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ORIGINAL ARTICLE

Risk hotspots for terrestrial plant invaders under climate change at the global scale

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Abstract Terrestrial plant invaders (TPIs) have a large potential to threaten plant diversity under climate change. To prevent the spread of TPIs under climate change, we must identify the risk hotspots for TPIs. However, the risk hotspots for TPIs have not yet been explicitly addressed at the global scale under climate change. Here, we selected 336 TPIs from the Invasive Species Specialist Group list and used species distribution modelling and Hot Spot Analysis to map the risk hotspots of TPIs based on the terrestrial ecoregions in the current, low and high gas concentration scenarios. The risk hotspots of TPIs were mainly distributed in South America, Europe, Australia, New Zealand and northern and southern Africa. Climate change may decrease the areas of hotspots that allow for TPI expansion, but the potential distribution probabilities of TPIs may increase in the high concentration scenario. Furthermore, TPIs, particularly herbaceous and woody ones, might still expand into critical or endangered ecoregions of these risk hotspots in the current, low and high concentration scenarios. We also need to focus on the impact of TPI expansion on both vulnerable and relatively stable ecoregions due to the increasing potential distribution probabilities of TPIs in risk hotspots and should integrate climate change into the risk assessment of plant invasion in the vulnerable and relatively stable ecoregions.

Keywords Plant invasion · Climatic change · GIS · Risk hotpot · Maxent modelling · Ecoregion · Hot Spot Analysis

Ji-Zhong Wan and Chun-Jing Wang have contributed equally to this work.

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Introduction

Terrestrial plant invaders (TPIs) pose an increasing threat to global biodiversity under climate change (Kalusová et al. 2013; Bellard et al. 2014). Climate change can promote the spread of TPIs into new habitats, increase the competitiveness of invasive plants relative to native species, alter ecosystem function and threaten native plant diversity (Hellmann et al. 2008; Richardson and Rejmánek 2011; Bai et al. 2013). However, the relationship between TPIs and climate change is complex (Hellmann et al. 2008). Varying patterns of climate change may result in different distributions of species at regional scales and even promote TPIs to expand widely over large geographic areas (Bradley 2010, 2012). Increases in the expansion of TPIs can enhance their chances of becoming established and naturalized under climate change (Thuiller et al. 2005; Wilson et al. 2009; Kalusová et al. 2013; Donaldson et al. 2014). Therefore, the definition of expansion ranges of TPIs under climate change plays an important role in the risk assessment of plant invasion at the geographic scale.

Ecologists often use species distribution models (SDMs) to project the overall geographic pattern of invasive plant species worldwide under a changing climate (Václavík and Meentemeyer 2009; Vicente et al. 2013). Some studies have also identified risk hotspots for invasive alien plants under climate change at the regional scale using SDMs (O'Donnell et al. 2012; Liang et al. 2014; Adhikari et al. 2015).

Furthermore, the definition of risk hotspots of plant invasion is useful and urgent for prioritization and management of TPIs (Adhikari et al. 2015). With the rapid development of global trade and the potential for explosive range expansion, climate change may promote the risk of TPI invasion at the global scale (Hellmann et al. 2008; Seebens et al. 2015). For example, global climate change promotes some TPIs from the USA to a range of new invasive species, including many from tropical and semi-arid Africa as well as the Middle East (Bradley et al. 2010a). Therefore, the question of how to determine the risk hotspots of TPIs at the global scale is becoming extremely relevant for the prevention and control of plant invasion.

Thuiller et al. (2005) suggested that SDMs could be used as a tool for predicting the risk of TPIs at a global scale based on global ecoregions. Ecoregions are designed to help users visualize and understand similarities across complex multi-variate environmental factors by grouping areas into similar categories (Olson et al. 2001). Climate change would provide potentially suitable areas for TPIs in ecoregions, which could promote TPIs to damage global ecosystems under climate change (Thuiller et al. 2005; O'Donnell et al. 2012; Bellard et al. 2013; Adhikari et al. 2015). For example, South African ecoregions would be invaded by TPIs under climate change (Donaldson et al. 2014). Hence, assessing the spread risk of TPIs at the ecoregion scale is important for the conservation of species diversity (Duursma et al. 2013; Adhikari et al. 2015). In this study, the ecoregions were integrated into the risk assessment of TPIs. Liang et al. (2014) suggested that the use of Hot Spot Analysis in the geographic information system (GIS) on defining risk hotspots of TPIs can facilitate invasive species risk assessment and improve the effectiveness of SDMs on the risk of plant invasion. Here, SDMs and Hot Spot Analysis in GIS were used to map the risk hotspots of TPIs based on the terrestrial ecoregions at the global scale.

In this study, 336 TPIs were selected from the Invasive Species Specialist Group (ISSG; http://www.issg.org/database/species/List.asp) list and Maxent was used to model the potential distributions of these 336 TPIs at the global scale. Then, Hot Spot Analysis was used to model the risk hotspots for TPIs as affected by climate change based on ecoregions at the global scale (Thuiller et al. 2005). Finally, some effective suggestions were proposed for conservation management.

Materials and methods

Ecoregion data

Ecoregions include basic characteristics, such as the stability of ecological function, long-term persistence of species composition and the consistent ecological dynamics of species; they contain a variety of ecosystems (Olson and Dinerstein 1998; Olson et al. 2001). Terrestrial ecoregions were defined based on the ecoregions of the World Wide Fund for Nature (WWF). These ecoregions include 867 distinct units within three degrees of protection for species diversity and their natural habitats [i.e. critical or endangered (CE), vulnerable (VU) and relatively stable or intact (RI)] based on a previous 30-year prediction of future conservation status given the current conservation status and trajectories (http://www.worldwildlife.org/biomes; Olson et al. 2001; Figure S1).

Bioclimatic data

Nineteen bioclimatic variables with 10-arc-minute spatial resolution were used for the environmental input layers of the SDM and as future bioclimatic variables. Data were downloaded from the WorldClim database (averages from 1950 to 2000 were used as current bioclimatic variables; http://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world). A Pearson correlation analysis was used to test the multi-collinearity among predictor variables. Among the highly cross-correlated variables (Pearson correlation coefficient $r > 0.9$ or < -0.9, $P < 0.05$), only one was selected for eliminating multi-collinearity effects in the estimates of parameters in the species distribution models (Merow et al. 2013; Fourcade et al. 2014). The remaining nine bioclimatic variables influence the habitat suitability of TPIs (Table S1; Gallagher et al. 2013). We relied on data from the Intergovernmental Panel on Climate Change's (IPCC) Fifth Assessment Report (AR5) as a reference for modelling the changing trends of TPI invasion (http://www.ipcc.ch/).

To model the future potential distribution of TPIs in the 2080 s (2071–2099), we used an average map of four global climate models (GCMs; i.e. bcc_csm1_1, csiro_mk3_6_0, gfdl.cm3 and mohc_hadgem2_es) and two greenhouse gas emission scenarios, the Representative Concentration Pathways (RCPs) 4.5 (mean 780 ppm; range 595–1005 by 2100) and 8.5 (mean 1685 ppm; range 1415–1910 by 2100), representing the low and high gas concentration scenarios, respectively (IPCC Fifth Assessment Report 2013; http://www.ccafs-climate.org/). The two scenarios predict different climatic changes due to differences in projected concentrations of greenhouse gases and other pollutants (http://www.ipcc.ch/).

Species data

We used 336 TPIs from the Invasive Species Specialist Group (ISSG) list from IUCN (http://www.issg.org/database/species/List.asp) to serve as a representative set of

TPIs with a high potential to invade habitats around the world (Table S2). These TPIs share the following characteristics: (1) imposing a significantly negative impact on plant diversity; (2) threatening a variety of ecosystems; (3) illustrating important issues on plant invasions, and (4) general functional traits that promote plant invasion and detailed records of invading non-native regions worldwide (http://www.issg.org/database/species/List.asp). Occurrence data, especially geographic coordinates, for each TPI were obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org; García-Roselló et al. 2014), the largest online provider of distribution records. We removed duplicate occurrences of recorded data for species in 10.0-arc-minute grid cells (16 km at the equator) to avoid any georeferencing errors (Merow et al. 2013). Previous studies have shown that using species with more than 100 records as input for SDMs decrease the negative effect of sampling bias on their performance (Wisz et al. 2008; Fourcade et al. 2014; García-Roselló et al. 2014). We examined enough occurrence records of TPIs to cover the present distributions of species as given in data from ISSG. (http://www.issg.org/database/species/List.asp; Bellard et al. 2014). The selected record number of each species was over 100. These TPIs included 142 woody plants, 151 herbaceous plants and 43 vines (Table S2).

Modelling potential distributions of TPIs

Maxent was used to model the potential distribution for each TPI from current presence-only species records and current, low and high gas concentration scenarios (Merow et al. 2013; Fourcade et al. 2014). The set of all pixels were regarded as the possible distribution space of maximum entropy. For the map cells predicted using Maxent, pixels with values of 1 had the highest degree of potential distribution probability and pixels with values of 0 had the lowest (Elith et al. 2011).

As suggested by Merow et al. (2013), the modelling sets were as follows: (1) the regularization multiplier (beta) was set to 1.5 to produce a smooth and general response that could be modelled in a biologically realistic manner (Saupe et al. 2014); (2) a tenfold cross-validation approach was used to remove bias due to recorded occurrence points (Merow et al. 2013); (3) the maximum number of background points was set to 10,000 (Merow et al. 2013); (4) the output format was logistic (Merow et al. 2013); and (5) all other settings were the same as described in Elith et al. (2011).

We evaluated the predictive precision of Maxent using the area under the curve (AUC) of the receiver operation characteristic (ROC) that regards each value of the prediction result as a possible threshold and then obtained the corresponding sensitivity and specificity through calculations. The area under the curve ranges from 0.5 (lowest predictive ability or not different from a randomly selected predictive distribution) to 1 (highest predictive ability). Models of each species with values above 0.7 were considered useful in our study. The AUC values of all of the 336 species were over 0.7, indicating a useful model performance (Hijmans 2012; Table S2). These 336 TPIs were also distributed worldwide based on the occurrence records.

Identifying the risk hotspots for TPIs

First, the map of each TPI potential distribution (originally at 16-km grid cell size; 10-arc-minute) was downscaled to 4.3-km grid cell size (2.5-arc-minute). If a species occurred in a 16-km grid cell, it was assumed to occur in each of the respective 4.3-km grid cell that had a suitable climate; otherwise, it was absent (Araújo et al. 2011). Then, we combined the Maxent results of all the TPIs to produce the maps of potential distribution of TPIs in the current, low and high concentration scenarios based on all the species and the plant types such as woody plants, herbaceous plants and vines, respectively (Figure S2).

Secondly, we calculated the potential distribution probabilities of all TPIs based on all the species in the ecoregions as follows (Alagador et al. 2011; Calabrese et al. 2014):

$$S_t = \sum_{j=1}^{n} X_j Y_j$$

where S_t is the potential distribution probabilities of TPIs in the ecoregion t; n is the total number of distribution pixels; X_j is an indicator of the potential distribution probabilities of TPIs in the pixel j of ecoregion t; and Y_j is the area percentage of the pixel j on the all the pixels of ecoregion t.

Next, we employed Optimizing Hot Spot Analysis using the false discovery rate to compute the regional risk hotspots of TPIs for ecoregions around the world (http://resources.arcgis.com/en/help/main/10.2/; Liang et al. 2014). Optimizing Hot Spot Analysis is a cluster analysis tool that, by computing the Getis-Ord Gi statistic, allows for the determination of the clusters of features with high values or features with low values based on global ecoregions (Liang et al. 2014). Optimizing Hot Spot Analysis was used to predict the current and future risk hotspots of TPIs for ecoregions based on the spatial correlation between the potential distribution probabilities of multiple TPIs in the ecoregions (http://resources.arcgis.com/en/help/main/10.2/; Liang et al. 2014). Thus, TPIs may have the ability to expand among the ecoregions at the global scale (based on the spatial correlation between the potential distribution probabilities of TPIs in the global ecoregions). In other words, the expansion pathways could be assessed by Optimizing Hot Spot Analysis (Liang et al. 2014). We calculated the potential distribution probabilities of TPIs based on the areas of risk hotspots of TPIs and the ecoregions belonging to the three protection degrees as described in Olson et al. (2001) in risk hotspots in the current, low and high concentration scenarios (Alagador et al. 2011; Calabrese et al. 2014):

$$C = \sum_{i=1}^{n} A_i B_i$$

where C is the potential distribution probabilities of TPIs in the risk hotspot areas in the current, low and high concentration scenarios; A_i is an indicator of the potential distribution probabilities of TPIs in the pixel i of the risk hotspot areas; B_i is the area percentage of the pixel i on all the pixels of risk hotspots of TPIs in the current, low and high concentration scenarios and of the ecoregions belonging to three protection degrees; and n is the total number of distribution pixels in the risk hotspot areas.

Finally, the following equation was used to compute the change in the potential distribution probabilities of TPIs based on the risk hotspot areas of TPIs and of the ecoregions belonging to the three protection degrees described by Olson et al. (2001) in the low and high concentration scenarios:

$$P = \frac{C_{\mathrm{Future}} - C_{\mathrm{Current}}}{C_{\mathrm{Current}}}$$

where P represents the change in the potential distribution probabilities of TPIs in the low or high concentration scenario, and C_{Future} and C_{Current} are the future and current potential distribution probabilities of TPIs, respectively.

Results

All of the climatic niche models had AUC values greater than 0.7 for both the training data sets, indicating that each model was accurate based on the 0.7 cut-off described in materials and methods (Table S2). The areas of risk hotspots of TPIs would decrease with increasing gas concentration at the global ecoregion scale. However, the potential distribution probabilities of all the TPIs would increase in the high concentration scenario (current: 106.294; low: 94.380; high: 136.280; Table 1). The risk hotspots of TPIs were mainly distributed in South America, Europe, Australia, New Zealand and northern and southern Africa in the current concentration scenario (Fig. 1). The areas of risk hotspots would decrease in South America, Australia and Africa and increase in northern Europe in the low concentration scenario (Fig. 1). The risk hotspots were distributed mainly in Europe, south-western Australia, New Zealand and Madagascar in the high concentration scenario (Fig. 1).

The risk hotspots of TPIs (based on all the species and plant types such as woody plants, herbaceous plants and vines) occurred mainly in the ecoregions of CE in the current, low and high concentration scenarios (the potential distribution probabilities of all the TPIs: current: 54.297; low: 48.962; high: 45.101; Table 1). The potential distribution probabilities of herbaceous TPIs were the largest for the risk hotspots of TPIs based on the ecoregions of CE in the current, low and high concentration scenarios (current: 28.900; low: 27.266; high: 24.534; Table 1). The potential distribution probabilities of vine TPIs for the ecoregions of CE were the lowest in the current, low and high concentration scenarios (current: 5.678; low: 4.469; high: 4.310; Table 1).

The potential distribution probabilities of TPIs would decrease in risk hotspots of TPIs in the ecoregions of CE, VU and RI in the low concentration scenario (Table 1) and would also decrease in the ecoregions of CE in the high concentration scenario (Table 1). However, they would increase in the ecoregions of VU and RI in the high concentration scenario (Table 1). The increasing trends of potential distribution probabilities of herbaceous TPIs were the largest in the ecoregions of VU and RI in the high concentration scenario (VU: +108.6 %; RI: +146.4 %; Table 1).

Discussion

Maps of risk hotspots of TPIs were produced at the global scale based on the plant types and the ecoregions using SDMs and Hot Spot Analysis in GIS. The potential distribution probabilities of TPIs would increase in the ecoregions that fall in risk hotspots in the high concentration scenario. TPIs, particularly herbaceous and woody plants, might still expand in the critical or endangered ecoregions of the risk hotspots in Europe, south-western Australia, New Zealand and Madagascar. However, overall the areas of risk hotspots of TPIs would decrease.

Some studies have shown that climate change would increase plant invasion at the global scale (Hellmann et al. 2008; Bradley et al. 2012; Seebens et al. 2015), but others have not found such an impact (Bellard et al. 2013, 2014; Gallagher et al. 2013). We found that, although TPIs may expand widely in South America, Europe, Australia, New Zealand and northern and southern Africa in the present days, the areas of TPI expansion would decrease in the future. Hence, climate change may not promote the TPI expansion at the global scale based on the decreasing areas

Table 1 Potential distribution probabilities of terrestrial plant invaders (TPIs) in risk hotspots under climate change

Types	Status	Current (probabilities)	Low (probabilities)	High (probabilities)	Change low (%)	Change high (%)
All	CE	54.297	48.962	45.101	−9.8	−16.9
	VU	22.788	21.682	39.195	−4.9	72.0
	RI	29.209	23.736	51.984	−18.7	78.0
Woody	CE	19.719	17.226	16.257	−12.6	−17.6
	VU	9.152	8.426	12.855	−7.9	40.5
	RI	12.827	9.894	15.990	−22.9	24.7
Herbaceous	CE	28.900	27.266	24.534	−5.7	−15.1
	VU	10.914	10.850	22.769	−0.6	108.6
	RI	12.262	10.658	30.216	−13.1	146.4
Vine	CE	5.678	4.469	4.310	−21.3	−24.1
	VU	2.722	2.406	3.570	−11.6	31.2
	RI	4.120	3.185	5.778	−22.7	40.2

Current, low and high represent the potential distribution probabilities of TPIs in risk hotspots in the current, low and high concentration scenarios, respectively. Change low and Change high represent the changes in the potential distribution probabilities of TPIs in risk hotspots in the low and high concentration scenarios, respectively

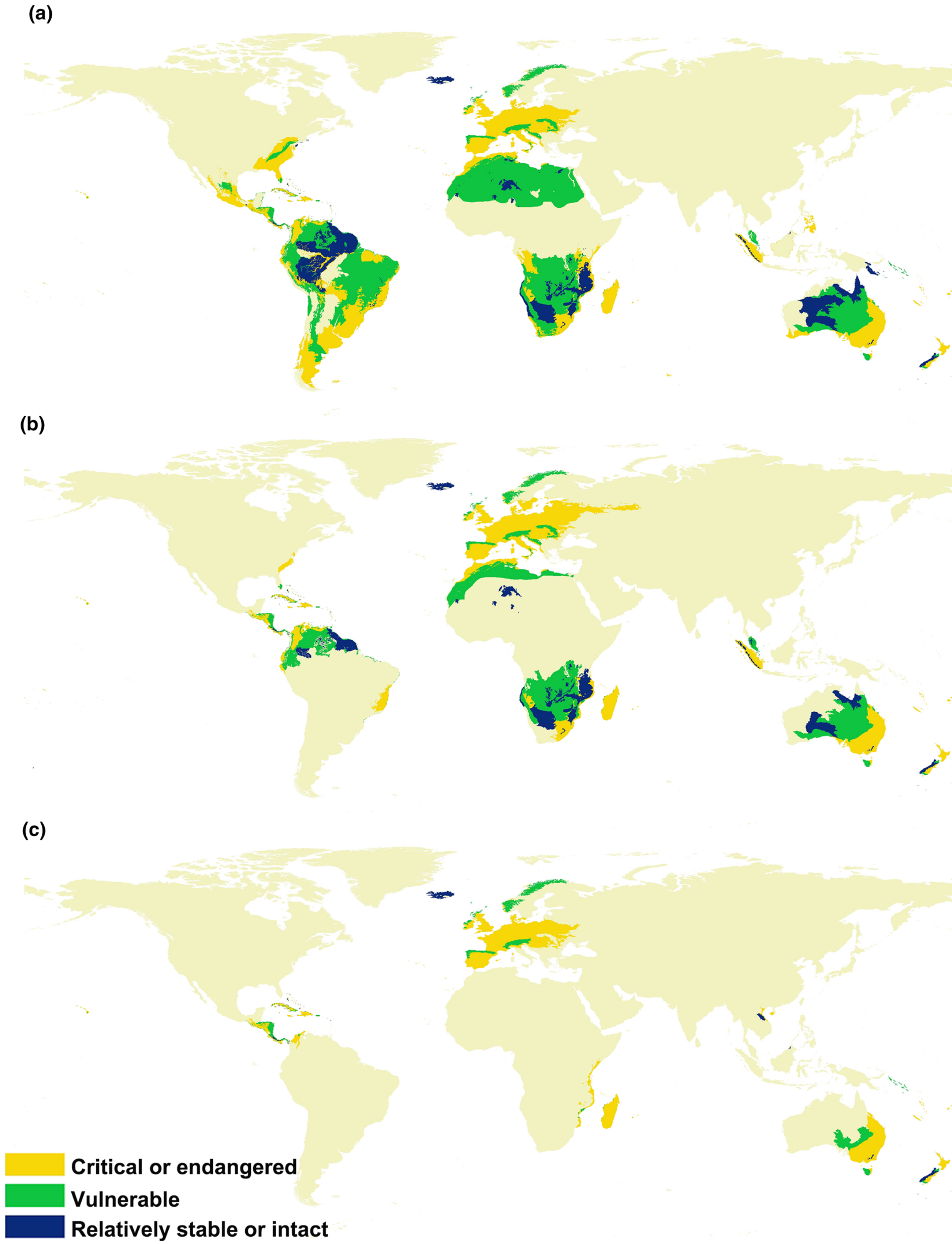
CE critical or endangered, *VU* vulnerable, *RI* relatively stable or intact

of risk hotspots for TPIs. However, the expansion potential of TPIs would be concentrated in the ecoregions of risk hotspots in Europe, south-western Australia, New Zealand and Madagascar under climate change (particularly, in the high concentration scenario; Table 1 and Fig. 1). To address and prevent these issues in the future, we suggest that Fig. 1 is regarded as the reference for global prevention and control of plant invasion.

TPIs are likely to expand in the CE ecoregions, particularly in Europe in the current, low and high concentration scenarios due to a high spreading ability (Fig. 1; Table 1). These ecoregions included rich plant diversity and threatened or endangered vascular plant species (Olson and Dinerstein 1998; Olson et al. 2001; Gorenflo et al. 2012). However, the plant diversity of these CE ecoregions in Australia and New Zealand may be threatened by climate change and the resulting plant invasion (Fig. 1; O'Donnell et al. 2012; Duursma et al. 2013; Beaumont et al. 2014; Bellard et al. 2014). Furthermore, herbaceous and woody TPIs had a high potential to expand in the CE ecoregions of South America, Europe, Madagascar and northern and southern Africa (Richardson and Rejmánek 2011; Beaumont et al. 2014; Bellard et al. 2014; Donaldson et al. 2014). As habitat suitability for TPIs expands with climate change, natural dispersal of TPIs could also promote invasion of ecoregions without the aid of human activities (Foxcroft et al. 2011; Colautti and Barrett 2013). TPIs have the ability to spread and occupy non-native habitats rapidly under climate change (Colautti and Barrett 2013). Hence, an effective management planning should be developed to prevent and control TPIs from expanding in CE ecoregions (Bradley 2010; Foxcroft et al. 2011; Meier et al. 2014).

Human impact, including human activity in CE ecoregions, may also aid the expansion of TPIs to risk hotspots under climate change (Spear et al. 2013; Melin et al. 2014). Human activities can provide invasion pathways for TPIs under climate change (Bradley et al. 2012; Donaldson et al. 2014; Seebens et al. 2015). Globalization facilitates the spread of TPIs as international commerce develops and as plants are introduced for horticulture or commercial purposes (Perrings et al. 2005; Bradley et al. 2010b; Donaldson et al. 2014; Melin et al. 2014; Seebens et al. 2015). For example, climate change can increase the invasion risk of *Lonicera japonica*, a common invasive horticultural vine in the USA (www.issg.org). *Acacia* species have also been introduced from Australia to South Africa as an ornamental and commercial species; however, they have become invasive (Donaldson et al. 2014). Furthermore, intensive anthropogenic activities greatly increase the chances of increasing pathways for TPIs (Spear et al. 2013). Hence, we need to integrate introduction dynamics into the management planning for preventing intentional or accidental introduction or dispersal of TPIs (Bradley 2010; Donaldson et al. 2014; Melin et al. 2014).

The finding that climate change may increase the expansion of TPIs, particularly herbaceous plants in the VU and RI ecoregions in the high concentration scenario, suggests that we need to employ methods of long-term monitoring for plant invasion (Duursma et al. 2013; Table 1). Previous studies have shown that TPIs would need appropriate temperatures with pronounced seasonality to spread (Bradley et al. 2010b, 2012). Also, extreme weather events, such as extreme seasonal differences in temperature within a year, can facilitate the formation of


(a)
(b)
(c)
Critical or endangered
Vulnerable
Relatively stable or intact

◀ **Fig. 1** Risk hotspots for terrestrial plant invaders (TPIs) based on the terrestrial ecoregions in the current (**a**), low (**b**) and high (**c**) concentration scenarios

expansion for TPIs in the VU and RI ecoregions (Bradley et al. 2010a, b; Diez et al. 2012). Hence, the detection of extreme climatic events is necessary for the prevention and control of TPIs.

Herbaceous TPIs may have the ability to expand in some VU and RI ecoregions of risk hotspots with low nutrition resources such as northern Europe and central Australia (Fig. 1; Eskelinen and Harrison 2014; Kremer 2014; Turner et al. 2014). Therefore, we should guard against the entry of TPIs into these VU and RI ecoregions to maximize their capacity to prevent and control plant invasion (Foxcroft et al. 2011; O'Donnell et al. 2012; Duursma et al. 2013). The challenge for biological conservationists is to minimize the opportunities for herbaceous TPIs to be introduced into new areas under climate change (Duursma et al. 2013). Establishing an early warning system for TPIs, particularly herbaceous plants, will improve the ability to prevent and control the movement of TPIs (Hellmann et al. 2008; Bradley et al. 2010a; Meier et al. 2014). Finally, the following measures should be purposed for the prevention and control of herbaceous TPIs in VU and RI ecoregions: (1) detailed monitoring of climate change (Bradley et al. 2010b); (2) more effective management of human activities (Meier et al. 2014); and (3) prevention of the introduction of herbaceous TPIs with a high ability to disperse naturally (Donaldson et al. 2014).

Conclusions

The identification of risk hotspots for TPIs could promote the development of prevention and control of plant invasion. TPIs, particularly herbaceous and woody ones, should be efficiently prevented and controlled in the critical or endangered ecoregions of Europe, south-western Australia, New Zealand and Madagascar in the current, low and high concentration scenarios. Attention should also be paid to the expansion potential of TPIs, particularly herbaceous ones in both vulnerable and relatively stable ecoregions in risk hotspots under climate change. The innovative evaluation approaches and tools are urgently needed for the projection of TPI expansion at the global scale. Furthermore, with accelerating economic globalization and rapid climate change, the risk evaluation of universal coverage for TPIs at global scale also is urgently required.

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