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ORIGINAL ARTICLE

Effects of ecoregional vulnerability on habitat suitability of invasive alien plants: an assessment using 13 species on a global scale

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Abstract

The development of new hypotheses can promote the explanation of mechanisms on plant invasion across different scales. We tested the hypothesis that ecoregional vulnerability can affect habitat suitability of invasive alien plants (IAPs) in non-native ranges. We used 13 IAPs, distributed around the world, and identified vulnerable ecoregions belonging to different biomes and biogeographical realms. Then, Maxent modeling was used to assess the habitat suitability of IAPs. We quantified the effects of ecoregional vulnerability on habitat suitability of IAPs as effect sizes using the log response ratio of habitat suitability. Ecoregional vulnerability had significant effects on habitat suitability for IAPs in invasive ranges across different biomes and biogeographical realms. Such effects may depend on the biomes and biogeographical realms of interest. Ecoregional vulnerability had positive effects on the habitat suitability of *Chromolaena odorata, Clidemia hirta, Imperata cylindrica, Melaleuca quinquenervia, Mikania micrantha, Prosopis glandulosa, Rubus ellipticus*, and *Tamarix ramosissima*. Vulnerable ecoregions of tropical and subtropical moist broadleaf forests and temperate broadleaf and mixed forests could result in large distributions and the highest habitat suitability of IAPs. The vulnerable ecoregions were mainly distributed in the biogeographical realms of Australasia, Nearctic, Neotropics, and Oceania. We tested a new hypothesis on disturbances and biological diversity based on ecoregional vulnerability over large scales. Our findings support the hypothesis that ecoregional vulnerability can increase habitat suitability of IAPs, promoting IAPs to expand in invasive ranges. Our study provides insight into the development of new hypotheses on the mechanisms of plant invasion over large scales.

Keywords Biogeographical realm · Biome · Effect size · Habitat suitability modeling · Plant invasion · Vulnerable ecoregion

Introduction

Invasive plants are likely causing an array of ecological, economic, and health impacts in invaded regions over a large spatial scale (Pimentel et al. 2005; Vilà et al. 2011; Early et al. 2016). Invasive plants can have adverse negative effects on ecosystems and change ecosystem functions in invaded regions (Hejda et al. 2009; Vilà et al. 2011; Early et al. 2016). For example, tree invasion can result in profound impacts on ecosystem processes such as biogeochemical cycling, carbon sequestration, and hydrology (Gómez-Aparicio and Canham 2008; Richardson and Rejmánek 2011). Hence, it is urgent to prevent and control plant invasion over large scales (even on the global scale) because plant invasion has a large potential to threaten global biodiversity and ecosystems (Hejda et al. 2009; Vilà et al. 2011; Early et al. 2016).

Numerous hypotheses (e.g., ecological niche hypothesis, enemy release hypothesis, and environmental disturbance hypothesis) explaining the mechanisms of plant invasion over large scales have been proposed (Hobbs and Huenneke 1992; Maron and Vilà 2001; Keane and Crawley 2002; Blumenthal 2006; MacDougall et al. 2009; Jeschke et al. 2012).

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Previous studies have shown that environmental disturbances may be the main drivers of invasive plant distributions, and rapid global change potentially promotes plant invasion around the world (Hobbs and Huenneke 1992; Broennimann et al. 2007; MacDougall et al. 2009). The knowledge of the impacts of environmental disturbances on plant invasions can promote our ability to prevent and control plant invasion, and assess the potential effects of plant invasion on biodiversity and ecosystems (Hobbs and Huenneke 1992; van Wilgen et al. 2008; Bradley et al. 2010; Beauséjour et al. 2015). Bradley et al. (2010) have shown that environmental disturbance can create a rapid and large-scale increase in resource availability for numerous IAPs. A biome is a community of multiple species that have common characteristics related to the environment in which they exist and can be found across different geographical scales (Olson et al. 2001). At multiple spatial scales, biomes are distinct biological communities that have formed in response to shared physical environmental conditions (Olson et al. 2001). Invasive plants can grow and survive together in non-native ranges where environmental conditions are similar to those in native ranges (van Wilgen et al. 2008; Faulkner et al. 2014; Rouget et al. 2015). Such biomes may constrain the distribution of invasive plants in invaded ranges (Faulkner et al. 2014; Rouget et al. 2015).

Previous studies have shown that such constraints of ecoregions on plant invasion may be due to similar environmental niches (e.g., temperature and precipitation) for the specific plant species across the different biomes and biogeographical realms at the large scales (Faulkner et al. 2014; Rouget et al. 2015; Wan et al. 2016). However, some studies have indicated that environmental disturbances lead to decreasing plant and animal diversity, which can promote succession of plant invasion coupled with human made or natural disturbances due to a result of plant–human associations or novel evolutionary histories, for example, enemy release. Numerous ecoregions are threatened by environmental disturbances, and the biodiversity in ecoregions has decreased sharply (Hobbs and Huenneke 1992; Maron and Vilà 2001; Keane and Crawley 2002; Blumenthal 2006; MacDougall et al. 2009; Kalusová et al. 2013; Faulkner et al. 2014; Taylor et al. 2016). Hence, many ecoregions are vulnerable due to environmental disturbances on biodiversity within biomes. However, few studies have focused on the mechanisms affecting ecoregional vulnerability on the invasion of invasive alien plants (IAPs) to test environmental disturbance hypotheses for the mechanisms on plant invasion.

Invasion biologists used habitat suitability as an important indicator of plant invasion and assess the risk of plant invasion for prevention and control (Thuiller et al. 2005; Crall et al. 2013; Faulkner et al. 2014; Wan and Wang 2018). High habitat suitability of IAPs can result in the success of plant invasion (Allen and Bradley 2016; Horvitz et al. 2017; Hulme 2017; Slodowicz et al. 2018). For example, Crall et al. (2013) used habitat suitability modeling (HSM) to target IAP surveys, and a number of studies applied risk assessment and HSM to prioritize invasive species and invasion regions for prevention and control management in a changing climate. Thuiller et al. (2005) used HSM to predict the risk of plant invasions based on habitat suitability concept. Faulkner et al. (2014) applied HSM to develop a simple and rapid methodology for invasive species watch lists at ecoregional levels on a global scale. Hence, HSM can be used to model the habitat suitability of IAPs across different ecoregions on a global scale. Considering environmental disturbance effects on the invasion of IAPs, we could use habitat suitability as the indicator of plant invasion at ecoregional level. To test environmental disturbance hypotheses upon plant invasion, we explored the effects of ecoregional vulnerability on habitat suitability of IAPs over large scales.

We propose one hypothesis: whether ecoregional vulnerability can affect habitat suitability of IAPs over large scales. For testing this hypothesis, we addressed two scientific issues as follows: (1) whether ecoregional vulnerability can affect habitat suitability of IAPs across different biomes, and (2) which biomes and biogeographical realms have high habitat suitability for IAPs in vulnerable ecoregions? Here, we used the 13 IAPs with enough occurrence records in non-vulnerable and vulnerable ecoregions [identified by the study of Olson and Dinerstein (1998)] from the list of “100 of the World’s Worst Invasive Alien Species” established by the invasive species specialist group as the case studies. We modeled the habitat suitability of IAPs in invaded ranges at the global scale using HSM (i.e., Maxent modeling) based on species occurrence data and environmental variables. Then, we quantified the effect sizes to assess the effects of ecoregional vulnerability on the habitat suitability of IAPs across different biomes. Finally, we proposed effective suggestions for the prevention and control of plant invasion.

Materials and methods

Assessing ecoregional vulnerability

The vector maps of the ecoregions used were downloaded from http://www.worldwildlife.org including 13 biomes belonging to grasslands, shrublands, and forests and seven biogeographical realms. Detailed information on the ranges and locations is further described in Olson et al. (2001). The vulnerability degrees of ecoregions were based on the conservation statuses of ecoregions as described by Olson and Dinerstein (1998). Olson and Dinerstein (1998) provided an estimate of the current ability of an ecoregion to maintain viable species populations, to sustain ecological processes, and to be responsive to short- and long-term environmental changes for vulnerability assessment. Such estimation was based on landscape-level vulnerability features, such as total habitat loss and the degree of fragmentation and threat, and degree of protection for global ecoregions (Olson and Dinerstein 1998; Olson et al. 2001). Hence, we used ecoregional vulnerability as the indicator of environmental disturbance (Olson and Dinerstein 1998; Keane and Crawley 2002; Blumenthal 2006; MacDougall et al. 2009; Kalusová et al. 2013). In our study, the vulnerability degrees of ecoregions included: (1) critical or endangered, (2) vulnerable, and (3) relatively stable or intact, where the ecoregions with critical or endangered (1) and vulnerable (2) statuses were considered the vulnerable regions and the relatively stable or intact (3) regions were considered non-vulnerable (Olson and Dinerstein 1998).

Species occurrence data

Species occurrence data were obtained from Global Biodiversity Information Facility (GBIF; http://www.gbif.org accessed in March 18, 2018; download link information as shown in Supplementary material). The invasive species specialist group (ISSG) of IUCN compiled a list of "100 of the World's Worst Invasive Alien Species". We used 13 IAPs (detailed information as shown in Table 1) from this list as the most geographically and taxonomically representative set of the most dangerous IAPs around the world, causing significant impacts on biodiversity and/or human activity in all ecosystems (Luque et al. 2014). All extracted occurrence data were rasterized as presences at a resolution of 10.0-arc-minute cells (16.0 km at the equator) to reduce the effect of sampling bias and to avoid errors associated with georeferencing, obvious misidentifications, and duplicate records per grid cell (Jarnevich et al. 2015; Meyer et al. 2016). The distribution of presence cells of each IAPs is an estimate of the spatial distribution for each species (Meyer et al. 2016). We identified the invaded ranges of IAPs based on the ISSG information (http://www.issg.org/). In our study, we focused on habitat suitability of IAPs across different biomes on the basis of the invaded ranges.

Environmental variables

We used 10.0-arc-minute data for the environmental layers as input for the HSMs based on climate and soil factors (Wan et al. 2016). Nineteen climatic variables with 10.0-arc-minute spatial resolution were downloaded from the WorldClim database (http://www.worldclim.org). Averages from 1950 to 2000 were used for climatic variables. We downloaded nine soil variable data at a 0.5-arc-minute spatial resolution from http://soilgrids.org/. We used resampled analyses in ArcGIS 10.2 (Esri, RedLands, CA) to translate the 0.5-arc-minute into 10.0-arc-minutes for soil variables. Among all available environmental variables, we removed those with Pearson correlation coefficients > |0.7| to avoid multi-collinearity effects in the parameter estimates of HSMs. Finally, four climatic variables (i.e., annual mean temperature; temperature seasonality; annual precipitation; precipitation seasonality) and seven soil variables (i.e., bulk density in kg / cubic-meter; cation exchange capacity in cmolc/kg; soil texture fraction clay in percent; coarse fragments volumetric in percent; soil organic carbon stock in tonnes per ha; soil pH * 10 in H_2O; soil texture fraction silt in percent) were determined for the assessment on habitat suitability of IAPs. These environmental variables can influence the distribution and physiological performance of IAPs (Thuiller et al. 2005; Morán-Ordóñez et al. 2017; Wan et al. 2017).

Assessing habitat suitability of IAPs

We used Maxent modeling (i.e., a common HSM) to assess the habitat suitability of IAPs across different biomes based on species occurrence data and relevant environmental variables (Phillips et al. 2006; Elith et al. 2011). Maxent is widely used to identify areas critical to the maintenance of tree populations based on presence-only species data (Phillips et al. 2006; Elith et al. 2011). The Clolog output format gives each map cell a value of 0–1, with 0 representing the lowest habitat suitability of a species and 1 the highest (Phillips et al. 2017). We set the regularization multiplier (beta) to two to produce a smooth and a general response, modeling the data in a biologically realistic manner (Radosavljevic and Anderson 2014). The maximum number of background points was set to 10,000 (Merow et al. 2013). We used a fourfold cross-validation approach (75% and 25% of occurrence data for training and test running, respectively) to remove bias with respect to recorded occurrence points (Merow et al. 2013). Other settings were the same as suggested in Merow et al. (2013). The receiver operating characteristic (ROC) curves regarded each value of the prediction as a possible judging threshold. We assessed the Maxent model performance using the area under the ROC curve (AUC). The performance of HSMs with AUC values over 0.7 were considered good (Phillips et al. 2006).

Assessing effects of ecoregional vulnerability on habitat suitability of IAPs

First, we used the jackknife method to assess the contribution of environmental variables to habitat suitability of IAPs and extracted the habitat suitability of occurrence data for avoiding the over-estimation due to potential habitat suitability produced by Maxent modeling (Phillips et al. 2006). We considered the environmental variable to be important if

Table 1 Results of AUC and contribution of environmental variables to habitat suitability of invasive alien plants (IAPs)

Species	Record	Training AUC	Test AUC	Bio1	Bio4	Bio12	Bio15	BLD	CEC	CLYPPT	CRFVOL	OCSTHA	PHIHOX	SLTPPT
Ardisia elliptica	63	0.952	0.928	**13.832**	**58.944**	12.361	2.594	0.954	0.003	0.000	1.604	4.026	0.033	5.650
Caulerpa taxifolia	72	0.942	0.919	**24.345**	**52.152**	1.885	12.532	0.028	0.870	3.484	0.456	2.622	0.550	1.077
Chromolaena odorata	990	0.913	0.910	**23.145**	**53.160**	10.369	4.097	0.012	1.194	0.685	0.208	0.065	1.065	6.000
Cinchona pubescens	140	0.975	0.971	7.674	**86.961**	2.202	0.339	0.280	0.158	0.267	0.023	1.082	0.146	0.869
Clidemia hirta	740	0.936	0.933	**13.450**	**66.349**	2.431	10.092	0.549	0.349	0.129	0.661	0.613	4.092	1.285
Imperata cylindrica	2,255	0.864	0.862	**61.168**	**21.074**	6.022	5.426	0.904	0.168	1.070	0.911	0.221	1.577	1.461
Melaleuca quinquenervia	298	0.968	0.964	**35.195**	**37.969**	14.303	4.358	0.168	0.706	0.573	2.137	0.134	1.753	2.704
Miconia calvescens	241	0.952	0.946	7.730	**77.633**	1.758	5.196	0.056	0.853	0.378	0.218	1.213	0.719	4.246
Mikania micrantha	735	0.932	0.930	**20.926**	**51.668**	14.490	5.152	0.006	0.394	0.048	0.019	0.923	0.802	5.573
Mimosa pigra	890	0.898	0.893	**37.038**	**51.031**	3.404	1.598	0.117	1.029	0.751	0.632	0.122	2.163	2.115
Prosopis glandulosa	650	0.958	0.957	**54.327**	**27.424**	8.433	0.522	5.699	1.380	0.303	0.325	0.055	0.872	0.660
Rubus ellipticus	103	0.980	0.974	**22.121**	**56.427**	3.337	2.698	0.126	0.781	0.293	0.668	2.688	8.665	2.198
Tamarix ramosissima	429	0.939	0.934	**34.428**	**32.503**	**18.077**	2.307	3.629	2.531	3.375	0.032	0.043	0.244	2.831

Record: the number of occurrence records; Bio1: annual mean temperature; Bio4: temperature seasonality (standard deviation *100); Bio12: annual precipitation; Bio15: precipitation seasonality (coefficient of variation). BLD: bulk density in kg / cubic-meter; CEC: cation exchange capacity in cmolc/kg; CLYPPT: soil texture fraction clay in percent; CRFVOL: coarse fragments volumetric in percent; OCSTHA: soil organic carbon stock in tonnes per ha; PHIHOX: soil pH * 10 in H_2O; SLTPPT: soil texture fraction silt in percent. Bold values represent the environmental variables with large contributions to habitat suitability of IAPs its contribution was at least 15% of the models for each IAP (Oke and Thompson 2015).

Then, we used independent-samples *t* tests to compare the mean habitat suitability of IAPs between the vulnerable and non-vulnerable biomes based on all and each species, respectively. We quantified the effects of ecoregional vulnerability on habitat suitability of IAPs as the effect sizes using the log response ratio of habitat suitability. For each IAP and biome, we computed the log response ratio of habitat suitability as: $\mathrm{RR} = \ln(Y_\mathrm{v}/Y_\mathrm{n})$, where RR is the log response ratio of mean habitat suitability based on an IAP or biome, and Y_v and Y_n are the mean habitat suitability of IAPs for one specific species based on the vulnerable and non-vulnerable biomes, respectively (Hedges et al. 1999; Strauss et al. 2008). We weighted RR by sample size using the following equation: $N_\mathrm{v} \times N_\mathrm{n}/(N_\mathrm{v} + N_\mathrm{n})$, where N_v and N_n are the number of occurrence records based on the vulnerable and non-vulnerable biomes, respectively (Hedges et al. 1999; Strauss et al. 2008).

Finally, we computed distribution areas (i.e., the number of occurrence records) and mean habitat suitability of IAPs in vulnerable ecoregions based on 14 biomes and seven biogeographical realms.

Results

Our modelings performed well because all the AUC values were over 0.900 (Table 1). Temperature had a larger contribution to habitat suitability for IAPs than precipitation and soil (Table 1). Annual mean temperature and temperature seasonality were the most important environmental variables for habitat suitability of IAPs (Table 1). Annual precipitation was the environmental variable for habitat suitability of *Tamarix ramosissima* (Table 1). *T. ramosissima* and *Melaleuca quinquenervia* had the highest habitat suitability in non-vulnerable and vulnerable ecoregions, respectively (Table 2).

We found that ecoregional vulnerability had significant effects on habitat suitability of IAPs in invasive ranges across different biomes and biogeographical realms worldwide ($P < 0.05$; Table 2). The habitat suitability of *Chromolaena odorata, Clidemia hirta, Imperata cylindrica, M. quinquenervia, Mikania micrantha, Prosopis glandulosa, Rubus ellipticus*, and *T. ramosissima* could be significantly affected by ecoregional vulnerability ($P < 0.05$; Table 2). Ecoregional vulnerability could have significantly negative effects on the habitat suitability of *P. glandulosa* ($P < 0.05$), and the habitat suitability of the other abovementioned IAPs was positively affected ($P < 0.05$; Table 2). Ecoregional vulnerability had the largest contribution to the habitat suitability of *I. cylindrica* and *M. quinquenervia* (Table 2). Although ecoregional vulnerability had no significant effects on the habitat suitability of *Ardisia elliptica, Caulerpa taxifolia, Miconia calvescens*, and *Mimosa pigra*, the habitat suitability of these four IAPs was very high in vulnerable ecoregions (Table 2).

The vulnerable ecoregions of tropical and subtropical moist broadleaf forests and temperate broadleaf and mixed forests could result in large distribution areas and the highest habitat suitability of IAPs (Fig. 1a). Although the habitat suitability of IAPs was relatively lower in the vulnerable ecoregions of tropical and subtropical grasslands, savannas

Table 2 Effect sizes of ecoregional vulnerability on habitat suitability of invasive alien plants (IAPs)

Species	Non-vulnerable		Vulnerable		Effect size	F	P values
	Mean	Count	Mean	Count			
Ardisia elliptica	0.640	12	0.736	47	1.345	1.598	0.211
Caulerpa taxifolia	0.825	2	0.620	29	− 0.535	0.716	0.405
Chromolaena odorata	0.543	61	0.673	920	12.237	22.392	< 0.0001
Cinchona pubescens	0.698	21	0.719	118	0.520	0.067	0.797
Clidemia hirta	0.646	126	0.685	601	6.071	4.217	0.040
Imperata cylindrica	0.498	179	0.691	2,002	53.786	144.984	< 0.0001
Melaleuca quinquenervia	0.494	43	0.792	229	17.123	49.977	< 0.0001
Miconia calvescens	0.737	31	0.695	209	− 1.594	0.791	0.375
Mikania micrantha	0.536	42	0.680	683	9.427	15.407	< 0.0001
Mimosa pigra	0.625	85	0.667	791	5.041	3.560	0.060
Prosopis glandulosa	0.730	129	0.678	516	− 7.571	5.143	0.024
Rubus ellipticus	0.671	7	0.765	94	0.852	0.803	0.372
Tamarix ramosissima	0.832	120	0.633	295	− 23.409	55.714	< 0.0001

Mean: mean habitat suitability of IAPs in non-vulnerable and vulnerable ecoregions; Count: distribution areas (i.e., the number of occurrence records) of IAPs in non-vulnerable and vulnerable ecoregions; Effect size: the log response ratio of mean habitat suitability based on non-vulnerable and vulnerable ecoregions across different IAPs. Bold values represent the significant differences of habitat suitability between non-vulnerable and vulnerable ecoregions for IAPs

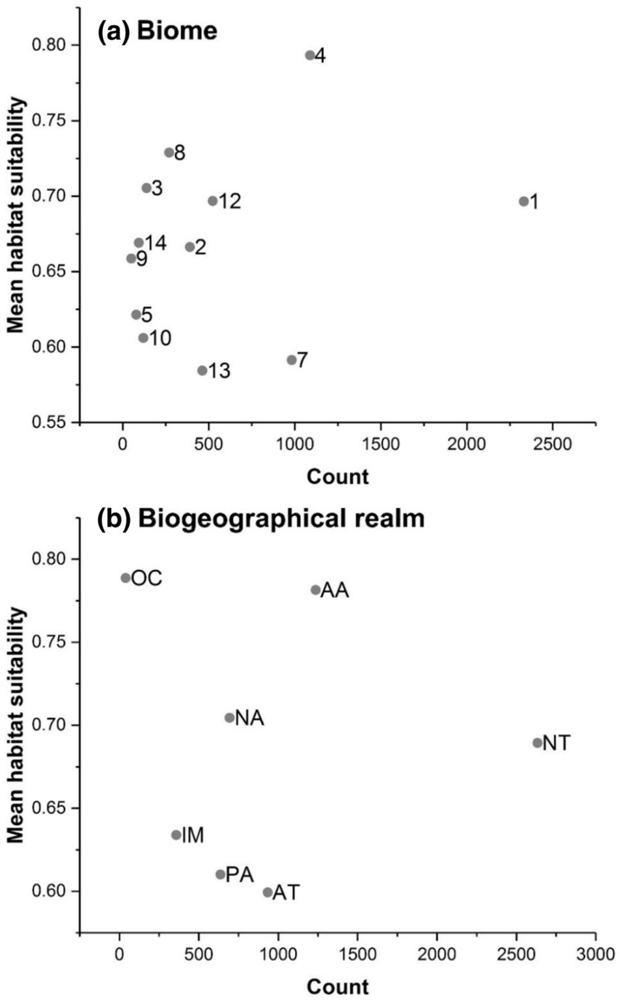

Fig. 1 Distribution areas and mean habitat suitability of invasive alien plants (IAPs) in vulnerable ecoregions based on different biomes (**a**) and biogeographical realms (**b**). Mean habitat suitability: mean habitat suitability of IAPs in each vulnerable ecoregion and biogeographical realm; Count: distribution areas (i.e., the number of occurrence records) of IAPs in each vulnerable ecoregion and biogeographical realm. Biome codes: 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; 12: mediterranean forests, woodlands and scrub; 13: deserts and xeric shrublands; 14: mangroves. biogeographical realm codes: *AA* Australasia, *AT* Afrotropics, *IM* IndoMalay, *NA* Nearctic, *NT* Neotropics, *OC* Oceania, *PA* Palearctic

and shrublands compared with the other biomes, the distribution areas were extremely large for IAPs (Fig. 1a). The distribution areas of IAPs were very small in vulnerable ecoregions of temperate grasslands, savannas and shrublands, but the habitat suitability of IAPs was higher in the vulnerable ecoregions than the other biomes, except for temperate broadleaf and mixed forests (Fig. 1a). These vulnerable ecoregions with high habitat suitability of IAPs were distributed in the biogeographical realms of Australasia, Nearctic, Neotropics, and Oceania (Fig. 1b). The vulnerable ecoregions of the Neotropics realm included the largest distribution areas of IAPs, and the Oceania realm had the highest habitat suitability for IAPs (Fig. 1b).

Discussion

Vulnerable areas and low biological diversity can promote the colonization and expansion of IAPs across different spatial scales (Naeem et al. 2000; Kennedy et al. 2002; Stohlgren et al. 2003; Fargione and Tilman 2005; Liao et al. 2015). Numerous ecoregions were vulnerable due to decreasing biological diversity and intensive human activities (Olson and Dinerstein 1998; Olson et al. 2001). Our findings indicated that ecoregional vulnerability had significant effects on habitat suitability of IAPs in invasive ranges and the habitat suitability of IAPs was extremely high across different biomes worldwide (Table 2; Fig. 1). Therefore, ecoregional vulnerability can drive IAPs into non-native ranges. Such effects of ecoregional vulnerability on habitat suitability of IAPs could vary with the changes of biomes and biogeographical realms. Hence, our study provides new insight into the prevention and control of plant invasion to better understand the dynamics of IAP expansion in vulnerable ecoregions at the global scale.

The mechanism of plant invasion success is a fundamental issue of invasion ecology (Richardson et al. 2000). We tested the effects of ecoregional vulnerability on habitat suitability for 13 IAPs and found that the habitat suitability of eight species including *C. odorata, C. hirta, I. cylindrica, M. quinquenervia, M. micrantha, P. glandulosa, R. ellipticus*, and *T. ramosissima* could be significantly affected by ecoregional vulnerability ($P < 0.05$; Table 2). This result supported the hypotheses that ecoregional vulnerability could lead to plant invasion in non-native ranges. Previous studies have shown that habitat disturbance and low biological diversity are the main drivers of plant invasion around the world (Hobbs and Huenneke 1992; Naeem et al. 2000; Stohlgren et al. 2003; Fargione and Tilman 2005). The intermediate disturbance hypothesis has shown that moderate levels of disturbance have been suggested to promote invasive plant richness by preventing competitive exclusion (Hobbs and Huenneke 1992; Kennedy et al. 2002; Roxburgh et al. 2004; Liao et al. 2015). Furthermore, some hypotheses have shown that lower species diversity favors plant invasions (Stohlgren et al. 2003; Roxburgh et al. 2004). The response of IAPs to disturbance and low biological diversity is stronger at smaller spatial scales than at larger scales (Hobbs and Huenneke 1992; Shea et al. 2004; Leishman et al. 2007). Our study showed that ecoregional vulnerability could affect habitat suitability of IAPs; therefore, new evidence is provided for hypotheses on the response of IAPs to disturbance and low biological diversity over large scales.

Ecoregions are defined as relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use changes over large scales (Olson and Dinerstein 1998; Olson et al. 2001). Large blocks of natural habitat, where species populations and ecological processes still fluctuate within their natural range of variation, are rapidly disappearing around the vulnerable ecoregions at the global scale (Olson and Dinerstein 1998; Olson et al. 2001; Hoekstra et al. 2005). Hence, the conditions of vulnerable ecoregions are consistent with the hypotheses on intermediate disturbance and low biological diversity on plant invasion, and promote plant invasion in non-native ranges. For example, *I. cylindrica* is an IAP that threatens diversity and forest productivity in terrestrial ecosystems (Otsamo 2000). The disturbance from cutover sites, minimum tillage cropping systems, reclaimed mined areas, and roadsides may promote *I. cylindrical* to establish rapidly in new habitats (Jose et al. 2002). Such areas with similar disturbance types exist widely in vulnerable ecoregions, which has a large potential to support plant invasion over large scales (Olson and Dinerstein 1998; Olson et al. 2001).

Our finding is that the effects of ecoregional vulnerability on habitat suitability of IAPs may vary with changes of biomes and biogeographical realms (Fig. 1). At the global scale, various biomes and biogeographical realms may face different disturbance levels and biological diversities (Olson and Dinerstein 1998; Olson et al. 2001; Hoekstra et al. 2005). We found that the vulnerable ecoregions of tropical and subtropical moist broadleaf forests and temperate broadleaf and mixed forests could result in large areas of distributions and the highest habitat suitability of IAPs indicating that the changes of disturbances and biological diversity could result in plant invasion (Olson and Dinerstein 1998).

The composition of tropical and subtropical moist broadleaf forests is dominated by semi-evergreen and evergreen deciduous trees (Olson and Dinerstein 1998; Olson et al. 2001). Disturbances, such as plowing, overgrazing, and excessive burning, lead to fragile habitats and low diversity for semi-evergreen, evergreen, and deciduous trees. *C. odorata* has a large ability to compete with native plants in environmental disturbance conditions of tropical and subtropical forests (De Rouw 1991; Goodall and Erasmus 1996). It can spread rapidly in degradation forests of South Africa, and threaten native vegetation (Goodall and Erasmus 1996). Temperate broadleaf and mixed forests also have large areas of habitat fragmentations, and many understory forest species are also unable to cross deforested areas (Olson and Dinerstein 1998; Bengtsson et al. 2000; Olson et al. 2001; Myers et al. 2015; Thom and Seidl 2016). Temperate grasslands, savannas and shrublands ecoregions have relatively low species richness, and are sensitive to disturbances, for instance, excessive burning or fire suppression, loss and degradation of riparian or gallery forest habitats and water sources, and overgrazing (Olson and Dinerstein 1998; Thom and Seidl 2016). Simmons et al. (2008) showed that *P. glandulosa* could affect the belowground herbaceous layer by changing water, nutrients and microclimate in temperate savanna. Habitat fragmentations and disturbances can enhance such change in biomes of savannas (Carvalho et al. 2009). Hence, *P. glandulosa* may have a negative effect on native species diversity of plant community in temperate broadleaf and mixed forests and temperate grasslands, savannas and shrublands. Hence, the habitat suitability of IAPs was highest in the vulnerable ecoregions of temperate grasslands, savannas and shrublands. Based on the hypotheses on intermediate disturbance and low biological diversity on plant invasion, IAPs can expand widely, and have extensive and significant impacts on native communities in vulnerable ecoregions (e.g., tropical and subtropical moist broadleaf forests, temperate broadleaf and mixed forests, and temperate grasslands, savannas and shrublands; Hobbs and Huenneke 1992; Olson and Dinerstein 1998; Naeem et al. 2000; Stohlgren et al. 2003; Fargione and Tilman 2005).

Furthermore, the vulnerable ecoregions with high habitat suitability of IAPs were mainly distributed in the biogeographical realms of Australasia, Nearctic, Neotropics, and Oceania (Fig. 1). Previous studies have shown that the climatic conservatism of IAPs between native and invasive ranges can drive plant invasion around the world (Petitpierre et al. 2012). We found that temperature was the main climatic variable of habitat suitability of IAPs (Table 1). Therefore, in the biogeographical realms of Australasia, Nearctic, Neotropics, and Oceania, combined with high disturbances and relatively low biological diversity in vulnerable ecoregions, IAPs can expand widely and invade into non-native regions due to the temperature conservatism of IAPs between native and invasive ranges (Petitpierre et al. 2012; Faulkner et al. 2014; Rouget et al. 2015). Once we understand the effects of ecoregional vulnerability on habitat suitability of IAPs, prevention and control measures could be proposed for plant invasion as follows: (1) using ecoregional vulnerability as the monitoring indicators of prevention and control of plant invasion (van Wilgen et al. 2008; Faulkner et al. 2014; Wan et al. 2018); (2) monitoring the disturbances from the small to large scales (Olson and Dinerstein 1998; Myers et al. 2015); and (3) listing the key risk biomes (e.g., tropical and subtropical moist broadleaf forests and temperate broadleaf and mixed forests) and biogeographical realms (e.g., Australasia, Nearctic, Neotropics, and Oceania; van Wilgen et al. 2008; Faulkner et al. 2014).

Abundant experimental and field evidence indicates disturbances and low biological diversity can affect habitat suitability of IAPs, resulting in plant invasion at small scales in non-native ranges (Naeem et al. 2000; Kennedy et al. 2002; Stohlgren et al. 2003; Fargione and Tilman 2005; Liao et al. 2015; Myers et al. 2015). Our study tested a new hypothesis on disturbances and biological diversity based on vulnerable ecoregions at the large scale using 13 species distributed worldwide. We found strong support for the hypothesis that ecoregional vulnerability can increase habitat suitability of IAPs and promote IAPs to expand in invasive ranges. The effects of ecoregional vulnerability on habitat suitability of IAPs may depend on the biomes and biogeographical realms of interest. Hence, our study promotes the development of new hypotheses on plant invasion based on disturbances and low biological diversity across different scales.

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