WILL GLOBAL CLIMATE CHANGE FACILITATE PLANT INVASIONS IN CONSERVATION AREAS?

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Abstract

Climate change may increase plant invasion risk, but few studies have paid attention to the relationship between climate change and plant invasion in conservation areas at a global scale. The primary objective of our study was to determine whether climate change would allow or even increase the likelihood that invasive alien plant species would invade conservation areas across the world and in particular regions. We modeled current and future potential distributions of invasive alien plant species using bioclimatic variables in the program Maxent. Our study found that global climate change would not lead to plant invasions in every conservation area, but it would provide the conditions for few invasive plant species to impact conservation areas in some regions. Greenhouse gas concentrations could aggravate the regional invasion of invasive plant species and make larger changes of ability of invasive plant species to invade conservation areas in low gas concentration scenario than high gas concentration scenario. Immediate measures must be taken to deal with this problem, such as developing global indicators of biological invasion and designing long-term management plans at different geographical scales.

Key words: Climate change; Conservation areas; Co-occurring species; GIS; Invasive alien plant species; Maxent.

Introduction

Climate change, including anomalous changes in temperature and precipitation, has the potential to limit species’ geographic distribution ranges (Chen et al., 2011), promote the invasion of alien species and threaten biological diversity (Caplat et al., 2013; Liang & Fei, 2014; Schlünzen et al., 2010). In the last decade it had been difficult for biological conservationists and government regulators to establish nature reserves because it was hard to predict the future distribution ranges of species due to climate change (Aratújo et al., 2011; Richardson & Whittaker, 2010). There is an additional complication in predicting whether a particular conservation area will be impacted by invasive alien plant species (IAPS), introduced plants with broad physiological niches (IAPS; Joppa et al., 2013; Richardson et al., 2000). Richardson & Rejmánek (2011) indicated that climate change provided a huge challenge for managing woody plant invasions due to strong and rapid dispersal ability and problematic management issues. Hence, we believe climate change will create the conditions for IAPS to invade the non-initial areas with high protection value, and consequently have extensive negative effects on the native species and the overall stability of the native ecosystem (Dimini et al., 2013). Unfortunately, the invasion of IAPS spread in global conservation areas (CAs) and the changing trends of IAPS may be disordered (Kelly et al., 2014). Hence, we must study the impact of climate change on the ecological invasion of CAs by IAPS and make the invasive trend of IAPS in CAs clear.

Both habitat fragmentation and biological invasion are major factors that lead to biodiversity loss and rapid climate change can exacerbate both processes (Kruess & Tscharntke, 1994; Chazdon, 2008). It is urgently necessary to provide predictions on the risk of biological invasion caused by climate change to particularly sensitive areas. Powell et al., (2011) showed that IAPS could affect biodiversity across at different spatial scales and we need to differentiate the impact of IAPS on biodiversity across these scales. Bellard et al., (2013) reported that climate change could promote future invasions in some areas of the world and Kuebbing et al., (2014) wrote that the invasion of multiple IAPS could potentially be worse for the native plant communities than the invasion of a single species. The main objective of our study is to predict the effect of climate change on co-occurring IAPS across space-time scales. We relied on data from the IPCC Fifth Assessment Report (AR5; http://www.ipcc.ch/) as a reference for modeling the changing trends of IAPS invasions.

Vicente et al., (2013) illustrated how climate change could drive IAPS into sensitive areas in the case of three Australian wattle (Acacia) species in northern Portugal. Conservation areas protect endangered ecosystems, habitats and species, but are increasingly under attack by IAPS in some regions of the world (Mitrovich et al., 2010; Le Maitre et al., 2011). The invasion of IAPS in CAs will cause several serious problems: 1) IAPS can occupy the habitat of native species so that many species can’t survive (Baldwin et al., 2003); 2) IAPS can change the ecological landscape and result in habitat fragmentation (Jauni & Hyvönén, 2010); 3) IAPS can break the composition of the community and ecosystem (Kuebbing et al., 2014), and 4) CAs will lose the ability to protect the native ecosystem (Le Maitre et al., 2011). It is important for global CAs to avoid invasion by IAPS, but scientists are not optimistic (Lee et al., 2013). Therefore, we should model the future invasion potential of IAPS to invade CAs and then propose feasible conservation strategies to prevent and reduce the risk of biological invasion (Le Maitre et al., 2011).
Species distribution models (SDMs) are widely used in biology to predict current and potential distributions of particular species in their current ecological niche (Merow et al., 2013). Predicting the potential distributions of IAPS in CAs using current and future environmental variables requires the use of SDM programs such as Maxent (Václavik et al., 2012). The advantages of using Maxent are as follows: it has the ability to use low sample sizes to finish modelling process that can drastically disturb both the performance and adjustments accuracy of the SDM (Papeş & Gaubert, 2007); it is insensitive to multicollinearity among environmental variables, that may otherwise overestimate the reliability of results (Evangelista et al., 2011); and it can assess the relative importance of each variable to the potential distribution of species using a jackknife test (Mariya & Robert, 2013). GIS can then be used to compute the area within CAs potentially containing IAPS (Vicente et al., 2013). We used SDM techniques for 36 IAPS from the IUCN list of the Invasive Species Specialist Group (ISSG) with the largest impact on biodiversity to evaluate the potential for IAPS to invade CAs (Bellard et al., 2013).

We used Maxent and GIS to build a framework to assess the current and future power of co-occurring IAPS to invade CAs under climate change on a global scale and in particular regions by modelling the current and future global potential distribution of IAPS using bioclimatic variables; by using GIS to assess the impact of multiple IAPS on global CAs and regional CAs; by analyzing the importance of each climatic variable in the model to the potential distribution of IAPS to determine the driving factors in the model that affected the ability of IAPS to invade CAs. Finally, we suggest effective measures to protect biodiversity in CAs around the globe.

Materials and Methods

**Species data:** 36 IAPS were selected from the ISSG list to serve as a representative set of the most widespread and dangerous IAPS of the world. These 36 IAPS share the following characteristics: 1) they can significantly impact biodiversity and human activity in a negative way; 2) they exhibit general functional traits that aid in plant invasion; and 3) they can invade a variety of plant habitats and communities across the world. This list includes 4 aquatic plants and 32 terrestrial plants (Bellard et al., 2013; Lowe et al., 2000). Occurrence record data, especially geographic coordinates, for each IAPS were downloaded from a variety of online databases including: 1) Global Biodiversity Information Facility (GBIF; www.gbif.org); 2) LIFEMAPPER (www.lifemapper.com); 3) SPECIESLINK (www.splink.cria.org.br); 4) Chinese Virtual Herbarium (CVH; www.cvherb.org.cn); and 5) IUCN/SSC Invasive Species Specialist Group (ISSG). Bellard et al., (2013) collected detailed species distribution records and we added CVH to our study because the locality information from China is not comprehensive and we gave up on the IUCN database not as did Bellard et al., (2013) because it lacked locality information, such as latitude and longitude. Occurrence points were recorded as present or absent in 2.5 arc-minute grid cells (4.3 km at the equator) to reduce the effect of sampling bias and to avoid any errors associated with georeferencing, obvious misidentifications and duplicate records in each grid cell. The presence point data of each IAPS is an estimate of the species’ distribution (Elith et al., 2011). Finally, we collected an average of 1,945 unique records from IAPS (the range of records for each species is from 52—26,506). These records cover the world, except the Sahara region, most regions of Russia, northern Canada and Greenland (Table 1 and Fig. S1).

**Bioclimatic data:** We used 2.5 arc-minute current and future data for the environmental layer input of the SDM. Seven current bioclimatic variables with 2.5-arc-minute spatial resolution (the same as future bioclimatic variables) were downloaded from the WorldClim database (averages from 1950-2000 were used as current bioclimatic variables; Table 2; Hijmans et al., 2005; http://www.worldclim.org). The bioclimatic variables with Pearson correlation coefficients between 0.85 and -0.85 were removed to eliminate the negative effects of multicollinearity on the adjustment of the SDM. These seven bioclimatic variables can influence the distribution and physiological performance of IAPS (Reid et al., 2014).

To model the future potential distribution of IAPS in the 2080s (2071-2099) we used four global climate models (GCMs): bcc_csm1_1, csiro_mk3_6_0, gfdl_cm3 and mohc_hadgem2_es and we used three greenhouse gas concentration scenarios (Representative Concentration Pathways (RCPs)) 2.6 (mean: 270 ppm; range: 140 to 410 by 2100), 4.5 (mean: 780 ppm; range: 595 to 1005 by 2100) and 8.5 (mean: 1685 ppm; range: 1415 to 1910 by 2100)) representing the lowest to highest gas concentration scenarios, respectively (Intergovernmental Panel on Climate Change (IPCC) 5th Assessment Report). We used 4 GCMs×3 RCPs to model a distribution of possible climate scenarios to estimate future IAPS distributions (http://www.ccafs-climate.org/).

**Conservation area data:** A global map of IUCN I–VI CAs was obtained from the World Database on Protected Areas (WDPA; Araújo et al., 2011; http://www.wdpa.org/). The total number of CAs is 115,506; and we selected 18,711 CAs with a large area (1-194166 2.5 arc-minute grids) to include in the study (Fig. 1). We did not include small CAs (the size smaller than 1 grid) in the study because 1) the CAs are too small for the grid size of the bioclimatic data and this set of CAs across the globe are a fair sampling to measure the impact of IAPS on every CA. We also expected to assess the power of IAPS to invade each CA of world, but the modeled precision of grid limited the size of target CAs. Hence, in this study, CAs we collected must cover the global geographical range of CAs. For instance, although some CAs are too small that we ignored in the certain latitudes and longitudes, we also can evaluate the CAs in the similar latitudes and longitudes, namely, regional geographical ranges and then estimate the ability of IAPS to invade the certain regional CAs because comparing with these small regional conservation areas, the large CAs contain the most information on extensive geographical ranges.
Table 1. Information on the IAPS species used for this study.

<table>
<thead>
<tr>
<th>Name</th>
<th>Family</th>
<th>Type</th>
<th>Record</th>
<th>AUC(_{\text{train}})</th>
<th>AUC(_{\text{test}})</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia mearnsii</td>
<td>Leguminosae</td>
<td>Land</td>
<td>1096</td>
<td>0.957</td>
<td>0.958</td>
<td>GBIF, SpeciesLink, ISSG</td>
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<tr>
<td>Ardisia elliptica</td>
<td>Myrsinaceae</td>
<td>Land</td>
<td>52</td>
<td>0.978</td>
<td>0.94</td>
<td>GBIF, SpeciesLink, CVH, ISSG</td>
</tr>
<tr>
<td>Arundo donax</td>
<td>Gramineae</td>
<td>Land</td>
<td>1826</td>
<td>0.906</td>
<td>0.899</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Caulerpa taxifolia</td>
<td>Caulerpaceae</td>
<td>Aquatic</td>
<td>85</td>
<td>0.977</td>
<td>0.954</td>
<td>GBIF, SpeciesLink, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Cecropia peltata</td>
<td>Moraceae</td>
<td>Land</td>
<td>417</td>
<td>0.96</td>
<td>0.95</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Chromolaena odorata</td>
<td>Compositae</td>
<td>Land</td>
<td>1003</td>
<td>0.922</td>
<td>0.918</td>
<td>GBIF, SpeciesLink, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Cinchona pubescens</td>
<td>Rubiaceae</td>
<td>Land</td>
<td>265</td>
<td>0.983</td>
<td>0.97</td>
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<tr>
<td>Cidemia hirta</td>
<td>Melastomataceae</td>
<td>Aquatic</td>
<td>1313</td>
<td>0.929</td>
<td>0.923</td>
<td>GBIF, SpeciesLink, ISSG</td>
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<td>Eichhornia crassipes</td>
<td>Poaceae</td>
<td>Land</td>
<td>1145</td>
<td>0.899</td>
<td>0.891</td>
<td>GBIF, SpeciesLink, CVH, ISSG</td>
</tr>
<tr>
<td>Euphorbia esula</td>
<td>Euphorbiaceae</td>
<td>Land</td>
<td>4361</td>
<td>0.869</td>
<td>0.866</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Fallopia japonica</td>
<td>Polygonaceae</td>
<td>Land</td>
<td>11495</td>
<td>0.765</td>
<td>0.767</td>
<td>GBIF, ISSG</td>
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<tr>
<td>Hedychium gardnerianum</td>
<td>Zingiberaceae</td>
<td>Land</td>
<td>179</td>
<td>0.988</td>
<td>0.98</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Hiptage benghalensis</td>
<td>Malpighiaceae</td>
<td>Land</td>
<td>98</td>
<td>0.989</td>
<td>0.976</td>
<td>GBIF, SpeciesLink, Lifemapper, ISSG</td>
</tr>
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<td>Imperata cylindrica</td>
<td>Gramineae</td>
<td>Land</td>
<td>4323</td>
<td>0.854</td>
<td>0.857</td>
<td>GBIF, SpeciesLink, CVH, ISSG</td>
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<tr>
<td>Lantana camara</td>
<td>Verbenaceae</td>
<td>Land</td>
<td>4574</td>
<td>0.944</td>
<td>0.946</td>
<td>GBIF, SpeciesLink, CVH, ISSG</td>
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<tr>
<td>Leucaena leucocephala</td>
<td>Leguminosae</td>
<td>Land</td>
<td>1161</td>
<td>0.904</td>
<td>0.905</td>
<td>GBIF, SpeciesLink, CVH, ISSG</td>
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<tr>
<td>Ligustrum robustum</td>
<td>Oleaceae</td>
<td>Land</td>
<td>109</td>
<td>0.99</td>
<td>0.99</td>
<td>GBIF, CVH, ISSG</td>
</tr>
<tr>
<td>Lythrum salicaria</td>
<td>Lythraceae</td>
<td>Land</td>
<td>26506</td>
<td>0.662</td>
<td>0.66</td>
<td>GBIF, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Melaleuca quinquenervia</td>
<td>Myrtaceae</td>
<td>Land</td>
<td>772</td>
<td>0.968</td>
<td>0.965</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Miconia calvecens</td>
<td>Melastomataceae</td>
<td>Land</td>
<td>499</td>
<td>0.957</td>
<td>0.958</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Mikania micrantha</td>
<td>Compositae</td>
<td>Land</td>
<td>1423</td>
<td>0.918</td>
<td>0.922</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Mimosa pigra</td>
<td>Leguminosae</td>
<td>Land</td>
<td>1441</td>
<td>0.904</td>
<td>0.895</td>
<td>GBIF, SpeciesLink, CVH, ISSG</td>
</tr>
<tr>
<td>Myrica faya</td>
<td>Myricaceae</td>
<td>Land</td>
<td>112</td>
<td>0.991</td>
<td>0.996</td>
<td>GBIF, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Opuntia stricta</td>
<td>Cactaceae</td>
<td>Land</td>
<td>1415</td>
<td>0.949</td>
<td>0.948</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Pinus pinaster</td>
<td>Pinaceae</td>
<td>Land</td>
<td>5510</td>
<td>0.85</td>
<td>0.851</td>
<td>GBIF, SpeciesLink, ISSG</td>
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<tr>
<td>Prosopis glandulosa</td>
<td>Mimosaceae</td>
<td>Land</td>
<td>672</td>
<td>0.951</td>
<td>0.952</td>
<td>GBIF, SpeciesLink, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Psidium cattleianum</td>
<td>Myrtaceae</td>
<td>Land</td>
<td>480</td>
<td>0.975</td>
<td>0.972</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Pueraria montana var. lobata</td>
<td>Leguminosae</td>
<td>Land</td>
<td>105</td>
<td>0.987</td>
<td>0.989</td>
<td>SpeciesLink, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Rubus ellipticus</td>
<td>Rosaceae</td>
<td>Land</td>
<td>321</td>
<td>0.981</td>
<td>0.98</td>
<td>GBIF, CVH, ISSG</td>
</tr>
<tr>
<td>Schinus terebinthifolius</td>
<td>Rutaceae</td>
<td>Land</td>
<td>970</td>
<td>0.953</td>
<td>0.953</td>
<td>GBIF, SpeciesLink, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Spartina anglica</td>
<td>Gramineae</td>
<td>Aquatic</td>
<td>586</td>
<td>0.977</td>
<td>0.978</td>
<td>GBIF, CVH, ISSG</td>
</tr>
<tr>
<td>Spathodea campanulata</td>
<td>Bignoniaceae</td>
<td>Land</td>
<td>210</td>
<td>0.956</td>
<td>0.966</td>
<td>GBIF, Lifemapper, ISSG</td>
</tr>
<tr>
<td>Sphagnotricol a trilobata</td>
<td>Compositae</td>
<td>Land</td>
<td>741</td>
<td>0.949</td>
<td>0.95</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Tamarix ramosissima</td>
<td>Tamaricaceae</td>
<td>Land</td>
<td>858</td>
<td>0.939</td>
<td>0.925</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Ulex europaeus</td>
<td>Leguminosae</td>
<td>Land</td>
<td>9656</td>
<td>0.787</td>
<td>0.791</td>
<td>GBIF, SpeciesLink, ISSG</td>
</tr>
<tr>
<td>Undaria pinnatifida</td>
<td>Alariaceae</td>
<td>Aquatic</td>
<td>59</td>
<td>0.992</td>
<td>0.986</td>
<td>GBIF, Lifemapper, ISSG</td>
</tr>
</tbody>
</table>

AUC\(_{\text{train}}\) is the training AUC of Maxent; AUC\(_{\text{test}}\) is the test AUC result from Maxent; Record: recorded occurrence points of each species. CVH: Chinese Virtual Herbarium; GBIF: Global Biodiversity Information Facility; ISSG: IUCN/SSC Invasive Species Specialist Group.

Fig. 1. The conservation areas considered in this study.

Fig. S1. The recorded occurrence localities of IAPS.
Modelling approach and evaluation: Maxent (ver.3.3.3k; http://www.cs.princeton.edu/~schapire/maxent/) was used to model the current and future globe potential distribution of 36 IAPS based on current and future bioclimatic data. Maxent was used to predict the potential distributions of IAPS with maximum entropy based on occurrence localities and environmental variables (Elith et al., 2011; Reid et al., 2014). Maxent predicted map cell values of 1—0 with 1 representing the highest habitat quality, and values close to 0 representing the lowest habitat quality for that species (Elith et al., 2011). Maxent estimates the relative contribution of each variable, which allows us to make biologically relevant inferences about the ecological processes that affect invasive species distributions (Elith et al., 2011).

In order to precisely predict potential distributions of IAPS, we tried to improve the modeling performance of Maxent by optimizing the analysis settings. We selected bioclimatic variables at a 2.5-arc-minute spatial resolution for Maxent modelling because although the fine resolution could improve the precision of Maxent, 0.5 arc-minute future climate scenarios might cause a false sense of accuracy (Ramírez-Villegas and Jarvis, 2010). We set the regularization multiplier (beta) to 1.5 to produce a smooth and general response which could be modeled in a biologically realistic manner (Duursma et al., 2013). The maximum number of background points was set to 10,000. We used 75% of the occurrence points for each species to train the model and the remaining 25% were used for testing. Then we ran 10 replicates for each species in each scenario and averaged the results (each run used a different random sample of points; Chetan et al., 2014). The other settings were the same as described in Reid et al., (2014). The jackknife test was used to analyze the importance of different bioclimatic variables with Maxent to determine factors that potentially allow IAPS to invade CAs (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 the corresponding sensitivity and specificity were then obtained through calculations. 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 each species with values above 0.75 were considered useful for our study. AUC values <0.75 were not considered in downstream analyses (Chetan et al., 2014).

The power of IAPS to invade CAs: We analyzed the power of IAPS to invade global CA.s in three different aspects: 1) the overall power of IAPS to invade global CAs; 2) the power of a single IAP species to invade CAs around the world and; 3) the power of multiple IAPS to invade each CA. We were able to get current and future potential distribution maps for each species in each scenario (Araújo et al., 2011).

First, we selected IAPS with AUC values larger than 0.75. To estimate the future potential distribution of a single IAPS in four concentration scenarios we superimposed the maps of future potential distribution of a single IAPS in 4 GCMs×3 RCPs of this study with the same weight. Many previous studies have set a presence/absence threshold for each individual species to estimate species richness through ensemble modeling. However, these thresholds are problematic and can produce bias in predictions. Therefore, we used the modified method of Calabrese et al., (2014) to compute the invasion extent of co-occurring IAPS in each pixel:

\[ E_j = \sum_{k=1}^{k} p_{i,k} \]

\( E_j \) represents the current or future invasion extent of co-occurring IAPS in pixel j; k is the number of species in pixel j; i is the species I; and \( p_{i,k} \) is the probability of the species i’ potential distribution in the pixel j. We averaged the distribution of co-occurring IAPS in RCP 2.6, 4.5 and 8.5 and analyzed the potential of co-occurring IAPS to invade CAs using the present distributions as a comparison (Bellard et al., 2013).

Secondly, we calculated the potential for a single IAPS to invade CAs around the world as follows:

\[ R_j = \sum_{i=1}^{n} A_i B_j \]

where \( R_j \) is the power of IAPS s to invade CAs around the world in the present or future; \( n \) is the total number of distribution pixels occupied by IAPS; \( A_i \) is an indicator of the distribution possibility of IAPS s (Maxent value) in grid i of CAs; and \( B_j \) is the distribution area percentage of IPAS s in CAs. We calculated this value for single IAPS under current conditions and in the 2080s (RCP 2.6, 4.5 and 8.5).

Then we calculated the change in the potential of one IAPS to invade all CAs around the globe as:

\[ B = R_{Future} - R_{Current} \]

where \( R_{Future} \) and \( R_{Current} \) are the future and current potential of a single IAPS to invade CAs around the globe.

Third, we calculated the potential of multiple IAPS to invade each CAs as follows:

\[ S_j = \sum_{i=1}^{n} X_i Y_j \]

where \( S_j \) is the current or future power of co-occurring IAPS to invade CA.; \( n \) is the total number of IAPS; \( X_i \) is an indicator of the distribution possibility of all IAPS (\( E_j \) values <0.75 were not considered in downstream analyses (Chetan et al., 2014).}

### Table 2. Environmental variables used.

<table>
<thead>
<tr>
<th>Code</th>
<th>Environmental variables</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bio1</td>
<td>Annual mean temperature</td>
<td>°C</td>
</tr>
<tr>
<td>Bio4</td>
<td>Temperature seasonality</td>
<td>SD*100</td>
</tr>
<tr>
<td>Bio6</td>
<td>Min. temperature of the coldest month</td>
<td>°C</td>
</tr>
<tr>
<td>Bio11</td>
<td>Mean temperature of the coldest quarter</td>
<td>°C</td>
</tr>
<tr>
<td>Bio12</td>
<td>Annual precipitation</td>
<td>mm</td>
</tr>
<tr>
<td>Bio14</td>
<td>Precipitation of the driest month</td>
<td>mm</td>
</tr>
<tr>
<td>Bio16</td>
<td>Precipitation of the wettest quarter</td>
<td>mm</td>
</tr>
</tbody>
</table>

Environmental variables were used as environmental layers for the species potential distribution models by Maxent; SD represents standard deviation.
value) in grid $i$ of CA $t$; and $Y_i$ is the distribution area percentage of all IAPS in CA $t$.

We calculated this value for each CA under current conditions and in the 2080s (RCP 2.6, 4.5 and 8.5).

\[ A_t = S_{Future} - S_{Current} \]

where $A_t$ is the change in the potential of multiple IAPS to invade CA $t$ and $S_{Future}$ and $S_{Current}$ are the future and current potential of all IAPS to invade each CA.

Fourth, we compared the future $R$, and $S$ (RCP 2.6, 4.5 and 8.5) with the present day to assess the uncertainty of power of one IAPS to invade all CAs and multiple IAPS to invade each CAs, respectively, using linear regression analysis in JMP 11.0 (SAS Institute Inc, Cary NC) and Origin 9.0 (OriginLab, Northampton, MA).

Finally, we compared $R$, $B$, $S$, and $A_t$ to further analyze the potential for IAPS to invade CAs around the globe under climate change with box charts made in Origin 9.0 (OriginLab, Northampton, MA).

**Results**

We used AUC values to evaluate 36 IAPS and we found that the AUC value of *Lythrum salicaria* was below 0.75, hence, we removed this species from the study. The AUC values of other species were over 0.75, indicating good model performance (Table 1). We found that IAPS were widely distributed over the Earth based on our occurrence records (Fig. S1).

Under all future climate scenarios, hotspots of multiple invasive species were similar to the present day invasive hotspots, such as the eastern and western United States, western and southern Europe, southwestern and southeastern Australia, New Zealand, eastern South America, eastern Madagascar, Mexico, southeastern Asia and southern China. However, the exact locations of invasive hotspots would shift in the future. Comparing with current hotspots, the future hotspots would aggravate obviously such as southern Europe, southeastern Australia and New Zealand. Some regions, such as central and northwestern South America and eastern-Europe, are lightly affected by IAPS, but our estimates suggest there will be more severe invasions in the future. Meanwhile, the CAs that these regions are invaded by IAPS at present and will also be future (Figs. 1 and 2).

With the greenhouse gas concentration increasing, the significant linear relationship of power of multiple IAPS to invade each CAs between the present day and future was decreasing gradually, namely, increasing uncertainty (RCP 8.5>4.5>2.6). The similar relationship is recorded for one IAPS to invade all CAs (Fig. 3). We found that the potential for IAPS to invade every CA on Earth didn’t obviously change in the future and the number of CAs with weak invasion scenarios will increase with increasing gas concentrations and the average power of IAPS to invade every CA will increase weakly (RCP 8.5>4.5>2.6>Current; ANOVA test: $p<0.05$; Fig. 4a). It is worth noting that high gas concentration scenarios significantly increased or decreased the potential for IAPS to invade CAs compared to low gas concentration scenarios. In some regions, particularly, a large number of CAs will experience serious invasions by IAPS under high gas concentrations (RCP 8.5>4.5>2.6; ANOVA test: $p<0.05$; Fig. 4b).

We found that the potential invasiveness of IAPS did not always change in the same ways in the current and future estimates (Fig. 5a). Some species, such as *Leucaena leucocephala* and *Mimosa pigra*, remain strongly invasive in all climate scenarios. Fig. 5b shows significant changes to the invasiveness of IAPS, such as *Chromolaena odorata* and *Spathodea campanulata*, with increased invasiveness in a high gas concentration scenario compared to a low gas concentration scenario (RCP 8.5>4.5>2.6; ANOVA test: $p<0.05$). A jackknife test revealed that annual mean temperature (Bio1), temperature seasonality (Bio4) and precipitation of the driest month (Bio14) were the most important climatic variables that influence the potential for IAPS to invade CAs around the globe (Fig. 6).

**Discussions**

In this study, we selected the most harmful and widespread IAPS which have the ability to spread and occupy new habitats (Lowe et al., 2000). Furthermore, the expansion of IAPS, as facilitated by climate change, will decrease the space available for native species, leading to ecosystem disorders and even species extinctions. Based on the AUC values, our predicted distribution of IAPS can be considered highly reliable and may accurately reflect the invasive power of IAPS (Chetan et al., 2014). Conservation areas play an important role in biological conservation around the globe, such as protecting endangered species and maintaining ecological balances (Amy et al., 1998). However, with the increase in human activities and rapid climate change, CAs are facing serious problems such as the invasion of IAPS (Lee et al., 2013; Vicente et al., 2013). By using ecological modeling, we were able to estimate the current and future impact of IAPS on CAs around the world, and our findings that annual mean temperature, temperature seasonality and precipitation of the driest month are driving the potential distributions of IAPS in our models suggested that we need to strengthen detection of these three climatic variables for warning the invasion of IAPS. However, further research will be necessary to assess the extent of IAPS invasions and the ecological drivers of IAPS invasions in different regions of world.

Bellard et al., (2013) reported that climate change could increase the trend of invasive species in some regions, indicating that IAPS could invade biodiversity hotspots around the world. We tested this hypothesis that the potential IAPS might invade CAs in some regions including which Bellard et al., (2013) mentioned and found that in our models, IAPS have a larger distribution in the future and that will include the CAs which protect these ecosystems. When we modelled the potential for global-scale biological invasions, our results showed that this level of invasion was not similar to the findings of Bellard et al., (2013). Accordingly, we focused on predicting the impact of single or multiple IAPS to invade regional CAs under several models of climate change.
Many previous studies have proposed that climate change will increase the invasion ability of IAPS. Chuine et al., (2012) reported that climate change might increase the invasion potential of the alien C₄ grass Setaria parviflora in the Mediterranean Basin. Kleinbauer et al., (2010) indicated that climate change might drive the invasive tree Robinia pseudacacia into nature reserves and endangered habitats due to climate warming and Bethany et al., (2010) showed that the results that climate change increases the risk of plant invasion in the Eastern US would compel people to make long-term management plans designed to reduce invasion risk proactively. We must prioritize the globe prevention and control of IAPS because climate change can promote the spread of these species into new regions and enhance their invasibility in non-native habitats (Buckley & Han, 2014). Climate change seems to drive one or more IAPS into some regional CAs, but overall global CAs are only marginally...
affected by changes in potential distributions of IAPS, indicating regional invasion of IAPS into CAs. This is consistent with the findings of Bellard et al., (2013) and Kuebbing et al., (2014). Although IAPS didn't obviously invade CAs on a global scale and some regions even showed a trend towards less invasion, IAPS will invade CAs of some regions more violently as greenhouse gases increase in the eastern and western United States, western and southern Europe and southern China. With increasing greenhouse gas concentration, the uncertainty of the invasion of IAPS into regional CAs would go up. Many CAs in high gas concentration scenario would be threatened more seriously than low gas concentration scenario while the power of many IAPS to invade CAs would be enhanced in the future. More importantly, the results that increasing uncertainty of IAPS to invade CAs made the great difficulties for prevention and control of IAPS in some regional CAs.

Fig. 5 The potential of each IAPS to invade global conservation areas. (a) The current and future ranges of IAPS in global conservation areas. (b) The changes of IAPS potentials to invade global conservation areas under different greenhouse gas concentration scenarios. Range: the range of power of IAPS to invade CAs; 2.6: RCP 2.6; 4.5: RCP 4.5; 8.5: RCP 8.5. The small block of the boxes: the mean values; the transverse line of the boxes: the medium values.

Millions of dollars have been invested in the globe control of IAPS and many scientists have proposed methods to prevent and control the invasion of IAPS (Pejchar & Mooney, 2009). McGeoch et al., (2010) developed a global indicator of biological invasion specifically for formulating invasive species policy. Le Maitre et al., (2011) described the usefulness of sustained investment to study the management and restoration of native habitats threatened by IAPS. Scientists proposed designing long-term management plans at the regional or national scale to create a mitigation strategy for IAPS invading CAs due to climate change (Van Wilgen et al., 2011; Bradley et al., 2011; Richardson & Rejmánek, 2011). For example, we could propose long-term plans to monitor the greenhouse gas concentration in CAs with high risks of IAPS because we know that high levels of greenhouse gases increase the potential for IAPS invasions. We also could investigate the actual distributions of IAPS in CAs such as the hotspots of IAPS (eastern and western United States, western and southern Europe, southwestern and southeastern Australia, and New Zealand). The most important issue is to clarify the impacts and interactions of multiple IAPS in order to better prevent and control IAPS (Kuebbing et al., 2013).

Fig. 6. Bioclimatic variables with a large effect in IAPS distributions and their ranges. The small block of the boxes: the mean values; the transverse line of the boxes: the medium values.

Conclusions and Recommendations

Our study found that globe climate change will not promote IAPS that will invade CAs across the globe, but climate change will potentially lead to growing regional distributions of one or multiple IAPS. The findings of Figs. 2, 4 and 5 showed these IAPS would invade CAs in some regions. We should attach importance to gas concentration scenarios that increase the uncertainty of power of IAPS to invade CAs and need to face the problem of regional invasion of IAPS into CAs along with growing greenhouse gas concentrations, especially high gas concentration scenario. Research on the relationship between climate change, IAPS and CAs should continue because many ecological processes are still unclear. A better understanding of the mechanisms that facilitate co-occurring IAPS could improve the...
precision of SDMs. Additionally, more invasive species need to be mapped and studied to understand their invasive potential. Our study provides a method to evaluate the present and future impact of IAPS and is a resource for the prevention and control of IAPS.

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References


