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Wind effects on habitat distributions of wind-dispersed invasive plants across different biomes on a global scale: Assessment using six species

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ABSTRACT

A number of widespread invasive plants are wind-dispersed, and wind may facilitate their dispersal and migration over a large distance. While wind is an important factor for seed dispersal and pollination, few studies have examined its potential to affect the habitat distribution of invasive plants over large spatial scales. We selected six of the world's worst invasive plants with wind-driving seed dispersal and pollination, and used wind speed as an indicator of wind. Environmental niche modelling was used to quantify the effects of wind on the habitat distribution of these invasive plants on a global scale and across 14 biomes. Wind had a negative effect on the habitat distribution of invasive plants in tropical and subtropical moist biomes, and a positive effect in Temperate Conifer Forests, Boreal Forests/Taiga, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands. We concluded that wind affected the habitat distribution of wind-dispersed invasive plants over a large scale, and this effect varied across different biomes. Thus, wind speed and biomes should be used as global monitoring indicators of invasion by wind-dispersed plants and wind speed variables should be included in the projection of habitat distributions of such invasive species when using ENM.

1. Introduction

Plant invasion is one of the main drivers of biodiversity loss around the world (Powell et al., 2011; Van Der Wal et al., 2008). Furthermore, rapid global change can promote the wide spread of invasive plants into non-native ranges, decrease ecosystem stability, and threaten native plant diversity (Hooper et al., 2012; Powell et al., 2011). Generally, invasive plants have broad physiological niches and/or some special traits; they may possess a strong ability to disperse seeds and respond quickly to changing environments (Higgins and Richardson, 2014; Hooper et al., 2012). Thus, over large spatial scales, many human-induced and natural spread pathways enable invasive plants to become established and naturalized in suitable environments (Donaldson et al., 2014; Hulme, 2009). For example, human activities such as agriculture, forestry, horticulture, trade, and transportation enable propagules to overcome various dispersal barriers and establish themselves in suitable habitats (Donaldson et al., 2014; Kalusová et al., 2013). When plant populations encounter a suitable environment in which to colonize, their maximum migration rate is strongly determined by natural dispersal (Higgins and Richardson, 2014; Richardson et al., 2000). For the prevention and control of plant invasion on a large scale, we need to understand the habitat distribution of invasives and the potential driving factors (Donaldson et al., 2014; Kalusová et al., 2013; Rejmanek

and Richardson, 1996).

A number of widespread invasive plants are wind-dispersed species, and wind can promote natural dispersal and migration over a long distance (http://www.issg.org). These wind-dispersed plants may have the ability to invade non-native ranges, leading to a high invasion risk (Bullock et al., 2012; Bullock and Clarke, 2000; Davis et al., 2004). Empirical studies have shown that wind is a common dispersal agent of seeds and pollens, and wind speed is an important driver of natural dispersal for invasive plants at community, local, and regional scales (Bullock et al., 2012; Bullock and Clarke, 2000; Lancaster and Baas, 1998; Soons and Bullock, 2008; Whitehead, 1962). Plant migration is a recognized ecological outcome of slowing near-surface wind speeds under conditions of sufficient seed release (Thompson and Katul, 2013). In the past years, global wind speeds have decreased substantially (Thompson and Katul, 2013; Young et al., 2011). Global change in wind speeds may create suitable habitats for plant invasion across different spatial scales (Bullock et al., 2012; Tackenberg, 2003). Hence, it is crucial to evaluate the effects of wind on plant invasion over large spatial scales, possibly even on a global scale. However, to our knowledge, to date, no studies have tested the effects of wind on the habitat distribution of invasive plants over large spatial scales.

A biome is a large community of plant species that have common characteristics due to similar environmental conditions (i.e. climate),

and is usually classified over a large spatial scale (Olson et al., 2001). Different biomes may provide habitats that favour the expansion of invasive plants to varying degrees (Faulkner et al., 2014; Rouget et al., 2015; van Wilgen et al., 2008; Wan et al., 2016). Ecologists and biological conservationists frequently use the concept of biomes to assess the invasion risk of plant species (Faulkner et al., 2014; Rouget et al., 2015; van Wilgen et al., 2008). Hence, we need to consider wind and biomes during the assessment of suitable habitats for invasive plants. Moreover, the concept of biomes can help us understand wind effects on the habitat distribution of invasive plants over a large spatial scale. To this end, we used environmental niche modelling (ENM) to explore the effects of wind on the habitat distribution of invasive plants across different biomes on a global scale.

ENM is the process of using computer algorithms to project the habitat distribution ranges of invasive plants based on occurrence records (locations where the species have been found) together with environmental variables (e.g. climate; Thuiller et al., 2005). It is widely used to project the habitat distribution of invasive plants over a large spatial scale and evaluate global invasion risk (Bradley et al., 2010; Jiménez-Valverde et al., 2011; Thuiller et al., 2005; Wan et al., 2016). The selection of a limited but relevant number of environmental variables is important when using ENM (Thuiller, 2014). Furthermore, the selection of environmental variables should be based on reasonable ecological assumptions of plant invasion (Thuiller, 2014). Considering the potential effects of wind on the dispersal and migration of wind-dispersed invasive plants, we can use ENMs to understand the effects of wind on their habitat distribution across different biomes, and support the application of ENMs on plant invasion assessment.

Here we tested the hypothesis that wind could potentially affect the habitat distribution of wind-dispersed invasive plants across different biomes. For this purpose, we selected six widespread, wind-dispersed, invasive plant species from the list of the worlds' 100 worst invasive alien species. Maxent was used to model their habitat distribution on a global scale based on two environmental datasets: i) climatic and ii) both climatic and wind speed variables (Lowe et al., 2000; Phillips et al., 2006). We computed differences in habitat suitability between the wind-dispersed invasive plants in these two models based on maps of their global habitat distribution and biomes. We then quantified the effects of wind on the habitat distributions of the plants across 14 biomes, and delineated the biomes that were positively affected by wind. Finally, we put forward some suggestions on the use of wind speed variables in ENM for the projection of habitat distribution of wind-dispersed invasive plants.

2. Materials and methods

2.1. Species data and occurrence records

The invasive species specialist group (ISSG) of IUCN compiled a list of '100 of the world's worst invasive alien species' (Lowe et al., 2000; http://www.issg.org/database/species/search.asp?st=100ss). Based on this list, we selected six invasive plants: *Cecropia peltata*, *Cinchona pubescens*, *Eichhornia crassipes*, *Mikania micrantha*, *Spathodea campanulata*, and *Tamarix ramosissima*. The species share the following characteristics around the world: 1) pollinating and spreading seeds via wind dispersal, 2) imposing a significantly negative effect on biodiversity, and 3) threatening a variety of endangered plant species and ecosystems (Lowe et al., 2000). Occurrence data, especially geographic coordinates, for each invasive plant were obtained from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org). These data were recorded as presence or absence within 2.5 arc-minute pixels (4.3 km from the equator) to reduce the effects of sampling bias and to avoid errors associated with georeferencing, obvious misidentifications, and duplicate records per grid cell. These records cover both native and invasive ranges (http://www.issg.org). The number of occurrence records ranged from 146 to 1315 (Table 1).

2.2. Biome data

The units of global biomes are ecoregions (Olson et al., 2001). Ecoregions can constrain the habitat distributions of invasive plants across different spatial scales (Faulkner et al., 2014; Rouget et al., 2015). Invasive plants can grow and survive together in non-native distribution ranges where climatic conditions are similar to those in their native ranges (Faulkner et al., 2014; Rouget et al., 2015; van Wilgen et al., 2008; Wan et al., 2016). Therefore, we used ecoregions as the basic units for assessing wind effects on the habitat distribution of the six invasive plants across different biomes (Faulkner et al., 2014; Rouget et al., 2015; Wang et al., 2017).

The ecoregions, including terrene and freshwater areas, were areas where there was spatial coincidence in characteristics of geographical phenomena associated with differences in the quality, health, and integrity of ecosystems (Olson et al., 2001). Delineation of the ecoregions was based on the biogeographic pattern of ecosystems and environmental management (Olson et al., 2001). Terrestrial ecoregions included 867 distinct units within 14 biomes (http://www.worldwildlife.org/biomes; Olson et al., 2001; Wang et al., 2017; Fig. 1).

2.3. Environmental variables

Climate factors are among the primary factors determining the overall distribution patterns of invasive plants across the globe. Current bioclimatic variables with a 2.5-arc-minute spatial resolution were used for the environmental input layers of the ENM, and were downloaded from the WorldClim database (averages from 1970 to 2000; Fick and Hijmans, 2017; www.worldclim.org). We removed these with absolute Pearson correlation coefficients larger than 0.8 to eliminate multicollinearity effects in the parameter estimates of ENMs. The resulting seven bioclimatic variables could influence the distribution and physiological performance of invasive plants (Petitpierre et al., 2017; Thuiller, 2014), and were 1) annual mean temperature (°C), 2) mean diurnal range (mean of monthly [max-min] temperature), 3) temperature seasonality (standard deviation * 100), 4) annual precipitation (mm), 5) precipitation during the driest month (mm), 6) precipitation seasonality (coefficient of variation) and 7) precipitation during the coldest quarter (mm). We downloaded the wind speed (m/s) data from January to December from the WorldClim database (averages from 1970 to 2000; Fick and Hijmans, 2017; www.worldclim.org). Therefore, we could establish two environmental datasets, i.e. bioclimatic and both bioclimatic and wind speed variables.

2.4. Habitat distribution modelling

Maxent (a commonly used ENM technique) was used to model habitat distribution for each of the six invasive plants based on occurrence records and the two environmental datasets (bioclimatic and both bioclimatic and wind speed variables; hereafter referred to as Climate and Wind Models, respectively). We used cloglog as the output of habitat suitability for invasive plants (Phillips et al., 2017). The cloglog transform is derived from the recently published interpretation of Maxent as an inhomogeneous Poisson process, giving it a stronger theoretical justification than the logistic transform by default (Phillips et al., 2017). All pixels were regarded as the possible habitat distribution space of maximum entropy. For the map predicted using Maxent, pixels with values of 1 and 0 represented the highest and lowest habitat suitability, respectively (Phillips et al., 2017). Furthermore, habitat suitability was determined in relation to the areas where climatic conditions of the study region were similar to the sites where occurrence localities had already been recorded.

Similar to previous studies (Merow et al., 2013; Radosavljevic and Anderson, 2014), our modelling sets were as follows: 1) the regularization multiplier (beta), set to 2, to produce a smooth and general response that could be modelled in a biologically realistic manner; 2) a

Species	Record	AUC$_{training}$		AUC$_{test}$		Training omission rate	
		C	W	C	W	C	W
Cecropia peltata	413	0.962	0.977	0.959	0.975	0.032 ± 0.031	0.028 ± 0.031
Cinchona pubescens	146	0.985	0.985	0.983	0.983	0.052 ± 0.037	0.050 ± 0.041
Eichhornia crassipes	1263	0.915	0.923	0.913	0.921	0.043 ± 0.032	0.051 ± 0.036
Mikania micrantha	1315	0.938	0.942	0.937	0.941	0.042 ± 0.031	0.041 ± 0.031
Spathodea campanulata	392	0.959	0.966	0.955	0.962	0.036 ± 0.032	0.031 ± 0.031
Tamarix ramosissima	514	0.950	0.955	0.947	0.951	0.043 ± 0.031	0.043 ± 0.030

C and W represent the Climate and Wind Models, respectively. Values of training omission rate are mean ± SD.
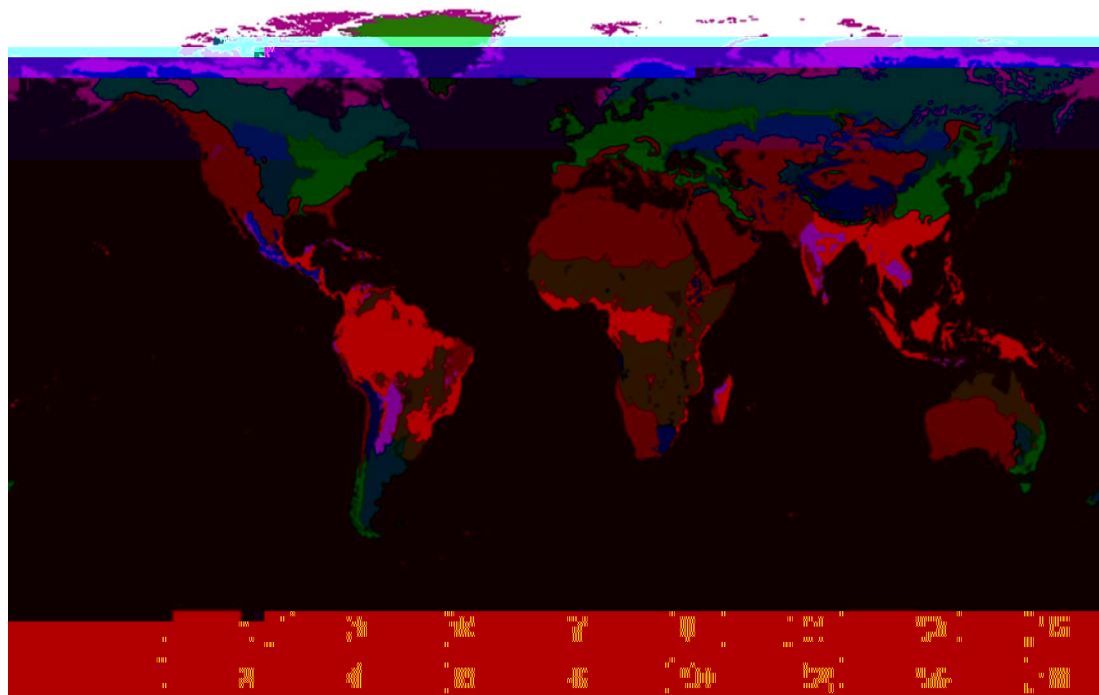

Fig. 1. The biomes are designated with different colours and numbers. 1 - Tropical and Subtropical Moist Broadleaf Forests; 2 - Tropical and Subtropical Dry Broadleaf Forests; 3 -

4-fold cross-validation approach to remove the bias of recorded occurrence points; 3) the maximum number of background points set to 10,000; and 4) other settings were identical to those described in Phillips et al. (2006).

We evaluated the predictive ability of Maxent using the area under the curve (AUC) of the receiver operation characteristic (ROC) that regarded each value of the prediction test as a possible threshold, and then obtained the corresponding sensitivities and specificities through calculations (see Phillips et al., 2006 for more details). The AUC values ranged from 0.5 (lowest predictive ability or not different from a randomly selected predictive distribution) to 1 (highest predictive ability). Models of species with values above 0.7 were considered useful in our study (Phillips et al., 2006). However, AUC is not enough for assessing the performance of Maxent modelling. Therefore, we also used the binomial test based on the training omission rate (Anderson and Gonzalez, 2011). The training omission rates were calculated as the proportion of the sample units within the grid cells that were predicted to yield the absence of the species for the occurrence records of training data (Anderson and Gonzalez, 2011; Phillips et al., 2006). These were 1-sided *P*-values for the null hypothesis that test points from the modelling techniques are no better than from a random prediction with the

same fractional predicted area. The binomial probabilities were based on seven common thresholds by Maxent modelling (see Phillips et al., 2006 for more details). A low omission rate (17%) is a necessary condition for a good model (Anderson and Gonzalez, 2011; Phillips et al., 2006). We used the paired-sample *t*-test to determine the difference between AUC and average training omission rates of Climate and Wind Models for the six invasive plants.

2.5. Analyses of wind effects on habitat distribution

First, we calculated Schoener's D to measure the similarities between predictions of habitat distribution by Climate and Wind Models based on habitat suitability of pixels for each invasive species using ENMTools 1.4.4 (see Warren et al., 2008, 2010 for detailed information). Schoener's D ranges from 0 (species having completely disparate habitat distributions) to 1 (species having identical habitat distributions; Warren et al., 2008).

Second, we evaluated changes in habitat suitability for invasive plants in each ecoregion. In each ecoregion, we computed the average habitat suitability of pixels for each wind-dispersed invasive plant using both Climate and Wind Models (Wan et al., 2016). We used the paired-

sample *t*-test to analyse the differences between the average habitat suitability in both Models across all the ecoregions. We also calculated the changes in average habitat suitability in each ecoregion as: CHS = $(X_w - X_c) / X_c$, where CHS is the change in average habitat suitability in an ecoregion, and X_w and X_c are average habitat suitability in the ecoregion based on Climate and Wind Models, respectively (Wan et al., 2016). A CHS value greater than zero indicated an increase in habitat suitability (Wan et al., 2016).

Third, we quantified the effects of wind on the habitat distribution of invasive plants in each biome. We calculated the mean habitat suitability across all ecoregions in each biome. Then, for each biome, we computed the log response ratio of habitat suitability as: RR = ln (Y_w / Y_c), where RR is the log response ratio of mean habitat suitability of invasive plants in a biome, and Y_w and Y_c are the mean habitat suitability of invasive plants across all ecoregions in the biome based on the Wind and Climate Models, respectively. We weighted RR by sample size using the following equation: $n_c * n_w / (n_c + n_w)$, where n_c and n_w are the number of ecoregions in the biome based on the Climate and Wind Models, respectively (Adams et al., 1997; Hedges et al., 1999).

Fourth, we delineated important biomes that were positively affected by wind. We extracted pixels (areas) with increased habitat suitability, and computed the proportion of these pixels in each biome. We considered the biomes with > 50% of these pixels to be 'important biomes' (Adhikari et al., 2015).

3. Results

All models had AUC values > 0.7 and training omission rates < 17% (Table 1; *P* < 0.05), indicating the good predictive abilities of the models. The training and test AUC values of the Wind Model were significantly larger than those of the Climate Model (*P* < 0.05), but the average training omission rates did not differ significantly between the two models.

Habitat distribution of the six wind-dispersed invasive plants mainly covered the tropical and sub-tropical regions of the world (Fig. 2). From a global perspective, the habitat distribution of the six wind-dispersed invasive plants based on the Wind Model was not consistent with that of the Climate Model (Fig. 2). The predictions of habitat distribution from the two models (Climate Model vs. Wind Model) differed most significantly for *C. peltata* (Schoener's D: 0.767), especially in South America, Central Africa, and Southeast Asia (Fig. 2).

Mean habitat suitability for all six wind-dispersed invasive plants across the biomes differed significantly between the Climate and Wind Models (*P* < 0.05), indicating that wind affected habitat distributions of invasive plants over large spatial scales (Fig. 3). Incorporating wind in the model resulted in large areas with increased habitat suitability for the plants across the 14 biomes (Figs. 1 and 3). Considering individual species, wind had the largest negative effect on the habitat distribution of *C. peltata* (RR = − 52.37) in Tropical and Subtropical Moist Broadleaf Forests, and the largest positive effect in Deserts and Xeric Shrublands (RR = 32.51; Table 2). Wind also greatly affected the habitat distribution of *C. peltata* in Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, Tropical and Subtropical Grasslands, Savannas and Shrublands, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands (Table 2). Wind had a large effect on the habitat distribution of *M. micrantha* in Tropical and Subtropical Moist Broadleaf Forests, *S. campanulata* in Temperate Conifer Forests, Temperate Grasslands, Savannas and Shrublands, Montane Grasslands and Shrublands, and Deserts and Xeric Shrublands, and *T. ramosissima* in Tropical and Subtropical Moist Broadleaf Forests (Table 2).

Considering the mean values of the proportion of habitats with increased suitability for the six wind-dispersed invasive plants, 10 of the 14 biomes were important biomes (with > 50% areas of average increased habitat suitability for the six wind-dispersed invasive plants, Table 3). Temperate Conifer Forests, Boreal Forests/Taiga, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands had > 50% areas of average increased habitat suitability for all six invasive plants (Table 3). Of the six invasive plants, *S. campanulata* had the largest proportion (> 90%) of areas with increased habitat suitability in Temperate Conifer Forests, Boreal Forests/Taiga, and Tundra (Table 3; Fig. 1). For *C. pubescens*, all 14 biomes were important biomes with > 50% of the areas having increased habitat suitability (Table 3; Fig. 1).

4. Discussion

Our study is the first case to quantify the effects of wind on the habitat distribution of wind-dispersed invasive plants across biomes, and to delineate biomes where there are large, positive effects of wind on habitat distributions of invasive plants on a global scale. We showed that wind might have positive effects on the habitat distribution of wind-dispersed invasive plants in biomes such as temperate forests, montane shrublands, and deserts and xeric grasslands, but have nega-
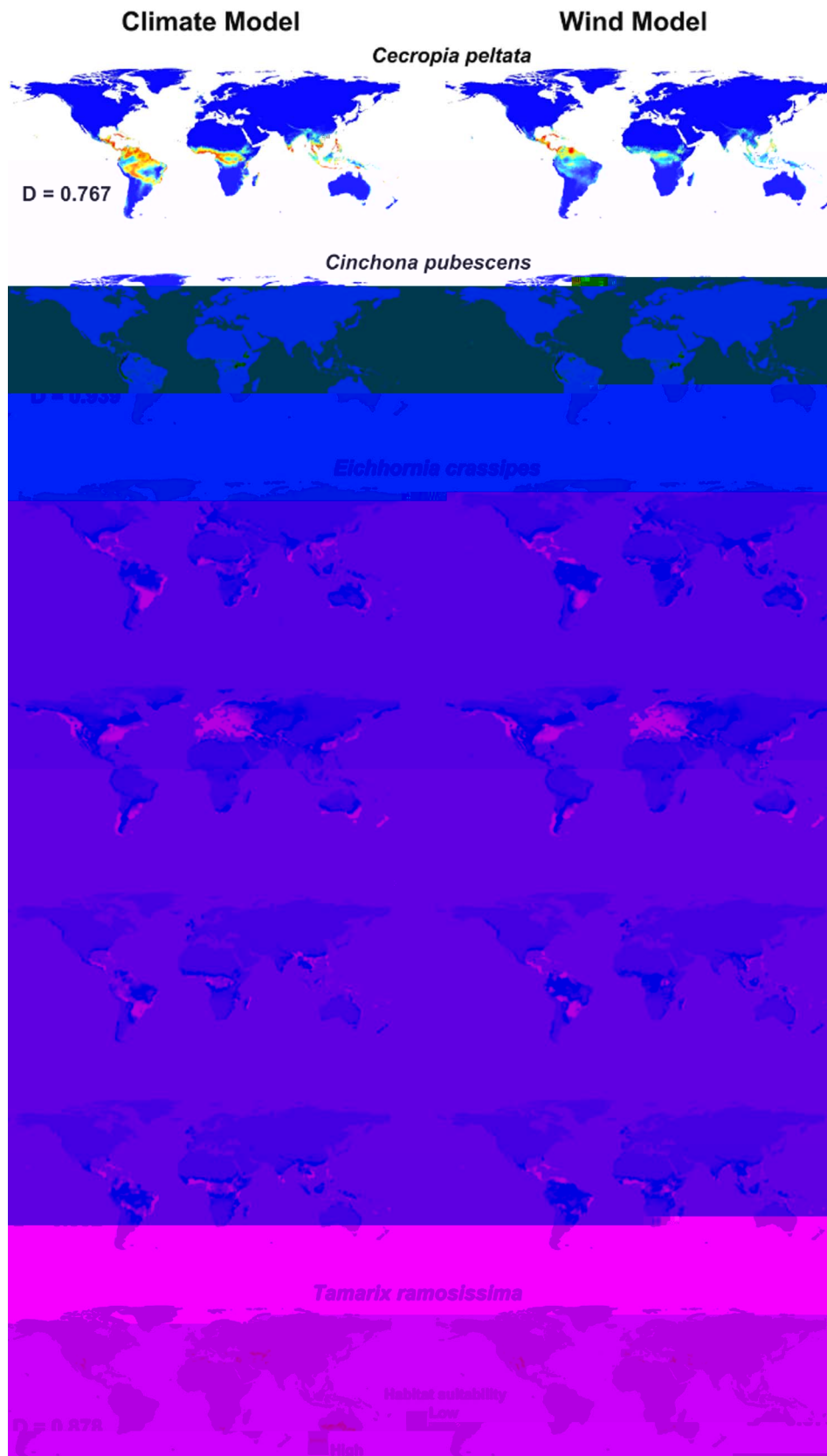
Fig. 2. Habitat distribution of each of the six wind-dispersed invasive species based on the Climate (left) and Wind Models (right) and the similarities between the two models measured using Schoener's D (D).

habitat distribution of *M. micrantha* and *T. ramosissima* in Tropical and Subtropical Moist Broadleaf Forests (Table 2; Fig. 3).

Wind speed had largely positive effects on the habitat distribution of *C. peltata* and *S. campanulata* in Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, Temperate Grasslands, Savannas and Shrublands, Montane Grasslands and Shrublands, and Deserts and Xeric Shrublands (Table 2; Figs. 1 and 3). *Cecropia peltata* is likely to survive and grow in warm climates ranging from montane to tropical
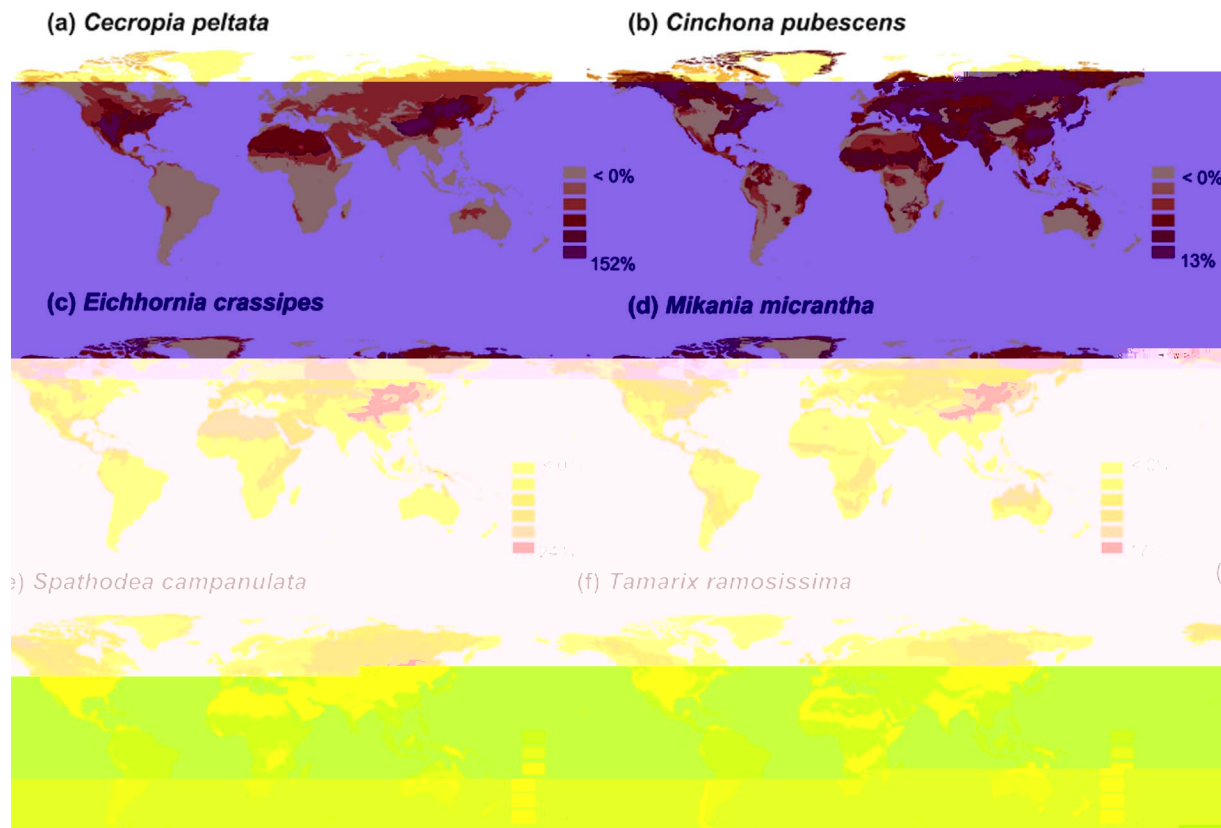
Fig. 3. Changes in habitat suitability of each of the six wind-dispersed invasive plants in the ecoregions. Positive values indicate the proportion of increased habitat suitability due to the wind effect, and the negative value (< 0%) represents decreased habitat suitability due to the wind effect.

conditions (Fleming and Williams, 1990), and *S. campanulata* has been widely introduced throughout tropical and subtropical regions of the world as an ornamental tree (Aide et al., 2000; Meyer, 2004). Hence, *C. peltata* and *S. campanulata* can adapt to a variety of environmental conditions. Wind may promote *C. peltata* pollination and *S. campanulata* seed dispersal on a large scale (Canham et al., 1990; Fleming and Williams, 1990). Hence, wind speed may be one of the most important factors promoting the spread of wind-dispersed invasive plants as their seeds and pollen can be dispersed across different biomes, over a large spatial scale.

4.2. Delineation of biomes with positive effects of wind on habitat distribution

Our results suggested that wind speed had a large, positive effect on the habitat distribution of wind-dispersed invasive plants across the biomes. The biomes with the greatest positive wind effects on the habitat distribution of all six wind-dispersed invasive plants included Temperate Conifer Forests, Boreal Forests/Taiga, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands. Plant invasion is the process by which alien plants could colonize non-native ranges by human introduction and/or natural spread (Rejmanek and Richardson, 1996; Richardson et al., 2000). Seed dispersal and pollination are the basic preconditions for the natural spread of invasive plants on a large scale (Rejmanek and Richardson, 1996; Richardson et al., 2000; Traveset and Richardson, 2006). Wind affects seed spread and pollination of wind-dispersed invasive plants in non-native ranges from montane to tropical biomes, and suitable wind speeds may lead to the invasion of wind-dispersed alien plants across different biomes (Bullock et al., 2012; Davis et al., 2004; Greene and Johnson, 1995; Skarpaas and Shea, 2007; Tackenberg, 2003). For example, temperate forests, and montane grasslands and shrublands are

Table 2
Wind effects on habitat distribution of the six wind-dispersed invasive plants in the 14 biomes.

Species	Biome													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cecropia peltata	− **52.37**	0.64	1.73	**22.91**	**16.22**	2.43	− **11.99**	**18.59**	8.39	**18.10**	− 3.22	− 6.61	**32.51**	− 4.246
Cinchona pubescens	− 0.16	1.57	0.10	8.18	6.36	4.08	0.02	1.92	2.43	2.89	2.12	1.25	5.22	0.328
Eichhornia crassipes	− 3.80	0.02	0.38	− 1.79	1.07	− 0.06	− 2.25	0.55	1.70	2.13	1.53	− 1.18	2.03	1.344
Mikania micrantha	− **14.64**	− 0.70	0.04	1.34	3.44	2.79	0.45	1.67	1.54	6.47	3.30	− 2.09	− 1.12	1.012
Spathodea campanulata	− 6.49	1.95	1.10	6.46	**13.14**	6.76	3.76	**11.58**	4.31	**14.52**	4.50	− 0.52	**16.71**	0.585
Tamarix ramosissima	− **25.80**	2.50	− 1.38	1.57	3.51	0.22	− 0.61	5.41	2.18	− 0.23	− 1.93	− 2.23	5.84	0.297

Values are response ratios of the habitat suitability of invasive plants in ecoregions calculated based on Climate and Wind Models. Bold values represent log response ratios over 10.0, indicating large positive wind effects; bold, italic values represent log response ratios smaller than − 10.0, indicating large negative effects. Codes for biomes are as follows: 1 - Tropical and Subtropical Moist Broadleaf Forests; 2 - Tropical and Subtropical Dry Broadleaf Forests; 3 - Tropical and Subtropical Coniferous Forests; 4 - Temperate Broadleaf and Mixed Forests; 5 - Temperate Conifer Forests; 6 - Boreal Forests/Taiga; 7 - Tropical and Subtropical Grasslands, Savannas and Shrublands; 8 - Temperate Grasslands, Savannas and Shrublands; 9 - Flooded Grasslands and Savannas; 10 - Montane Grasslands and Shrublands; 11 - Tundra; 12 - Mediterranean Forests, Woodlands and Scrub; 13 - Deserts and Xeric Shrublands; 14 - Mangroves.

Table 3
The proportion (%) of areas with increased habitat suitability for the six wind-dispersed invasive plants in the 14 biomes.

Species	Biome													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cecropia peltata	12.1	25.3	**76.7**	**62.2**	**69.8**	**68.8**	30.3	**74.8**	45.0	**64.6**	39.4	31.5	**76.1**	17.8
Cinchona pubescens	**59.5**	**81.3**	**61.0**	**86.0**	**81.3**	**95.4**	**66.7**	**51.5**	**79.4**	**55.0**	**79.8**	**67.5**	**59.2**	**64.8**
Eichhornia crassipes	18.5	26.1	**68.2**	**54.5**	**52.3**	**53.5**	31.9	**54.3**	47.3	**63.3**	**73.2**	46.1	**56.3**	**69.3**
Mikania micrantha	22.9	32.6	**67.7**	**67.3**	**67.2**	**71.1**	45.4	**70.5**	43.0	**73.9**	**81.2**	33.6	36.5	**58.8**
Spathodea campanulata	22.6	**50.4**	**89.4**	**74.1**	**92.9**	**97.2**	32.3	**79.6**	**52.6**	**76.0**	**91.0**	**56.3**	**74.8**	**53.9**
Tamarix ramosissima	11.7	44.7	32.8	37.0	**52.6**	**58.5**	37.6	**51.7**	48.7	**50.2**	23.5	35.2	36.7	38.5
Mean	24.6	43.4	**66.0**	**63.5**	**69.3**	**74.1**	40.7	**63.7**	**52.7**	**63.8**	**64.7**	45.0	**56.6**	**50.5**

Bold values represent important biomes with over 50% areas having increased habitat suitability. Codes for biomes are as follows: 1 - Tropical and Subtropical Moist Broadleaf Forests; 2 - Tropical and Subtropical Dry Broadleaf Forests; 3 - Tropical and Subtropical Coniferous Forests; 4 - Temperate Broadleaf and Mixed Forests; 5 - Temperate Conifer Forests; 6 - Boreal Forests/Taiga; 7 - Tropical and Subtropical Grasslands, Savannas and Shrublands; 8 - Temperate Grasslands, Savannas and Shrublands; 9 - Flooded Grasslands and Savannas; 10 - Montane Grasslands and Shrublands; 11 - Tundra; 12 - Mediterranean Forests, Woodlands and Scrub; 13 - Deserts and Xeric Shrublands; 14 - Mangroves.

biomes with relatively low plant diversities and little human activity (Olson et al., 2001). There is a high invasion risk for these biomes (Kennedy et al., 2002). Wind-dispersed invasive plants (e.g. *C. pubescens*) could potentially expand via wind dispersal, and wide niche distributions of invasive plants may enhance such a potential (Higgins and Richardson, 2014; Rejmanek and Richardson, 1996; Richardson et al., 2000). Therefore, wind speed can be used as a global monitoring indicator of plant invasion in biomes such as Temperate Conifer Forests, Boreal Forests/Taiga, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands.

Furthermore, wind may greatly enhance habitat suitability (over 50%) of species in the biomes, particularly *C. pubescens* for which wind increased its habitat suitability by over 50% in all 14 biomes (Table 1). Wind could be a good indicator for the assessment of plant invasion risk (Thompson and Katul, 2013). We need to pay attention to the spread of *C. pubescens* around the world due to the large areas of increased habitat suitability (Table 3). *Cinchona pubescens* is a widely cultivated tropical species that invades a variety of forest and non-forest habitats (Buddenhagen et al., 2004). It spreads by wind-dispersed seeds, and vegetatively via suckers up to several meters away from the original tree once established (Buddenhagen et al., 2004). Hence, appropriate wind speeds may promote the expansion of *C. pubescens* across different habitats of biomes. Although some invasive plants do not occur over large areas, because of the positive effects of wind on habitat distribution, wind speed may still have significant effects in some biomes, for example, *C. peltata* in Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, and Deserts and Xeric Shrublands. Hence, our results provide a reference for the introduction of wind-dispersed non-native plants, with a perspective on the relationship between wind and species distribution. We need to delineate hotspots of biomes with positive effects of wind on habitat distribution, and consider wind speed effects for the prevention and control of plant invasion (Buddenhagen et al., 2004; Trueman et al., 2014).

4.3. Implications for environmental niche modelling

The training and test AUC were significantly larger in the Wind than in the Climate Model, suggesting that including wind speed as an input variable could improve the predictive capabilities of ENMs (Anderson and Gonzalez, 2011; Phillips et al., 2006). It is clear that the selection of reasonable environmental variables can improve the predictive abilities of ENMs (Petitpierre et al., 2017; Thuiller, 2014), and temperature and precipitation are the main drivers of the habitat distribution of plants (Bradley et al., 2010; Petitpierre et al., 2017). However, ENMs may under- or over-estimate habitat suitability for invasive plants when using temperature and precipitation variables alone (Gallardo et al., 2015; Petitpierre et al., 2017). Hence, some abiotic variables, including human footprint, soil factors, and elevation, are integrated to project the habitat distribution of invasive plants using ENMs (Gallardo et al.,

2015; Hoffman et al., 2008; Padalia et al., 2014). Our study showed, perhaps for the first time, that wind speed is also an important input variable for modelling habitat distribution of wind-dispersed invasive plants using ENMs (Tables 1 and 2).

Our results also suggested that the predictive ability of ENMs might depend on biomes. For example, ENMs using temperature and precipitation variables potentially over-estimated the habitat distribution of *C. peltata*, *M. micrantha*, and *T. ramosissima* in Tropical and Subtropical Moist Broadleaf Forests, and under-estimated that of *C. peltata* in Temperate Conifer Forests, Boreal Forests/Taiga, Temperate Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands (Table 2; Fig. 3). Faulkner et al. (2014) has developed a simple, rapid methodology for invasive species watch lists based on biomes and conditions of temperature and precipitation. As in previous studies, we suggested that wind speed variables should be included and biomes should be considered when projecting the habitat distribution of wind-dispersed invasive plants for invasion assessment using ENMs (Faulkner et al., 2014; Rouget et al., 2015; van Wilgen et al., 2008; Wan et al., 2016).

5. Conclusions

Wind potentially has negative effects on the habitat distribution of wind-dispersed invasive plants in tropical and subtropical moist biomes, and positive effects in temperate forests, montane shrublands, deserts, and xeric grasslands. Thus, it is necessary to integrate wind speed and biome data in the assessment of habitat distribution of wind-dispersed invasive plants on a large spatial scale, and this could be useful when coming up with strategies for the prevention and control of invasive plants. Wind speed should be used as an input environmental variable for the projection of habitat distribution of plants across different biomes to improve the performance of ENMs. However, because our study was limited by the amount of available data for ecological validation, more studies should be carried out for verification, including field investigations, ecological monitoring and precision trainings, and validations of ENMs. With accelerating economic globalization and rapid climate change, the risk evaluation of universal coverage for wind-dispersed invasive plants and environmental variables is also urgently required.

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