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Predicting the potential distribution of *Lantana camara* L. under RCP scenarios using ISI-MIP models

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Abstract Projections of anthropogenically-induced global climate change and its impacts on potential distributions of invasive species are crucial for implementing effective conservation and management strategies. *Lantana camara* L., a popular ornamental plant native to tropical America, has become naturalized in some 50 countries and is considered one of the world's worst weeds. To increase our understanding of its potential extent of spread and examine the responses of global geographic distribution, predictive models incorporating global distribution data of *L. camara* were generated. These models were used to identify areas of environmental suitability and project the effects of future climate change based on an ensemble of the four global climate models (GCMs) within the Inter-Sectoral Impact Model Intercomparis on Project (ISI-MIP). Each model was run under the four emission scenarios (Representative Concentration Pathways, RCPs) using the Maximum entropy (Maxent) approach. Future model predictions through 2050 indicated an overall expansion of *L. camara*, despite future suitability varying considerably among continents. Under the four RCP scenarios, the range of *L. camara* expanded further inland in many regions (e.g. Africa, Australia), especially under the RCP85 emission scenario. The global distribution of *L. camara*, though restricted within geographical regions of similar latitude as at present (35°N~35°S), was projected to expand

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equator-ward in response to future climate conditions. Considerable discrepancy in predicted environmental suitability for *L. camara* among GCMs highlights the complexities of the likely effects of climate change on its potential distribution and the need to improve the reliability of predictions in novel climates.

1 Introduction

Ornamental plants are the largest pool of non-native species purposely introduced into new regions of the world for horticultural, landscaping or agricultural purposes. These species are gaining much attention because some of them have become naturalised and invaded ecosystems in their adventive range causing detrimental ecological and economic impacts across the globe. Introductions for ornamental purposes are reinforced by consumer demand for novel species and complicated by limited understanding of the invasion risks posed by these purposeful introductions (McNeely et al. 2001). Concern over the negative consequences of invasive ornamental species has increased in recent years as global trade and travel have rapidly expanded. The introduction of these invasive species threatens the stability and diversity of native ecosystems and these effects may be further exacerbated by global climate change. It is widely recognized that the ornamental horticulture industry is a primary path way for plant invasions worldwide (Reichard and White 2001; Bell et al. 2003). Therefore, there is a pressing need to identify areas of suitable habitat for invasive ornamental plants and to closely monitoring of these sites to prevent potential introduction or further range expansion.

Various modeling approaches have been developed and are available for assessing regions that are potentially susceptible to invasion across a range of scales (Guisan and Zimmermann 2000). Among these modeling approaches, bioclimatic envelope models such as CLIMEX, Domain, GARP, and Maxent have been extensively used for predicting the potential distributions of invasive species on the basis of their ecological and climatic profiles (Beaumont et al. 2005), with the assumption that climate is the primary determinant of the distribution of plant species (Andrewartha and Birch 1984; Baker et al. 2000; Kriticos et al. 2003). Once the climatic requirements or ecological tolerances of a species are characterized, the models can be employed to project its potential range in new regions or under future climate change scenarios to estimate the geographical distribution of suitable conditions. The bioclimatic envelope modelling approach has its foundations in ecological niche theory for which the fundamental ecological niche is defined as the set of environmental conditions and resources that allow a given species to survive and reproduce in the absence of biotic interactions. The realized niche encompasses a narrower range of conditions and resources in which a viable population is maintained in the presence of competitors and predators (Hutchinson 1957; Begon et al. 1996). This distinction between fundamental and realized niches is important in the context of bioclimatic modelling, particularly with regard to the methodologies used to characterize bioclimatic envelopes (Pearson and Dawson 2003).

Lantana camara L. (lantana; Verbenaceae), a hybrid species of tropical American origin, has spread across tropical and sub-tropical Africa, Asia and Australia in around 60 countries where it was introduced as a garden ornamental or a hedge plant (Day et al. 2003). As one of the world's ten worst weeds (Sharma et al. 2005), *L. camara* was reported infesting millions of hectares of natural and cultivated lands, causing great ecological and economic damage (Vardien et al. 2012). Along with its high reproductive output, reductions in manual weeding, herbicide tolerance, and reduced competition from other weedy species have allowed

L. camara to proliferate and spread successfully. Moreover, the high adaptability of this species to a wide range of climatic conditions has also allowed it to thrive in diverse habitats such as riverbanks, mountain slopes, valleys, pastures, and commercial forests where it forms impenetrable stands that obstruct access and use (Baars and Neser 1999). There has been some modeling methods were employed to investigate the potential distributions of *L. camara*. For instance, Taylor and Kumar (2013) used CLIMEX, a climate-matching model to estimate the potential distribution of *L. camara*. Priyanka and Joshi (2013) used Maxent model, a correlative niche modeling method to predict distribution of *L. camara* in the western Himalayan regions of India. Although these studies revealed that climate change may lead to shifts in distribution of *L. camara* at global or regional scales, current knowledge of this species potential distribution is still limited given its continued spread by humans, rapid land use changes, and complexities of climate variability which may exacerbate its spread.

Most of bioclimatic envelope modeling on invasive species, for instance, distribution predictions of *L. camara*, were based upon SRES-based emission scenarios and climate projections from the phase 3 of the coupled model intercomparison project (CMIP3). However, recent studies have demonstrated that new scenarios are required to explore the impact of different climate policies and the role of adaptation in more detail (Moss et al. 2010). A recent new set of emission scenarios referred to as Representative Concentration Pathways (RCPs), integrating socioeconomic development descriptions with climate change projections and with assumptions about climate mitigation and adaptation policies has been developed by CMIP5. The RCPs have been used as the basis for simulations with earth system models, producing projections of the magnitude and pattern of climate change during this century and, in some cases, as far out as 2300 (Taylor et al. 2012a). These new sets of emission scenarios are considered to be an important development in climate research and provide a potential foundation for further research and assessment, including emission mitigation and impact analysis (van Vuuren et al. 2011a). Currently, there are simulations from global climate models (e.g. the Intersectoral Impact Model Intercomparison Project (ISI-MIP, www.isi-mip.org)) which offer a unique opportunity for this analysis by providing multi-model ensembles of climate-change impacts across different sectors in a consistent scenario frame work. In our view, it is critical to project and evaluate species distributions using a more realistic climate scheme and the latest model simulations.

We used the consensus of *L. camara* suitability models representing a range of modeling approaches driven by the four GCMs from ISI-MIP to identify present areas of potential distribution and project the effects of future climate change during the 2050s. We investigated the spatial patterns of *L. camara* habitat changes from its current distribution to future potential occupied areas using the maximum entropy ecological niche modeling technique. Ultimately, the aim of this work is to provide valuable distribution information to assist land managers to most effectively plan and implement early detection and rapid response (EDRR) programs for this increasingly widespread invasive shrub.

2 Materials and methods

2.1 Occurrence data collection

Presence records of *L. camara* were retrieved from the Global Biodiversity Information Facility (GBIF; www.gbif.org/), Pacific Island Ecosystems at Risk (PIER) and Tropicos

Database (http://www.tropicos.org/). Resources from South Africa, Chinese Virtual Herbarium databases as well as online flora databases or reports from some Asian countries (Jafri 1974; Thakur et al. 1992) were also included. Coordinates of all locations were checked following (Hijmans et al. 1999) for low bias and errors. Geo-referencing was conducted with the Alexandria Digital Library Gazetteer (http://www.alexandria.ucsb.edu/) when necessary. Duplicate records were deleted and filtered spatially so that only one point occurred within each grid cell (~10 km×10 km). Thus, a total of 2307 documented global presence records were obtained for constructing the models.

2.2 Environmental variables

Several environmental geodatasets including climate, topography and human impacts were acquired and evaluated for their usefulness to predict *L. camara* invasions. A total of 19 bioclimatic variables representing annual trends, seasonality and extreme environmental conditions between 1950 and 2000 with a spatial resolution of 5arc-min (~10 km×10 km) were obtained from the WorldClim 1.4 database (version 1.4, http://www.worldclim.org) (Hijmans et al. 2005). Elevation data was also obtained from the WorldClim database. The human influence index (Hii, 1995–2004), an estimate of human influence obtained by incorporating four data types (i.e., human settlement, land transformation, accessibility, and electrical power infrastructure) as proxies for human influence was taken from the Last of the Wild data collection (Wildlife Conservation Society 2005) for model generation. This index was used because numerous alien species (e.g. *L. camara*) have been reported to be associated with human modified landscapes, international trade and transportation (Leprieur et al. 2008; Taylor et al. 2012b). Data values range from 0 to 64, corresponding to no or maximum human influence on a habitat. The HII dataset was re-sampled to a resolution of 5 arc-min to match the bioclimatic variables using a bilinear interpolation function, which is considered to be more realistic than the simpler nearest-neighbor method (Phillips et al. 2006). The topographic wetness index (TWI, also referred to as the compound topographic index), an estimate of predicted water accumulation in a defined area, was derived from the HYDRO1k product of the United States Geological Survey (USGS 2009) and re-sampled to maintain the 5 arc-min resolution. This index was used because it provides the spatial distribution of soil moisture within fields, potential surface runoff, ponding water, or water saturation after heavy rainfalls (Beven and Kirkby 1979) and has been employed for predicting species' distribution (e.g. Cohen et al. 2010). High TWI values are generally found for converging, flat terrain, while low values are typical of steep, diverging areas (Schmidt and Persson 2003).

To reduce the high collinearity and minimize model overfitting, the relative strengths of each predictor variable was first evaluated using Maxent's jackknife test. Variables with contributions of less than 1 % to the model prediction were eliminated. By pair-wise correlation analyses, the variable with the lower predictive power was removed, thereby one variable was selected for pairs with a correlation coefficient >|0.80|. Ultimately, the full set of 22 environmental variables was reduced to a subset of less correlated and more significant variables, including minimum average temperature of the coldest month (bio6), annual precipitation (bio12), and precipitation of warmest quarter (bio18) (Table 1). Whether TWI and HII correlated with any of the bioclimatic variables was also tested by extracting the HII and climate values for each grid cell and performing cross-correlation analysis with the data. No strong correlations were found between TWI (or HII) and climate variables (all *R* values<0.5).

3 Results

3.1 Predictors and model performance

The jack-knife procedure revealed that the distribution of *L. camara* was most constrained by minimum average temperature of the coldest month (bio6), which accounted for 48.50 % of the explained variation. The human influence index (HII, 15.32 %) and precipitation of warmest quarter (bio18, 11.11 %) accounted for the next highest variation (Table 1). Precipitation of driest month (bio14) and annual precipitation (bio12) were also important predictors with mean contributions of greater than 5 %. Other variables such as mean diurnal range (bio2), maximum temperature of warmest month (bio5) explained only a minor portion of the variance (no greater than 1 %) and will not be used for predicting the potential impacts of climate change on *L. camara* distribution. The probability of occurrence was maximal for variable bio6 ranging between 3.4 and 5.5 °C, precipitation of warmest quarter ranging from 277 to 507 mm, and values of human influence index varying between 15 and 50. The AUC of the independent test set for the model was 0.862, and was significantly higher than the null-model AUC (median=0.624, $P<0.05$), indicating that the model performed better than expected by chance. Mean Cohen's Kappa (0.578) and TSS values (0.654) also confirmed what the AUC values indicated in the reliability of model predictions.

Average projections of important thermal and moisture predictors for *L. camara* under each RCP are shown in Fig. S1. Annual mean temperature (bio1) for cells with the presence of *L. camara* was projected to rise by 1.2~1.8 °C for RCP2.6, 1.5~2.2 °C for RCP4.5, 1.3~2.1 °C for RCP6.0 and 1.9~2.8 °C for RCP8.5, depending on the GCMs used by 2050, relative to the baseline period 1950~2000. All four GCMs projected an average warming of 1.0~2.2 °C for the minimum temperature of the coldest month (bio6). Average annual precipitation (bio12) was projected to vary by −22.1~113.6 mm for RCP2.6, −52.6~92.7 mm for RCP4.5, −60.6~82.6 mm for RCP6.0 and −105.4~78.7 mm for RCP8.5. Precipitation of warmest quarter (bio18) in 2050 were projected to decrease across the four GCMs for RCP4.5 by 1.8~13.4 mm relatively to the baseline. Similar decreasing of this variable were projected for RCP2.6 and RCP6.0, except HadGem2-ES model (Fig. S1).

3.2 Current predicted distributions

Predictive maps for *L. camara* under current climate conditions successfully identified areas of high probability occurrence (Fig. S2). *L. camara* has a geographically wide potential distribution covering large parts of the tropics and adjacent subtropical regions. Its distribution is especially widespread within the Southern Hemisphere but also extends to North America including Florida and coastal areas along the Gulf of Mexico. In the Americas, regions most suitable for *L. camara* were located mainly in the southeastern United States, southern Mexico extending to Costa Ricaand Panama, Peru, central-eastern Argentina, Uruguay and southeastern Brazil. In Africa, regions projected to be highly suitable for *L. camara* were located along a relatively narrow belt extending from Guinea, southwestern Nigeria, and Uganda to Kenya, where another downward-suitable belt was present along the southeastern border of the continent. Much of Ethiopia, southern and eastern parts of Madagascar also comprised highly suitable habitats for this invasive shrub. In Asia, southern China, northern areas of Pakistan, India and Nepal, southeastern coastal areas of Sri Lanka as well as parts of several southeastern Asian countries also had high probabilities of suitable habitats for *L. camara* colonization.

Other favorable areas for this invasive shrub included eastern edges of Australia, the northern coastline of New Zealand, and several Pacific islands including Fiji, Vanuatu, Samoa and New Caledonia.
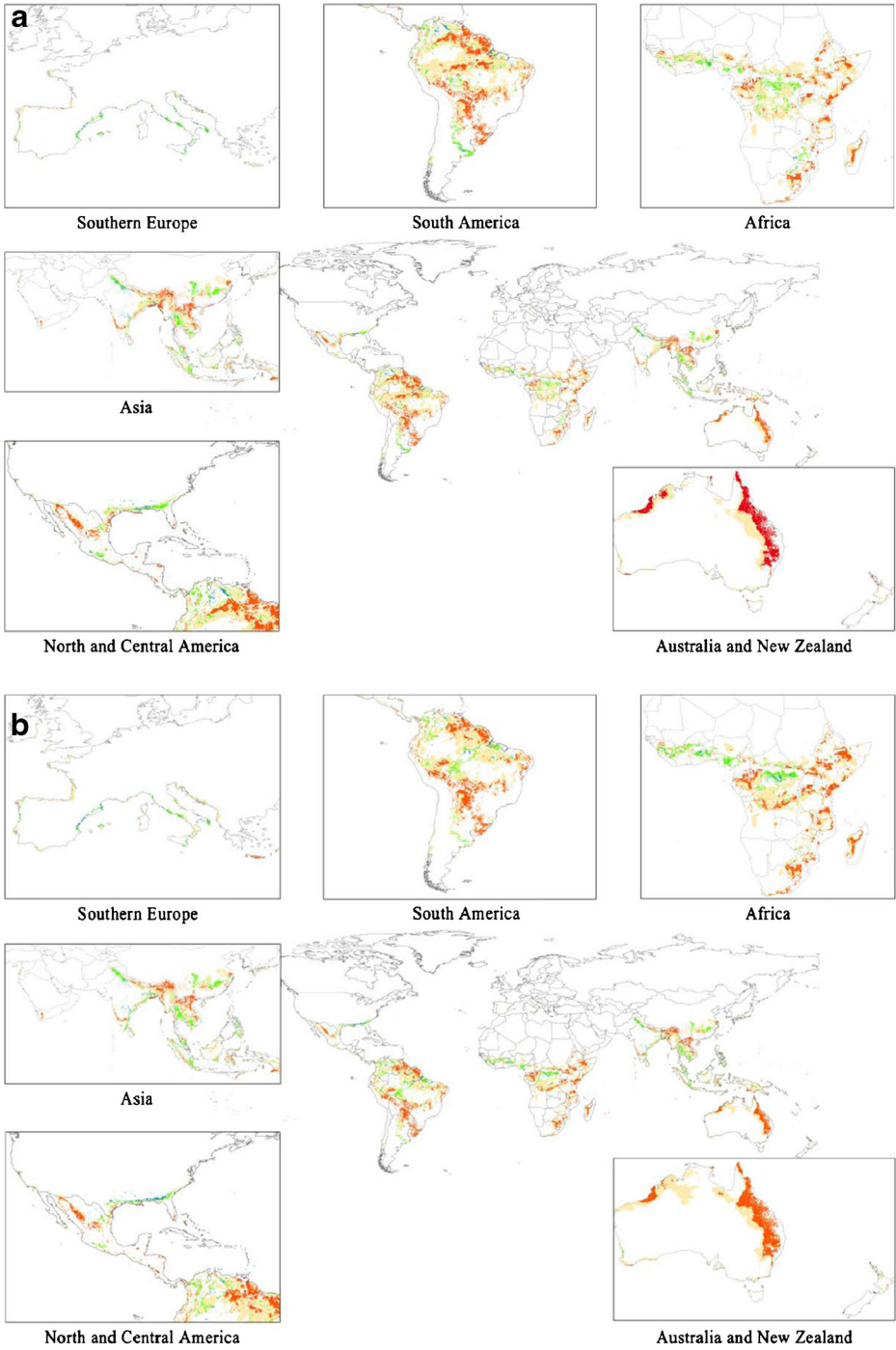
3.3 Global range shifts under climate change

Future model projections revealed possible changes in the potential distribution of *L. camara*. Under the four RCP emission scenarios, the ensemble model projected declines in suitability (Fig. 1, blue, four GCMs) in a small proportion (0.08 %~ 0.25 %) of scattered regions located primarily in the southeastern United States, northwestern Venezuela, central and eastern Brazil, eastern Ghana, and northern Zaire. Decreasing distribution probabilities were also found in Asia, such as the border areas of India (except the western border), northern Thailand, southwestern Malaysia, Indonesia, and the Philippines. Regions currently unsuitable for *L. camara* colonization but projected to become suitable by 2050 (Fig. 1, red, four GCMs, 2.52 %~ 3.62 %) included northern Mexico, parts of several South American countries, including Suriname, French Guiana, and Guyana. Similar probabilities shifts were also identified in fragmentary regions mostly adjacent to currently suitable areas.

Model predictions using the GCMs tested under different RCP scenarios were highly variable in their range shift projections. Model predictions using the GCMs tested under different RCP scenarios were highly variable in their range shift projections, with agreements of 7.3 to 9.1 % among the four GCMs for the same RCP (Fig. S3). Agreement between the model predictions was greatest under the RCP8.5 emission scenario. Regions with consistently favorable environments for *L. camara* were located mainly in southern U.S. states, large parts of Central America, and east-central South America. Other suitable regions included Africa (eastern edges, parts of western regions) as well as eastern Madagascar, southern China, northeastern India, parts of Southeast Asia, coastal areas of eastern Australia, and Pacific Island regions.

Under the RCP8.5 emission scenario, there were fewer new habitat losses and more suitable habitat gains when compared with the other scenarios, especially for the HadGem2-ES, MIROC- ESM- CHEM, and NorESM1-M models. Under the RCP2.6, RCP4.5 and RCP6.0 scenarios, the HadGem2-ES model predicted slight changes in range shifts for most habitats (i.e. about 97 % of grid cells were retained). The lowest habitat losses and gains under each of the other three RCPs were estimated by the HadGem2-ES model, whereas the greatest habitat losses were derived from the MIROC-ESM-CHEM model. Ensemble global estimated turn-over rates under the RCP8.5 scenario were higher (42.13 %±0.835) than the other RCPs and were highest of all the models used. Among the four GCMs, the NorESM1-M model predicted the highest turnover rates under all the RCPs, whereas the HadGem2-ES model predicted the lowest turnover rates, especially under the RCP6.0 scenario, where turnover rates were about one-half of those estimated by the NorESM1-Mmodel (Table 2).

Fig. 1 Projected global change in *L. camara* habitat suitability under the four emission scenarios: **a** RCP2.6, **b** ▶ RCP4.5, **c** RCP6, and **d** RCP8.5 by 2050, showing agreement among the four GCMs. *Black areas* indicate predicted current distribution regions. Areas with current suitability that is retained are indicated in *white*. Areas with current suitability that decreases are indicated in *green* (agreement of two GCMs) and *blue* (agreement of four GCMs), whereas areas not suitable in the current time period but suitable in the future are shown in *light yellow* (agreement of two GCMs) and *red* (agreement of four GCMs)
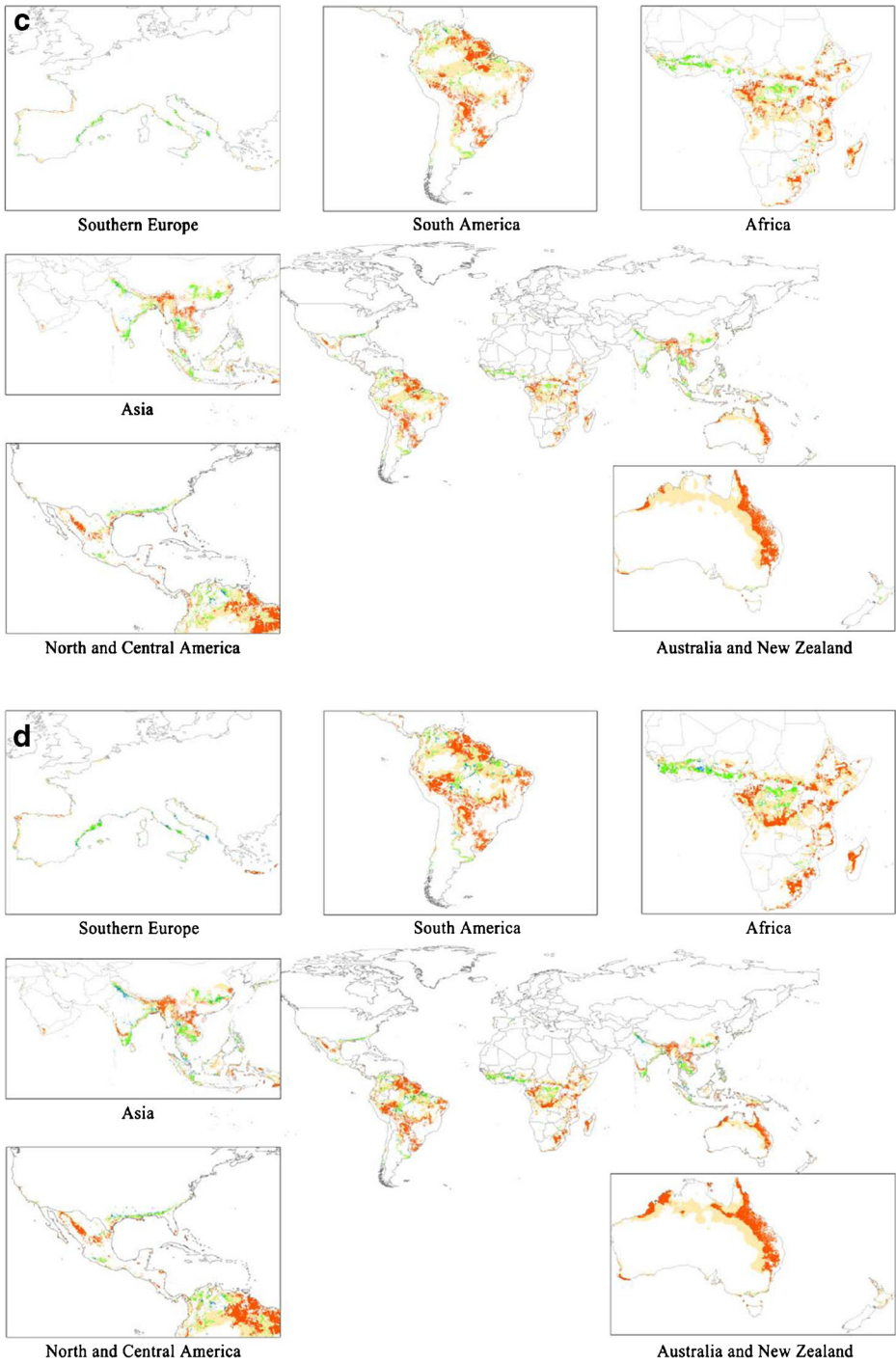
a

Southern Europe   South America   Africa

Asia

North and Central America   Australia and New Zealand

b

Southern Europe   South America   Africa

Asia

North and Central America   Australia and New Zealand

Fig. 1 continued.

3.4 Future continental range shifts

Ensemble mean change and variation among the four GCMs evaluated for five major
L. camara colonization regions are shown in Fig. S4 (A-F). The effects of climate change
on future suitability varied considerably among continents, with suitable areas increasing
substantially in Oceania (10.6 %~16.4 %, averaged model predictions) across the four RCP
levels, followed by Africa (5.7 %~8.1 %). In particular, increases in suitable areas in Australia
and New Zealand accounted for 9.9 to 15.7 % of their territory when averaged across all the
RCPs. The increase in suitable area was lowest (average values no greater than 0.5 %) under
the four RCP scenarios in Europe. With an increase in RCP levels, projected suitable areas
expanded except in America. The predicted net change in suitable areas for all continents
varied little across the GCMs used under the RCP8.5 scenario (Fig. 2).

Differences in global continental range shifts under the RCP scenarios were investigated
(Fig. S4 (F)). The predicted range gain shown on the right side of the coordinate axes were
substantially larger than the range loss, despite range gains or losses within a specific continent
concentrated in similar latitudinal locations. Projected changes of potential suitable habitats
using the IPSL-CM5A-LR and NorESM1-M models were higher than obtained from the
HadGem2-ES and MIROC-ESM-CHEM models. Future habitat gains and contractions for
L. camara mostly occurred in −20~10°N within America and Africa. The latitudinal extent of
this species in Asia and Oceania was 15~30°N and −15~30°N respectively. In Europe, two
habitat gains were detected at latitude ranges of 0~5°N and 35~45°N, though their magnitude
was smaller than in other continents. In general, the effects of future climate change on global
geographical shifts of *L. camara* were characterized by distinct habitat gains mostly at lower
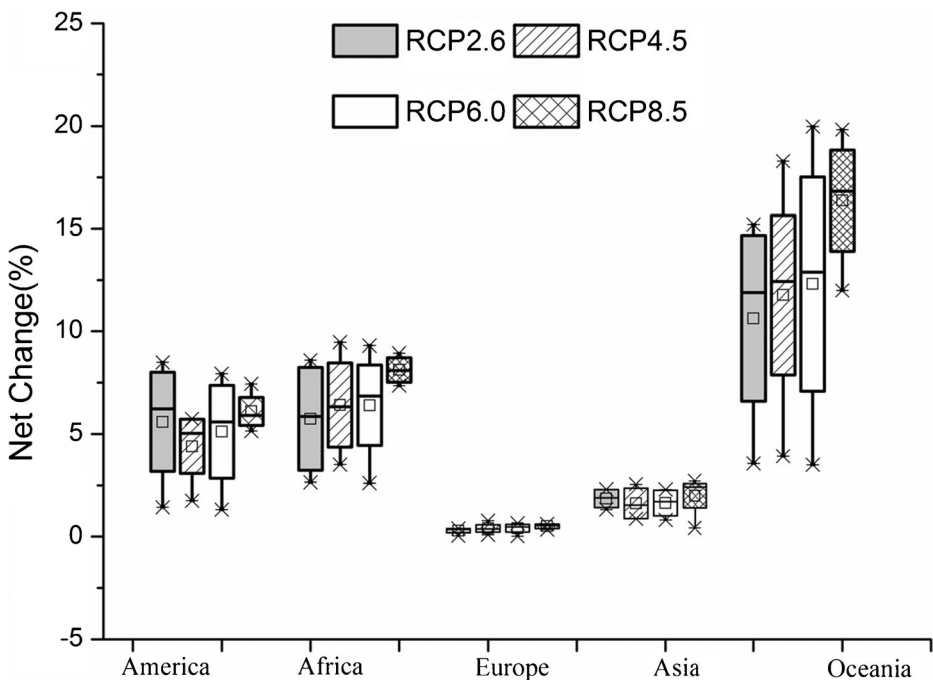

Fig. 2 Averaged net changes in *L. camara* suitability projected by the four GCMs under the four RCPs across
the five continents

latitudes, but Europe showed a somewhat mixed response. All four ISI-MIP models revealed habitat gains for this invasive species trending southward globally.

Under the four RCP emission scenarios, the range of *L. camara* expanded further inland in many regions, and was especially noticeable under the RCP8.5 level. In Africa, the range of *L. camara* shifted to parts of Tanzania, eastern Gabon, central and northwestern Congo, western Madagascar as well as the western border of Swaziland extending into Lesotho. In Australia, there was a considerable inland range expansion in southeastern Queensland and the wet tropics. Increases in new suitable habitats were found in parts of South Australia, Victoria and northern Tasmania. In Asia, a typical range shift was detected in China most notably using the HadGem2-ES and NorESM1-M models. In China, *L. camara* was predicted to spread from southeastern coastal areas (e.g. Guangdong, Hainan, Hongkong, Taiwan and southern Sichuan) to marginal areas in eastern regions.

4 Discussion

4.1 Potential distribution and range shifts

The effects of future climate on the predicted range of *L. camara* were discernible (Fig. 1). Some regions were identified as vulnerable to invasion; some invaded areas were projected to contract as they would no longer be climatically suitable, and some regions exhibited habitat gains and increased potential to be invaded. These findings highlight the complex effects of climate change on the potential geographical distribution of *L. camara* rather than simply increasing invasion risk. Predictions of further inland range expansion of this species under future climate conditions are consistent with previous findings (Taylor et al. 2012b; Taylor and Kumar 2013). These shifts in the projected potential range were relatively restricted considering the physiological tolerance limits to temperature and precipitation of this species. Therefore, the distribution of *L. camara* in the coming decades may not occur uniformly but rather more patchily reflecting the availability of favorable microhabitats (Taylor et al. 2012b). In a recent pot experiment, Zhang et al. (2014) reported that elevated temperatures led to significant increases in growth of *L. camara* along with physiological and allelopathic effects. These findings further suggest that global warming resulting from climate change is likely to facilitate invasion of *L. camara* into new regions of the world. However, given the increasing influence of direct or indirect human-induced spread of invasive species, caution is needed when interpreting the capacity or extent of species to shift their range in response to climate change.

The estimated change in the latitudinal range of *L. camara* was primarily concentrated between the 30°N and-20°S latitudes, although the suggested global distribution range occurs between 35°N and 35°S (Day et al. 2003). One exception to this projected distributional change in range was found in Europe, where changes occurred at latitudes between 35°N and −45°N. Compared with current climatic conditions, annual mean temperature (bio1) and minimum average temperature of the coldest month (bio6) across the RCP levels in Europe increased 1.9~3.5 and 1.2~2.5 °C respectively. Future fluctuations in temperature were moderately higher while precipitation declined less than in other regions, which may afford *L. camara* new opportunities to colonize European regions. Indeed in previous studies, the magnitude of future global warming was predicted to be especially high in northern latitudes (ACI 2005) such as northern Europe, and thus the likelihood of climate-induced range shifts of

invasive species would likely be more pronounced in these regions (Rahel and Olden 2008). As a major pantropical highly adaptable weed, *L. camara* may survive in natural ecosystems in these regions and will raise additional concerns about its deleterious economic and environmental impacts under future climate change. Compared with the pole-ward or altitudinal range expansion documented for numerous invasive species in response to climate change (Parmesan and Yohe 2003; McLachlan et al. 2005), the global distribution of *L. camara*, was largely restricted to the same geographical regions currently colonized. There was a equator-ward tendency however of this species expanding in response to future climate conditions.

4.2 Comparison of results and uncertainties

Based on the predicted global geographic shifts of *L. camara*, many regions of the tropics, subtropics, and warm temperate regions were modeled as having suitable climatic conditions for colonization by this species, which is consistent with current global distribution records. Compared with findings derived using the CLIMEX software (Taylor et al. 2012c), predictions of *L. camara* invasion using Maxent were more conservative despite similarities in its distribution between the two modeling approaches, especially on the African continent. CLIMEX predictions indicated that most of eastern and central Africa, parts of West Africa as well as eastern Madagascar were suitable for *L. camara*, which markedly exceeds its current known distribution in Africa. However, Maxent in this study predicted a much smaller possible range of *L. camara* fitting well with these occurrence points. Discrepancies in model projections between Taylor et al. (2012c) and the present study may be largely due to differences in the modelling methods and environmental data sets employed. The CLIMEX model predictions of a broader distribution of *L. camara* in former study was based on direct physiological measures of how a species responds, in terms of growth or tolerance for example, to specific abiotic conditions such as temperature, moisture and light (Helmuth et al. 2005). On the other hand, Maxent assesses those areas presenting suitable environmental conditions for colonization by *L. camara* based on correlations between a species' geo-referenced location data and environmental variables. Thus, CLIMEX projects the fundamental niche onto environmental space while Maxent projects the realized niche onto space. The fundamental niche, representing the ecophysiological limits to the persistence of *L. camara*, is more extensive than the realized niche, and the realized niche always occurs within the fundamental niche (Brown et al. 1996).

When assessing future changes in the geographic distribution of species with correlative models (i.e. Maxent), one fundamental assumption is the principle of niche conservatism, which states that species tend to preserve their ancestral niche requirements over time and space (Holt and Gaines 1992; Wiens et al. 2010). For invasive *L. camara*, its complex history of introductions, as well as morphological or genetically differences from original ancestral populations, could favor niche shifts due to adaptive evolution (Smith and Smith 1982; Sanders 2006; Clements and DiTommaso 2011). Recent studies have revealed the different directions of niche change in this species among continents (i.e. expansion in India vs. contraction in Australia and Africa) (Goncalves et al. 2014). However, whether the principle of niche conservatism held for this species was not tested in these previous studies or this study. Correlating current climate with the observed species distribution may therefore not identify the full potential climatic range of the species. Another important factor which has received limited attention is the effect of equilibrium state and geographic background conditions on predicting habitat changes in *L. camara* based on future climate change

scenarios (Zhu et al. 2014). Distribution of *L. camara* may not be in equilibrium with its environment (as is the case with most invasive species), due to biotic interactions, dispersal characteristics, and human management of the landscape. Therefore, the realized niches used in correlative bioclimatic envelope methodologies may not represent absolute limits to species' ranges and thus future distributions may show very different realized niches (Pearson and Dawson 2003; Huntley et al. 2010). The assumption of equilibrium is particularly violated when niche models are calibrated over a large geographic area in a non-equilibrium state (Gallien et al. 2012). If invasive *L. camara* is not in equilibrium with its environment, the climate niche quantification and transferability will be limited. In contrast, since mechanistic models (i.e. CLIMEX) do not assume equilibrium or a relationship between species occurrence and environmental data, models based on physiological restrictions to species ranges are expected to identify the absolute environmental limits more precisely (Roura-Pascual and Suarez 2008). However, mechanistic models have other limitations, such as not providing information on the current distribution of a species, nor including non-climatic factors that play important roles in determining species distributions and the dynamics of distribution change (e.g. biotic interactions, dispersal process, genetic adaptation) as well as the different tolerance ranges of individuals of a species (Soberon and Peterson 2005). Despite some questioning of the validity of bioclimatic envelope modelling strategies, it is stressed that the spatial scale at which these models are applied is of fundamental importance (Pearson and Dawson 2003). A corresponding modelling framework for addressing the environment-biota relationship in a hierarchical manner was proposed, which identified correlative models as more appropriate at global, regional and landscape scales than mechanistic models, which seem to be more accurate at finer spatial scales (Guisan and Zimmermann 2000; Soberon and Peterson 2005). Since we employed the correlative niche modelling method Maxent in this study for predicting and interpreting at broad spatial scales, where climatic factors tend to be the primary controls on distribution of *L. camara*, influences of non-climatic factors are minimized and is thus a valuable first approximation as to the potential effects of climate change on species' range expansion. For the development of bioclimatic envelope models and their major applications in the future, a strategy involving both correlative and mechanistic approaches should be conceived, and data on biotic interactions, species' adaptability to new climatic conditions as well as species' dispersal capabilities would be incorporated into distribution models for more robust predictions of a species' potential range (Roura-Pascual and Suarez 2008; Kearney and Porter 2009).

4.3 Predictions under RCPs scenarios and implications

Future projections of the potential distribution of *L. camara* under a set of RCP scenarios suggested an overall expansion in territory susceptible of being colonized. Although changes in climatic suitable regions varied among the continents, the models indicated that all continents currently colonized by *L. camara* would be susceptible to increased spread with rising RCP levels by 2050, most notably in Oceania and Africa. Our findings contrast those of Taylor and Kumar (2013) in which climatically suitable areas for *L. camara* were generally projected to contract globally under future climate change. Besides the different modeling algorithms and predictors employed, other possible reasons for the contrasting predictions may be due to the set of scenarios and GCMs used. The radiative forcing prescribed in the SRES and RCP scenarios can lead to different average temperature responses as well as seasonal and annual temperature and precipitation extremes. Climate changes simulated in the CMIP3 and CMIP5 ensembles are not directly comparable because of the differences in prescribed forcing

agents (e.g. CO_2 and aerosols) between the SRES and RCP scenarios (Rogelj et al. 2012). It is difficult to determine the exact cause of the discrepancy of GCM outputs between the two studies. Nevertheless, the results are helpful in improving our understanding of model responses to a specific radiative forcing and highlight the uncertainties in predicting species distribution shifts under future climates.

Considering the aggressive growth and reproductive habit of *L. camara*, its broad ecological tolerance and high adaptability, it is likely that with climate change, currently isolated areas of infestation in some regions of the world (e.g. coastal areas of eastern Australia, parts of Southeast Asia) will further expand. Effective regulatory strategies focused on limiting human-facilitated propagation and movement of this species, as well as close monitoring and preventive approaches must be developed and implemented. For regions such as parts of Africa that have been identified as being especially prone to increased invasion by *L. camara* under all climate models and scenarios, a more in depth understanding of the factors that affect the population dynamics of invasive species over time could have clear implications for the management and restoration of invaded ecosystems (Ramaswami and Sukumar 2013). For instance, the functional relationships and interactions between the various cultivars of *L. camara* and insect herbivores should be investigated to improve the likelihood of developing successful biological control programs (Cilliers and Neser 1991). In either case, to what extent climate determines changes in the natural distribution of aspecies and the role that other non-climatic factors play need to be considered for more robust estimates of potential range shifts with climate change (Pearson and Dawson 2003). It should be noted that using only climatic variables as explanatory variables for scenarios may produce large uncertainties and difficulties in interpreting model projections. Aside overall climatic conditions, information about habitat availability and human activity are likely to be more influential at a local scale (e.g.Willis and Whittaker 2002). For instance, a case study of *L. camara* in Australia by Taylor et al. (2012b) revealed that land-use plays an important role in determining habitat availability and hence colonization potential. When incorporating land-use data into the modelling process, more constrained distribution projections with both the reference climate and climate change scenarios were derived, which provided land managers a more accurate assessment of where management efforts would need to be targeted (Taylor et al. 2012b). These limiting factors, not included in our analysis, map help local decision-makers identify areas vulnerable to potential invasion by *L. camara*.

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