scale. The environmental suitability of a location, as predicted by the MaxEnt model, varied from 0 to 1. The Jenks's natural breaks method in ArcGIS was used to convert the environmental suitability scores of MaxEnt to suitability maps with four categories of suitability based on the 10th percentile training presence logistic threshold (marginal value): optimally suitable area (>0.6), intermediately suitable area (0.4 to 0.6), marginally suitable area (marginal value to 0.4), or unsuitable area (less than the marginal value; Wan et al. 2014; Yang et al. 2013). Then, the raster calculator in ArcGIS was used to calculate the area of the potential geographic distributions of the seven species.

Environmental Niche Overlap Analysis

Schoener's (1968) *D*, implemented in ENMTools, was used to measure niche overlap between pairs of parasitic and crop species (Jiao et al. 2016; Legault et al. 2013; Warren et al. 2008). Schoener's *D* values can range from 0 to 1, with values closer to 0 representing a small degree of niche overlap, and values closer to 1 representing a high degree of niche overlap (Warren et al. 2008, 2010). Based on the predictions of the MaxEnt models, the areas with potential niche overlap of the five parasitic plant species and the two host plant species were visualized for the suitability area (the combination of the marginally, intermediately, and optimally suitable areas) in ArcGIS. The MaxEnt model with the highest performance was selected, and then the Reclassify tool in ArcGIS was used to convert the potential distribution area into 0/1 raster files, where 0 indicates unsuitable and 1 indicates suitable. After that, the raster calculator of ArcGIS was used to overlay the environmental suitability results of each pair of species to identify the potential overlapping distribution areas.

Results and Discussion

Current Global Distribution

Kernel density estimation maps of the current records of the five parasitic species and the two host species are shown in Supplementary Figure S1. In the final SDMs, the number of bioclimatic variables ranged from 7 (*C. japonica*) to 10 (alfalfa), and the number of soil variables ranged from 10 (*C. europaea*) to 13 (soybean; Table 1; Supplementary Figure S2). Among the bioclimatic variables, the annual mean temperature (Bio1) was important in the SDMs of all species (Supplementary Figure S3). Among the soil variables, the topsoil gravel content was important in the SDMs of all species (Supplementary Figure S3). The mean value and standard deviation of the AUCs for the models developed for *C. approximata*, *C. australis*, *C. chinensis*, *C. europaea*, *C. japonica*, soybean, and alfalfa were 0.994 ± 0.002 , 0.970 ± 0.010 , 0.980 ± 0.006 , 0.965 ± 0.010 , 0.984 ± 0.003 , 0.950 ± 0.007 and 0.927 ± 0.001 , respectively, indicating excellent model performance.

We found that for all seven species, the bioclimatic variables were more important determinants of their distributions than soil variables. For the *Cuscuta* species, which are stem parasites and do

not grow in the soil (at least not after having attached to a host stem), this is not surprising, as the soil should only affect them indirectly through the soil preferences of their hosts. Among the climatic factors, the annual mean temperature (Bio1) was a particularly strong determinant of the environmental suitability for all seven species. For some species, isothermality (Bio3, Supplementary Figure S3) also played a strong role. Similarly, Ren et al. (2020) showed for *C. chinensis* that annual mean temperature and isothermality were the most important climatic factors determining the suitable environment. In other words, our study showed that the seven species are more sensitive to temperature variables than to precipitation variables. This could reflect that they might use crops that grow on irrigated lands as hosts and are therefore less restricted by natural precipitation.

Current and Future Suitable Areas

The host species soybean has most of its currently suitable area (marginally to optimally suitable area) in eastern Asia, Europe, and North America (Supplementary Figure S4a). By 2070, its suitable area will increase by 58.0% (RCP 2.6) to 61.9% (RCP 8.5), and its optimally suitable area will increase by 22.3% (RCP 2.6) to 30.0% (RCP 6.0; Table 2; Supplementary Figure S4). The other host species, alfalfa, has most of its currently suitable area in Europe, but also has some suitable area on other continents (Supplementary Figure S5a). Until 2070, its suitable area will increase by 144.7% (RCP 2.6) to 152.8% (RCP 6.0), but its optimally suitable area will completely disappear under all four scenarios (Table 2; Supplementary Figure S5). Its marginally to intermediately suitable area will not only increase in Europe, but also in other parts of the world, particularly in Australia, western North America, and southern South America (Supplementary Figure S5).

The parasitic species *C. approximata* has most of its currently suitable area in Europe, South America, South Africa, Pakistan, Iran, and Australia (Supplementary Figure S6a). Until 2070, its suitable area will slightly increase by 8.0% (RCP 4.5) to 17.3% (RCP 2.6), and its optimally suitable area will decrease by 15.3% (RCP 8.5) or increase up to 4.8% (RCP 4.5; Table 2; Supplementary Figure S6). Most of the currently suitable area for *C. australis* is in eastern Asia, Europe, South America, and Australia (Supplementary Figure S7a). Until 2070, its suitable area will decrease by 18.2% (RCP 6.0) to 24.3% (RCP 8.5), and its optimally suitable area will increase by 0.4% (RCP 4.5) to 24.7% (RCP 8.5; Table 2; Supplementary Figure S7). Most of the currently suitable area for *C. chinensis* is in eastern and southeast Asia, but it also has suitable areas on other continents (Supplementary Figure S8a). Until 2070, its suitable area will increase by 2.9% (RCP 8.5) to 10.6% (RCP 6.0), and its optimally suitable area will increase by 1.1% (RCP 6.0) to 5.7% (RCP 4.5; Table 2; Supplementary Figure S8). Most of the currently suitable area for *C. europaea* is in central China and Europe (Supplementary Figure S9a). Until 2070, its suitable area will increase by 77.3% (RCP 8.5) to 83.0% (RCP 6.0), but its optimally suitable area will completely disappear in all four scenarios (Table 2; Supplementary Figure S9). For *C. japonica*, most of its currently suitable area is in eastern Asia, but it also has suitable areas on other continents (Supplementary Figure S10a). Until 2070, its suitable area will increase by 21.1% (RCP 8.5) to 22.8% (RCP 2.6), and its optimally suitable area will decrease by 37.9% (RCP 4.5) to 31.6% (RCP 8.5; Table 2; Supplementary Figure S10).

The five *Cuscuta* species in our study are, like most species in this genus (Nickrent 2020), holoparasitic plants that absorb nutrients, carbohydrate, and water from their host plants via

Table 2. Sizes of the areas for the different suitability classes of the five parasitic and two host plants under the current climate and potential future climates in 2070.

Species	Historical periods ^a	Habitat suitability area				Total
		Marginal	Medium	Optimal	km ²	
<i>Cuscuta approximata</i>	1960–1990	1,498,682	974,181	589,236	3,062,099	
	2061–2080 (RCP2.6)	1,769,890	1,297,252	525,028	3,592,170	
	2061–2080 (RCP4.5)	1,488,370	1,201,656	617,614	3,307,640	
	2061–2080 (RCP6.0)	1,645,239	1,176,590	583,666	3,405,495	
	2061–2080 (RCP8.5)	1,609,860	1,227,173	499,360	3,336,393	
<i>Cuscuta australis</i>	1960–1990	10,000,073	2,761,083	1,133,157	13,894,313	
	2061–2080 (RCP2.6)	7,013,623	2,651,411	1,181,934	10,846,968	
	2061–2080 (RCP4.5)	6,989,836	2,764,847	1,138,050	10,892,733	
	2061–2080 (RCP6.0)	7,249,678	2,742,416	1,368,460	11,360,554	
	2061–2080 (RCP8.5)	6,428,677	2,677,681	1,413,473	10,519,831	
<i>Cuscuta chinensis</i>	1960–1990	957,546	2,596,687	1,811,817	5,366,050	
	2061–2080 (RCP2.6)	936,771	2,922,017	1,870,907	5,729,695	
	2061–2080 (RCP4.5)	989,236	3,015,355	1,915,393	5,919,984	
	2061–2080 (RCP6.0)	1,090,402	3,010,086	1,831,915	5,932,403	
	2061–2080 (RCP8.5)	899,812	2,782,310	1,839,518	5,521,640	
<i>Cuscuta europaea</i>	1960–1990	339,556	1,138,351	420,399	1,898,306	
	2061–2080 (RCP2.6)	806,549	2,652,163	0	3,458,712	
	2061–2080 (RCP4.5)	762,740	2,637,259	0	3,399,999	
	2061–2080 (RCP6.0)	860,594	2,613,172	0	3,473,766	
	2061–2080 (RCP8.5)	827,173	2,539,405	0	3,366,578	
<i>Cuscuta japonica</i>	1960–1990	321,566	1,508,242	1,351,072	3,180,880	
	2061–2080 (RCP2.6)	351,449	2,696,951	858,186	3,906,586	
	2061–2080 (RCP4.5)	357,922	2,671,057	838,464	3,867,443	
	2061–2080 (RCP6.0)	315,619	2,699,886	877,004	3,892,509	
	2061–2080 (RCP8.5)	327,964	2,600,225	923,974	3,852,163	
Soybean	1960–1990	6,317,048	3,787,203	2,993,827	13,098,078	
	2061–2080 (RCP2.6)	9,853,065	7,180,879	3,662,250	20,696,194	
	2061–2080 (RCP4.5)	10,331,349	6,660,668	3,730,522	20,722,539	
	2061–2080 (RCP6.0)	10,568,157	6,618,214	3,887,842	21,074,213	
	2061–2080 (RCP8.5)	10,450,054	7,080,841	3,669,325	21,200,220	
Alfalfa	1960–1990	576,966	3,321,038	966,654	4,864,658	
	2061–2080 (RCP2.6)	2,091,155	9,810,235	0	11,901,390	
	2061–2080 (RCP4.5)	1,623,936	10,473,388	0	12,097,325	
	2061–2080 (RCP6.0)	1,914,640	10,382,986	0	12,297,626	
	2061–2080 (RCP8.5)	1,969,514	10,011,815	0	11,981,329	

^aRCP, representative concentration pathway.

haustoria (Albert et al. 2008; Zhang et al. 2020). Their distributions might thus be largely determined by the distributions of their hosts. Indeed, a previous study indicated that the environmental suitability of the host (soybean) can influence the environmental suitability of the parasite (*C. chinensis*; Ren et al. 2020). That study also found that the parasite is likely to benefit from climate change, which is in agreement with our finding that four of the five *Cuscuta* species, just like the two Leguminosae hosts, are projected to have larger suitable ranges by 2070. The only exception was *C. australis*, but interestingly, although its suitable range will decrease, the percentage of this range that will be optimally suitable will actually increase. So this species might also benefit from climate change. On the other hand, while *C. europaea* and alfalfa are projected to have larger suitable ranges, they will no longer have any optimally suitable areas, suggesting that overall they might not benefit strongly from climate change. It should be noted, however, that we only considered climatic and edaphic factors for predicting species' distributions, although other factors (e.g., biological factors, human activities) may also restrict the potential distributions of the species (Guan et al. 2021; Zou et al. 2020). In particular, as mentioned earlier, the parasitic species might be protected from climatic limitations (e.g., through irrigation of the crops) and from some biotic factors (e.g., competition alleviated by weeding). Therefore, our results only predict the potentially suitable area and not the area that will actually be occupied by the species in the future.

Changes in Environmental Niche Overlap between Parasitic and Host Plants

Based on Schoener's *D*, as well as on the absolute area, the host species soybean currently has the largest niche overlap with *C. australis* and the lowest with *C. approximata* (Table 3; Figure 1; Supplementary Figures S11, S13, and S15). Based on Schoener's *D*, the host species alfalfa currently has the largest niche overlap with *C. europaea* and the lowest with *C. chinensis* (Table 3; Figure 2; Supplementary Figures S12, S14, and S16). However, in terms of absolute area, alfalfa has the largest overlap with *C. australis* (Table 3).

By 2070, these patterns will remain largely the same for both host species, although there will be changes in the degree of overlap of the hosts with each of the five parasites, depending on the specific RCP scenario considered (Table 3) and on whether one considers the relative or the absolute overlap. For soybean, the relative niche overlap (Schoener's *D*) will slightly decrease for a couple of *Cuscuta* species by RCP combinations (the strongest decrease will be -5.8% for the relative overlap with *C. japonica* in RCP 8.5), but in most cases will slightly increase (the strongest increase will be +9.0% for the relative overlap with *C. australis* in RCP 2.6; Table 3; Supplementary Figures S11 and S15). However, the absolute overlap of soybean will decrease for *C. australis* (by up to -12.8% for RCP 8.5) and increase for all other *Cuscuta* species

Table 3. Schoener's *D* values and the absolute overlapping area between the five parasitic and two host plants in the current climate and under potential future climates in 2070.^a

Species	Period ^b	Soybean		Alfalfa	
		<i>D</i>	Area	<i>D</i>	Area
			km ²		km ²
<i>Cuscuta approximata</i>	1960–1990	0.2473	206,699	0.4508	1,611,291
	2061–2080 (RCP2.6)	0.2619	927,964	0.4655	3,353,405
	2061–2080 (RCP4.5)	0.2602	825,141	0.4571	3,123,447
	2061–2080 (RCP6.0)	0.2527	679,563	0.4504	2,751,749
	2061–2080 (RCP8.5)	0.2482	720,060	0.4501	3,127,963
<i>Cuscuta australis</i>	1960–1990	0.5489	7,689,648	0.4879	3,025,743
	2061–2080 (RCP2.6)	0.5984	7,278,207	0.4923	3,645,238
	2061–2080 (RCP4.5)	0.5757	7,101,541	0.4775	3,767,632
	2061–2080 (RCP6.0)	0.5806	7,123,295	0.4842	3,954,835
	2061–2080 (RCP8.5)	0.5583	6,706,509	0.4676	3,491,380
<i>Cuscuta chinensis</i>	1960–1990	0.4734	4,620,624	0.2876	22,205
	2061–2080 (RCP2.6)	0.4771	5,156,190	0.2805	190,064
	2061–2080 (RCP4.5)	0.4711	5,262,776	0.2750	112,533
	2061–2080 (RCP6.0)	0.4591	5,239,216	0.2564	115,017
	2061–2080 (RCP8.5)	0.4570	5,016,860	0.2587	32,744
<i>Cuscuta europaea</i>	1960–1990	0.4123	1,061,799	0.5675	1,430,410
	2061–2080 (RCP2.6)	0.4220	2,401,881	0.5786	2,618,215
	2061–2080 (RCP4.5)	0.4214	2,398,569	0.5796	2,597,816
	2061–2080 (RCP6.0)	0.4205	2,363,116	0.5736	2,595,107
	2061–2080 (RCP8.5)	0.4163	2,342,039	0.5771	2,494,316
<i>Cuscuta japonica</i>	1960–1990	0.4330	3,151,147	0.3232	32,518
	2061–2080 (RCP2.6)	0.4247	3,788,106	0.3127	239,368
	2061–2080 (RCP4.5)	0.4175	3,762,137	0.2978	174,407
	2061–2080 (RCP6.0)	0.4124	3,843,281	0.2917	154,912
	2061–2080 (RCP8.5)	0.4079	3,747,007	0.2976	115,544

^aSchoener's *D* values can range from 0 to 1, with values closer to 0 representing a small degree of niche overlap, and values closer to 1 representing a high degree of niche overlap.

^bRCP, representative concentration pathway.

(by up to +348.9% for *C. approximata* in RCP 2.6; Table 3; Supplementary Figures S11 and S15). Similarly, for alfalfa, the relative niche overlap will slightly decrease for about half of the *Cuscuta* species by RCP combinations (the strongest decrease will be –10.8% for the relative overlap with *C. chinensis* in RCP 6.0), but slightly increase for the other half (the strongest increase will be +3.3% for the relative overlap with *C. approximata* in RCP 2.6; Table 3; Supplementary Figures S12 and S14). On the other hand, the absolute overlap of alfalfa will increase for all *Cuscuta* species (from a minimum of +15.4% for *C. australis* in RCP 8.5 up to +636.1% for *C. japonica* in RCP 2.6; Table 3; Supplementary Figures S12 and S16).

Most *Cuscuta* species are generalists that can use many species as hosts (Kelly et al. 1988), but whether a potential host will actually be infested by a *Cuscuta* species will depend on their actual ranges. In its current distribution, mainly in eastern Asia, soybean is mainly infested by *C. chinensis* and *C. australis*. In line with this, the current potential environmental niche overlap values are high for those host–parasite combinations. However, the overlap in potentially suitable area will decrease for *C. australis*. On the other hand, it will increase for the other four *Cuscuta* species. As *C. japonica* already has its main distribution in eastern Asia, it is most likely that this could become a more problematic parasite for soybean in the future. Furthermore, as more and more soybean is grown on other continents, like Europe, it is likely that the European *Cuscuta* species might become more problematic. This might be exacerbated by the fact that some of the *Cuscuta* species are spreading outside their native continents, where they might come into contact with soybean.

In its current distribution, alfalfa is mainly infested by *C. europaea* and *C. approximata*. In line with this, the current

potential environmental niche overlap values are high for those host–parasite combinations. However, alfalfa's highest absolute area of potential overlap is with *C. australis*, indicating that if both species continue to spread outside their native ranges, the realized niche overlap might increase considerably. While the relative overlap in environmental suitability with some of the *Cuscuta* species might decrease for alfalfa, under some RCP scenarios, the absolute area of potential niche overlap will increase considerably for all *Cuscuta* species. So the potential area where alfalfa might be infested with any of the five *Cuscuta* species is also likely to increase with ongoing climate change and naturalization of host and parasites.

Studies have shown that numerous weed species have already invaded regions where they are nonnative (Pyšek et al. 2017). Species distribution modeling can help in identifying key areas for monitoring and developing efficient management programs. In this study, we found that the marginally to optimally suitable area for both host species will increase by the year 2070 for all four RCP scenarios, although the optimally suitable area for alfalfa will actually disappear. For most of the *Cuscuta* species, the marginally to optimally suitable area will also increase. An exception is *C. australis*, which will lose suitable area, although the remaining suitable area will increase in suitability. As the suitable areas for both hosts and parasites increase overall, the relative overlap in suitable area, as indicated by Schoener's *D*, changes only within a relatively narrow range from –10.8 to +9.0%. However, in absolute terms, the change in overlap of suitable area ranges from –12.8% up to +636.1%. Overall, our results indicate that larger parts of the globe will be suitable for both soybean and alfalfa but that these crops could also suffer from *Cuscuta* parasitism in larger parts of their

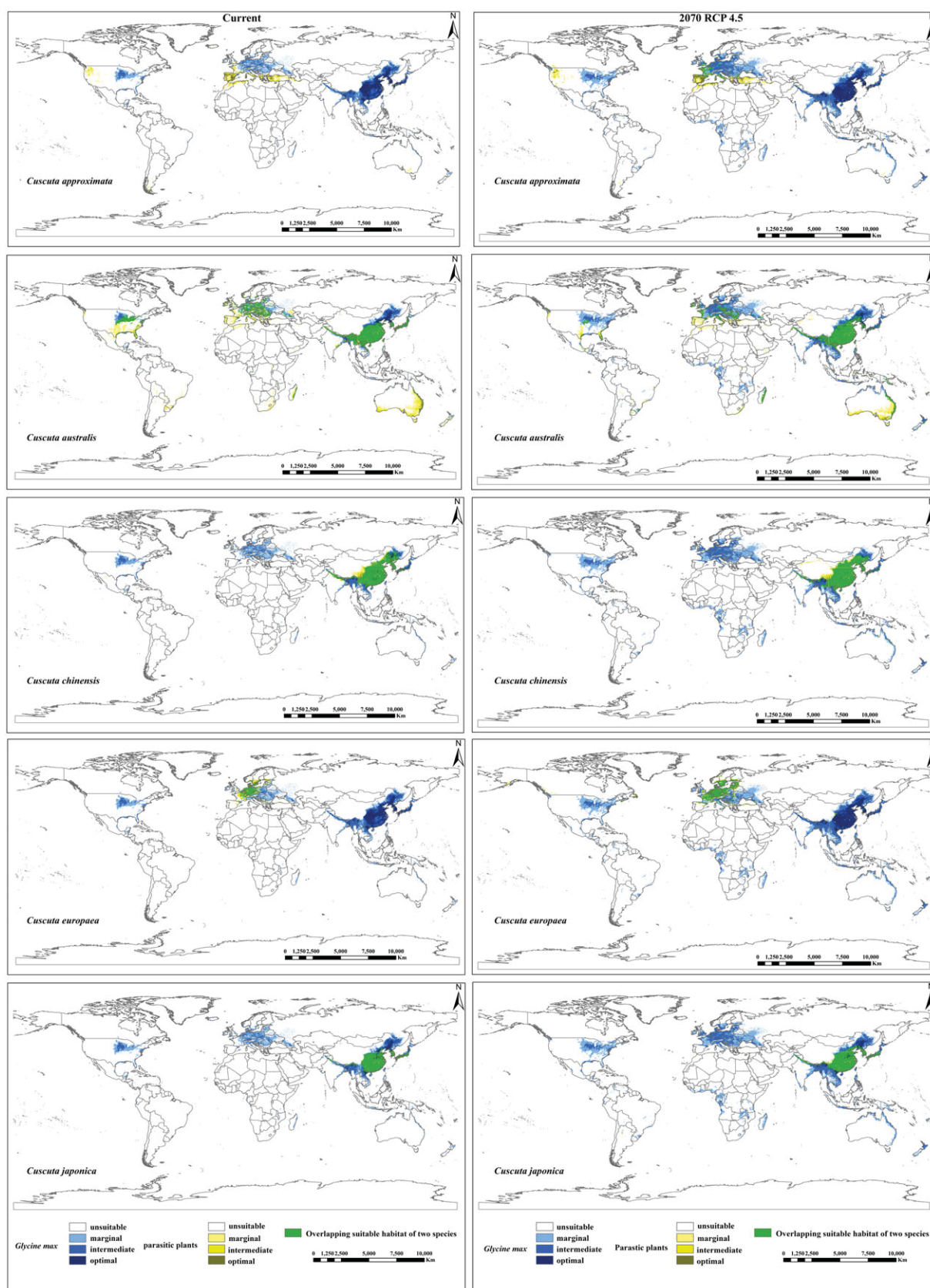


Figure 1. Maps showing the overlap of suitable habitat between soybean and five *Cuscuta* species in the current climate (left) and potential future climatic scenario representative concentration pathway (RCP) 4.5 in 2070 (right). Based on the value of the 10th percentile training presence logistic threshold, four suitability categories were distinguished: optimally suitable area (>0.6), intermediately suitable area ($0.4-0.6$), marginally suitable area (marginal value- 0.4), or unsuitable area (less than the marginal value).

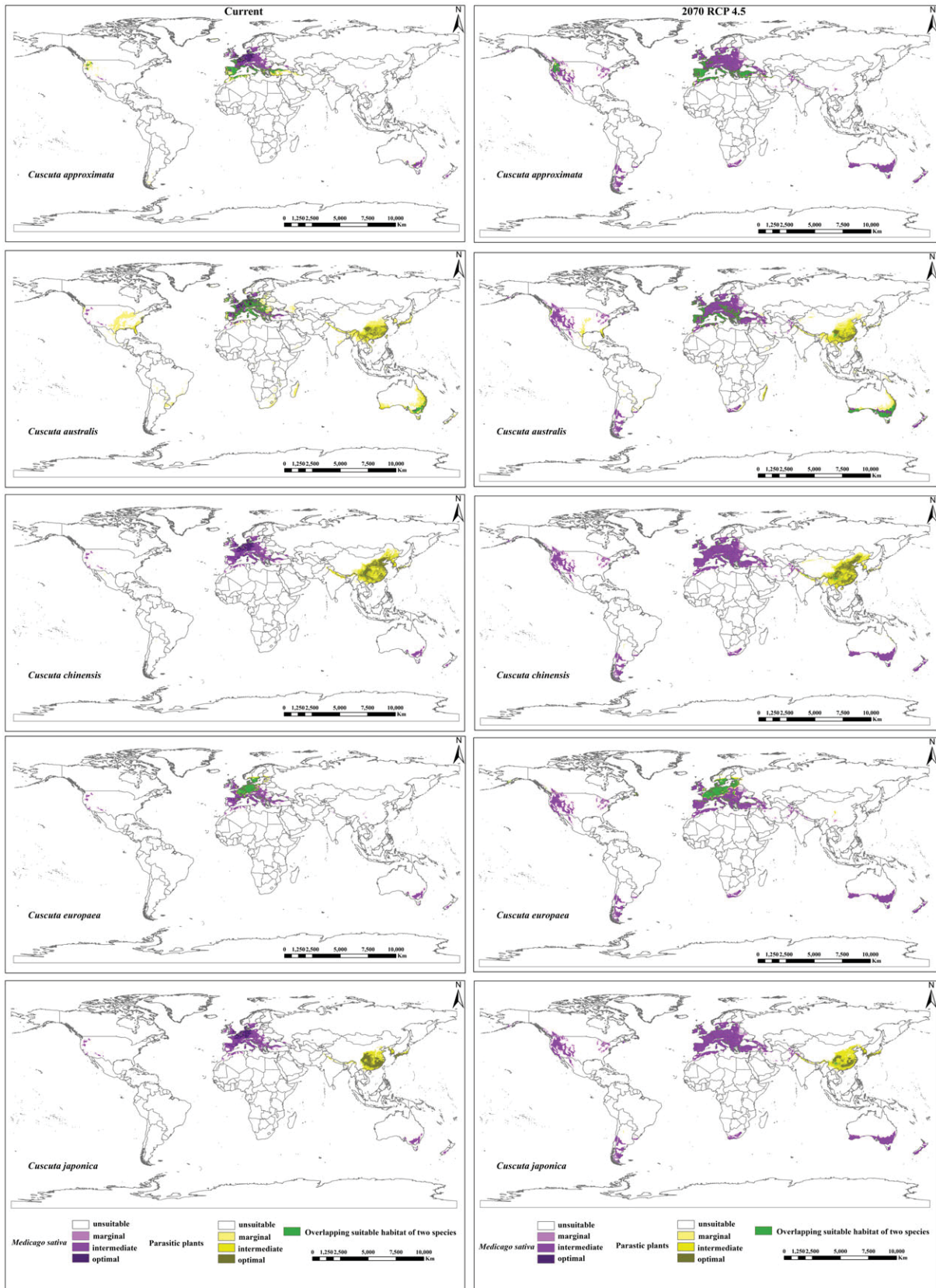


Figure 2. Maps showing the overlap of suitable habitat between alfalfa and five *Cuscuta* species in the current climate (left) and potential future climatic scenario representative concentration pathway (RCP) 4.5 in 2070 (right). Based on the value of the 10th percentile training presence logistic threshold, four suitability categories were distinguished: optimally suitable area (>0.6), intermediately suitable area (0.4–0.6), marginally suitable area (marginal value–0.4), or unsuitable area (less than the marginal value).

suitable ranges. These results might be helpful to increase awareness among crop protection services across the globe and might help national crop-health authorities to prepare for changes in crop pest risks.

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