Upward Shifts in *Ageratina adenophora* Global Distributions in Response to Future Climate Change Scenarios

Gu Changjun *et al*: Upward Shifts in *Ageratina adenophora* Global Distributions in Response to Future Climate Change Scenarios

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We confirm that the authors have no conflict of interest.

Abstract

Aim: Invasive alien species (IAS) threaten ecosystems and humans worldwide, and future climate change may accelerate the expansion of IAS. Predicting the suitable distributions of IAS can prevent their further expansion. *Ageratina adenophora* is a invasive weed over 30 countries in tropical and subtropical regions. However, the potential suitable distribution of *A. adenophora* remains unclear along with its response to climate change. This study explored and mapped the current and future potential distributions of *Ageratina adenophora*.
Location: Global
Taxa: Asteraceae *A. adenophora (Spreng.)* R.M.King & H.Rob. Commonly known as Crofton weed.
Methods: Based on *A. adenophora* occurrence data and climate data, we predicted its potential distribution of this weed under current and future (four RCPs in 2050 and 2070) by MaxEnt model. We used ArcGIS 10.4 to explore the distribution characteristics of this weed and the 'ecospat' package in R to analyse its altitudinal distribution changes.
Results: The area under the curve value (>0.9) indicated excelled model performance. Among environment factors, Mean Temperature of Coldest Quarter contributed most to the model. Globally, the suitable habitat for *A.adenophora* invasion decreased under climate change scenarios, although regional increase were observed, including in six biodiversity hotspot regions. The potential suitable habitat of *A.adenophora* under climate change moved toward regions with higher elevation.
Main Conclusions: Temperature was the most important variable influencing the distribution of *A. Adenophora*. Under the background of warming climate, the potential distribution range of *A.adenophora* will shrink globally but increase regionally. The distribution of *A.adenophora* will shift toward higher elevation under climate change. Mountain ecosystems are of special concern as they are rich in biodiversity and sensitive to climate change, and increasing human activities provide more opportunities for IAS invasion.

KEY WORDS: Invasive alien species, Ecological niche modelling, Climate change, Range shift, *Ageratina adenophora*, MaxEnt

1 Introduction

Invasive alien species (IAS) are recognized as one of the main drivers of global environmental change (Simberloff et al., 2013). IAS lead to biodiversity loss (Bellard, Cassey, & Blackburn, 2016; Clavero & Garciaberthou, 2005), affect the ecosystem function and services (Vilà et al., 2010), and cause economic losses (Diagne et al., 2020; Ekesi, De Meyer, Mohamed, Virgilio, & Borgemeister, 2016; Paini et al., 2016). Climate change and anthropogenic activities such as international trade, tourism, and road network expansion, play important roles in the expansion of IAS (Bertelsmeier, Luque, Hoffmann, & Courchamp, 2015; Bertelsmeier, Ollier, Liebhold, & Keller, 2017; Wan & Wang, 2018) by providing opportunities for IAS to spread and accelerating IAS expansion (Wang, Wan, Qu, & Zhang, 2017). IAS are commonly believed to be closely related to climate change (Alexander et al., 2016; Rodríguez-Merino, García-Murillo, Cirujano, & Fernández-Zamudio, 2018; Zhao, Liu, & Zhou, 2013), and (Richardson & Rejmánek, 2011) predicted that climate change will accelerate IAS invasion. However, the relationship between IAS and climate change remains unclear since their interaction is quite complex (Merow, Bois, Allen, Xie, & Silander, 2017). Exploring the spatial patterns of potentially suitable areas for IAS at present and in the future is an effective way to prevent the further expansion of IAS (Fournier, Penone, Pennino, & Courchamp, 2019; Kaiser & Burnett, 2010; Keller, Lodge, & Finnoff, 2007). A number of recent studies have analysed the potential changes in IAS distributions under multiple climate change scenarios at regional and global scales. Species distribution models (SDMs) have been widely applied in the early detection IAS (Ahmad et al., 2019; Padalia, Srivastava, & Kushwaha, 2014; Rodríguez-Merino et al., 2018; Srivastava, Griess, & Padalia, 2018; Zhang et al., 2015; Zhao et al., 2013) by mapping potential IAS distribution and quantifying the relationships between IAS and environmental factors based on occurrence-only data and species habitat conditions (eg., climate, soil conditions, and terrain).

Ageratina adenophora (Sprengel) R. King and H. Robinson (synonym: Eupatorium adenophorum Sprengel), also known as Crofton weed, is regarded as one of the most serious invasive species in Asia, Africa, and Oceania. *A. adenophora* is native to Mexico (Qiang, 1998) and was introduced as an ornamental plant to other regions, including the United Kingdom (Auld & Martin, 1975), Hawaii (Muniappan, Raman, & Reddy, 2009), Australia (Auld, 1969), India (Bhatt et al., 2012; Poudel, Jha, Shrestha, & Muniappan, 2019a), South Africa (Kluge, 1991a), Nepal (Tiwari, 2005), and Italy (Del Guacchio, 2013). *A. adenophora* is thought to have invaded southwestern Yunnan province of China from Myanmar in the 1940s (Chen et al., 2019; Fang, Wang, & Zhang, 2019; Shen, 2019; Wang & Wang, 2006) and is classified as one of the worst IAS in China (Yan, Zhenyu, Gregg, & Dianmo, 2001; Zhang et al., 2008). After *A. adenophora* became established in Yunnan province, it moved eastward and northward into other provinces at a high speed of approximately, 20 km per year (Sang, Zhu, & Axmacher, 2010).

The ecological attributes of *A. adenophora* contribute to its invasive ability. First, it possesses strong sexual and asexual reproductive capacity (Feng, 2008). According to (Parsons, 1992), a typical plant can produce up to 10,000 seeds per season,including 7,000 viable seeds. The seeds are capable of discontinuous germination, which prolongs their viability (Shen, Zhao, & Liu, 2011). Furthermore, the size are, facilitating their spread by wind and water; the seeds of *A. adenophora* can disperse over both short and long distances (Wang et al., 2011; Zhang et al., 2008). *A. adenophora* also possesses a strong allelopathic effect, allowing it to compete with native species (Heather et al., 2011; Zhong, Duan, & Jia-Xiang, 2007). Research has shown that *A. adenophora* can alter the soil microbial community, which may inhibit native species and benefited its own growth (Niu, Liu, Wan, & Liu, 2007; Xu et al., 2012). In combination with the above traits, the high stress tolerance (Li, Qiang, & Qian, 2008a; Rivera, Villaseñor, & Terrazas, 2017) and high morphological plasticity (Shen, 2019; Zhao, Liuwenyao, & Meng, 2012) of *A. adenophora* make it an 'ideal' weed (Baker, Baker, & Stebbins, 1965). The invasion of *A. adenophora* has significantly influencd the native biodiversity and resulted in enormous economic losses (Hui, Hai-Gen, & Liu, 2007; Xianming, Yujie, Xuejun, & Shucun, 2013; Xu et al., 2006; Yu et al., 2014). Various countermeasures against *A. adenophora* invasion have been implemented, including chemical control and biological control based on its invasion mechanism; however, no single control approach is effective (Yang, Gui, Liu, & Wan, 2017).

Preventing the invasion of IAS into new potentially suitable regions is thought to be the most effective way of controlling the damage and costs to both the ecosystem and economy (Fournier et al., 2019). SDMs play an important role in risk assessment and conservation (Jiménez-Valverde et al., 2011) as they can be used to investigate the relationships between species occurrence data and the background environmental conditions (Yue, Zhang, & Shang, 2019a). Predictions can then be made based on these relationships (Galletti, Ridder, Falconer, & Fall, 2013; Yang, Kushwaha, Saran, Xu, & Roy, 2013; Zhang, Yao, Meng, & Tao, 2018). The prediction of potentially suitable areas for species makes it possible for policymakers to enact measures to prevent IAS invasion. Numerous modelling methods are available for prediction, including the generalized linear model (He, Chen, Potter, & Meentemeyer, 2019), evolutionary algorithms (Gobeyn et al., 2019), random forest (Fern, Morrison, Wang, Grant, & Campbell, 2019), bayesian hierarchical logistic mixed model (Rocchini et al., 2019) and the Maximum Entropy (MaxEnt) model (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). Although it is difficult to identify the most appropriate method (Elith, Kearney, & Phillips, 2010), MaxEnt was applied in this study because of demonstrated ability to predict species distributions and superior performance compared to other presence-only SDMs (Abolmaali, Tarkesh, & Bashari, 2018; Galletti et al., 2013; Qin et al., 2017; Tererai & Wood, 2014; Yi, Cheng, Yang, & Zhang, 2016; Zhang et al., 2018).

This study aimed to addressed the following qustions: i) What are the potential spatial patterns of *A. adenophora* under current conditions and under different future climate change scenarios? (ii) Where are the high-invasion-risk regions at present and in the future? (iii) What will happen to the invasion range of *A. adenophora* under climate change on global and regional scales? We hope that the findings of this study contribute to preventing the further invasion of *A. adenophora.*

2 Materials and methods

2.1. Environmental variables

For climate data, 19 bioclimatic variables were obtained from the WorldClim dataset (http://www.worldclim.org/), with a 1-km spatial resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The WorldClim dataset has been widely used in species distribution modelling (He et al., 2019; Jiao et al., 2019; Tan, Li, Lei, & Xie, 2019; Yue, Zhang, & Shang, 2019b). Two versions of the WorldClim dataset are available (version 2.0 and version 1.4). The dataset includes past and future (version 1.4 only) climate conditions at four different resolutions (10 min, 5 min, 2.5 min, and 30 s). Version 1.4 with a resolution of 30 s was selected for use in this study, and the average data for the years 1970–2000 were used to represent the current climate conditions. The climate projections in WorldClim come from the Fifth Assessment Report of the Intergovernmental Panel on Climate Change and have been downscaled and calibrated. To indicate future climatic scenarios, we chose the data for 2050 and 2070 under four representative concentration pathways (RCPs): RCP26, RCP45, RCP60, and RCP85 (Ahmad et al., 2019). Soil data were downloaded from (http://soilgrids.org) at a resolution of 1-km, and 12 soil variables were selected to indicate the soil conditions (Staff, 2014). Terrain factors were derived from digital elevation model data, which were downloaded at (http://srtm.csi.cgiar.org/) and included elevation, slope, and aspect. We obtained land cover data at 1-km resolution from the the EarthEnv dataset (https://www.earthenv.org/landcover), which integrates multiple global land-cover datasets (Tuanmu & Jetz, 2015). For many applications in biodiversity and ecology, existing remote sensing-derived land cover products are limited by inconsistency issues and their typically non-continuous nature. The consensus product with the generalized scheme better captures land-cover heterogeneity and has improved utility for modelling species distributions. Two versions of the dataset are available: the full version and reduced version. The former dataset integrates GlobCover (2005-06; v2.2), the MODIS land-cover product (MCD12Q1; v051), GLC2000 (global product; v1.1), and DISCover (GLCC; v2); the latter only includes the first three datasets. In this study, we used the full version which includes 12 land-cover classes. The values of each land-cover class range from 0 to 100, representing the consensus prevalence in percentage.

To avoid model overfitting caused by multicollinearity between the selected variables (Dormann et al., 2013), Pearson's correlation analysis was performed and only those variables with correlation coefficient (r^2) < 0.75 were selected (see Supporting Information). For instance, if absolute value of the cross-correlation coefficient between two variables exceeded 0.75, only the variable that captured more information was selected (Table 1).

2.2. Species occurrence data

Species occurrence data were downloaded from the Global Biodiversity Information Facility (https://www.gbif.org/, accessed 03 September 2018) and the Chinese Virtual Herbarium (http://www.cvh.ac.cn/, accessed 03 September 2018). Furthermore, we collected some samples during the fieldwork in the Tibetan Plateau in 2016. A total of 5,474 occurrence points were initially recorded. Occurrence records are often biased toward geographically convenient or environmentally friendly (e.g., areas near cities or areas with high population density), resulting in sampling bias in geographic space. Thus, spatial thinning was performed to remove the spatial autocorrelation and sampling bias. Grid cells with dimensions of 10×10 km were created, and a single occurrence point was selected randomly from each cell with more than one occurrence point (Ahmad et al., 2019). A total of 741 unbiased occurrence data points from regions in Asia (74 points), Africa (68 points), Australia (344 points), Oceania (70 points), North America (101), and South America (two points) were saved in CSV format (Figure 1). The native and introduced regions were delineated according to the biogeographical distribution scheme of the United States Department of Agriculture's Germplasm Resource Information Network (https://npgsweb.ars-grin.gov, accessed 04 September 2019).

2.3. Modeling approach and spatial analysis

We applied Maxent, version 3.3.3k (available athttp://biodiversityinformatics.amnh.org/open_source/maxent/) (Phillips, Anderson, & Schapire, 2006)) to predict the potential distribution of *A. adenophora*. As one of the most effective presence-only algorithms available, Maxent has been shown to perform better than other models and its quite robust when the occurrence points are in small size (Elith et al., 2006; Jarnevich, Holcombe, Barnett, Stohlgren, & Kartesz, 2010; Wisz et al., 2008). Seventy percent of the occurrence points were selected for model training, while the other 30% were used for model validation. The model output represented the probability of presence from 0 to 1 (Phillips & Dudík, 2008). The area under the curve (AUC) of the receiver operating characteristic (ROC) curve was used to evalute the model performance. The AUC value ranges from 0 to1, an AUC value between 0.5 and 0.7 indicates that the model performance is not acceptable, AUC in the range of 0.7-0.9 indicates good performance, and AUC >0.9 indicates the highest predictive ability (Abdelaal, Fois, Fenu, & Bacchetta, 2019; Phillips et al., 2006).

The most commonly used framework combines occurrence records from both the native and introduced regions by using distribution data from the native range, this strategy makes use of those occurrence records that are likely to be in equilibrium with the regional environment while also including records from introduced regions which may provide additional information about expansion into novel ranges. Four arbitrary categories of invasion risk for *A. adenophora* were defined as No Risk (NR, <0.2), Low Risk (LR, 0.2–0.4), Moderate Risk (MR, 0.4-0.6), and High Risk (HR, >0.6) based on predicted habitat suitability (Xu, Zhuo, Wang, Ye, & Pu, 2019; Zhang et al., 2018; Zhang et al., 2019). In this study, we defined a region as an under-risk (UR) region when its risk category was LR, MR, or HR. Based on the predicted results for the current climate conditions and eight RCPs, the risks of invasion by *A. adenophora* in different areas were calculated using ArcGIS 10.4.1 based on the four arbitrary categories defined above. To explore the variation in the distribution of *A. adenophora* with altitude under climate change scenarios, the 'ecospat' package in R was applied (Di Cola et al., 2017).

3 Result

3.1 Model performance and main variables

The AUC value for *A. adenophora* obtained using the MaxEnt model was 0.97 (Figure 2), indicating excellent model performance. The jackknife test of the model indicated that the following major variables contribute significantly to the distribution of *A.adenophora* (Table 2): Mean Temperature of Coldest Quarter (bio11, 47.5%), Evergreen Broadleaf Trees (consensus_full_class_2, 22.9%), Urban/Built-up (consensus_full_class_2, 6.5%), Barren (consensus_full_class_2, 5.8%), Mean Temperature of Warmest Quarter (bio10, 2.8% of variation), Cation exchange capacity of soil (cecsol_m_sl3_1km_ll, 2.2%), Soil pH (phihox_m_sl3_1km_ll,1.4%), Coarse fragments volumetric (crfvol_m_sl3_1km_ll,1.3%), and Precipitation Seasonality (bio15,1.1%). Among the variable types, climate factors made the largest contribution to the distribution of *A. adenophora* in our model (51.4%), with Mean Temperature of Coldest Quarter having the largest contribution (47.5%). Land cover variables were the second most influential, with Evergreen Broadleaf Trees having the greatest contribution among land cover factors. Soil conditions and terrain factors had relatively small contributions to the distribution of *A. adenophora*.

Based on the response curves of the eight environmental variables to distribution probability (Figure 3), the suitable ranges with respect to the different variables are as follows. The suitable Mean Temperature of Coldest Quarter ranges from 2°C to 22°C. *A. Adenophora* is adapted to Evergreen Broadleaf Trees and Urban/Built-up regions. The probability of *A. Adenophora* distribution decreases with decreasing Barren land. The suitable range of Mean Temperature of Warmest Quarter is −2.5°C to 31°C. The probability of *A. Adenophora* distribution increases with increasing soil Cation Exchange Capacity. According to petri dish experiments conducted by (Lu et al., 2006), the optimal soil pH for *A. adenophora* ranges from 5.5–6.5, with maximum germination occurring at pH 5.7. As soil Coarse Fragments Volumetric increases, the probability of *A. adenophora* distribution decreases, particularly for values exceeding 20%. Precipitation Seasonality (Coefficient of Variation) have little influence on the distribution of *A.adenophora*. According to the model, temperature had a strong effect on the distribution of *A. Adenophora*, and this species prefers a warm climate. Among land cover types, *A. Adenophora* is mainly distributed in Evergreen Broadleaf Trees, Urban/Built-up, and Barren lands. Globally, evergreen broadleaf trees are mainly distributed in subtropical and warmer temperate regions, it shows the obvious similarity between this land cover and species occurrence points. Compared to temperature and land cover variables, soil conditions and precipitation factors have little effect on the distribution of *A. adenophora*.

3.2 Current invasion pattern of *A. adenophora*

Figure 4 shows the percentages of areas in different risk categories under current climate conditions. According to the global map of potential *A. Adenophora* distribution, the total area of UR regions was 5,364,220.33 km^2, of which 306,172.76 km^2 was classified as HR. The areas of MR and LR regions were 1,271,142.83 km^2 and 3,786,904.74 km^2, respectively. Most UR regions for *A. adenophora* invasion were located in Mexico, the eastern coastal part of the United States, the southern part of Chile, the central parts of Peru and Bolivia, the southern coastal part of South Africa, most parts of Ethiopia and Madagascar, the eastern coastal part of Australia, most parts of the central Himalaya in India and Nepal, the southwestern region of China, most of Taiwan, the eastern parts of Myanmar, most parts of Laos and the Korean peninsula, and large parts of Japan. Among these regions, the regions classified as HR are mainly distributed in Chile, the eastern coastal part of Australia, and the central Himalaya.

There are currently 36 recognized biodiversity hotspot regions (BHRs) worldwide. Figure 5 shows the estimated potential invasion range of *A. adenophora* in these BHRs. At present, 3,813,692.44 km^2 of the UR area is found in BHRs, accounting for approximately 71% of the total UR area in the world; the BHR areas classified as LR, MR, and HR are 2,542,359.97, 996,626.20, and 274,706.27 km^2, respectively. The BHR areas classified as LR, MR, and HR account for approximately 67.14%, 78.40%, and 89.72% of the total worldwide areas classified as LR, MR, and HR, respectively. The BHR containing the largest UR area (531,980.29 km^2) is the Indo-Burma BHR in Southeast Asia, which comprises all non-marine parts of Cambodia, Laos, Myanmar, Thailand, and Vietnam along with parts of southern China. This area also contain the largest LR area (372,108.89 km^2) and MR (141,323.95 km^2) area and is one of the most biologically important regions on the planet. Among BHRs, the Forests of East Australia BHR has the largest area are classified as HR (64,041.83 km^2) and also the largest UR proportion (83.72%) of the total area. This BHR consists of a discontinuous coastal stretch along the Australian states of Queensland and New South Wales and extends inland and further west to include the New England Tablelands and the Great Dividing Range. The areas classified as HR and MR in the Forests of East Australia BHR account for approximately 26% and 29% of the BHR's total area, respectively.

3.3 Potential distribution of *A. adenophora* under different future climate change scenarios

The potential suitable regions for *A. adenophora* invasion were analysed under the eight different future climatic scenarios (RCP2.6, RCP4.5, RCP6.0, and RCP8.5 in 2050 and 2070). The results indicate that the potential distribution range of *A.*

adenophora will shrink under all RCPs (Figure 6, Table 3). Compared to current conditions, the increase in the area classified as NR ranged from 1.23% under RCP2.6 2070 to 1.71% under RCP8.5 2070. The area classified as LR decreased under all RCPs compared to current conditions, with the decrease ranging from 30.44% (RCP2.6 2070) to 45.64% (RCP8.5 2070) with an average of 35.6% (the largest decline among risk categories). The areas classified as MR and HR also decreased with respect to current conditions, with average decreases of 23.39% and 23.92%, respectively. Analysing the spatial patterns of the potential distribution regions indicated that the decreases in areas classified as LR and MR compared to current conditions were mainly distributed in the southern parts of Mexico, Guatemala, Nicaragua, Costa Rica, the central parts of Peru and Bolivia, the southern parts of Chile, Nigeria, the southern parts of South Africa, western Madagascar, the central Himalaya, western and eastern Myanmar, Northern Laos, southwestern China, the entire Korean Peninsula, and Japan (Figure 6). Although the UR areas in different categories generally showed the same shrinking trend under the future climate change scenarios, the opposite trend was observed in some regions. For example, some areas categorized as NR or LR for *A. adenophora* invasion under current climate conditions will become MR or even HR areas under future climate change scenarios, including Northwestern California, southern Chile, southern South Africa, the central Himalaya, and Southwestern China (western Tibet). In summary, the regions suitable for *A. Adenophora* invasion (those classified as LR, MR, or HR) decreased under the future climate change scenarios, although the opposite trend was observed on a regional scale.

Similarly, the UR area within BHRs decreased under the future climate change scenarios compared to under current conditions. According to the predicted results, the UR area in BHRs will decrease from 3,813,692.44 km^2 under current conditions to an average of 2,486,854.44 km^2 under the eight RCPs, with the largest decrease (decreased by 1,682,145.406 km^2) occurring under RCP8.5 in 2070. The average decreases in areas classified as LR, MR, and HR within BHRs were 38.09%, 28.66%, and 26.54%, respectively, with the largest corresponding decreases being 49.61% under RCP8.5 in 2070, 34.49% under RCP8.5 in 2070, and 30.39% under RCP2.6 in 2050, respectively.

In 29 out of 36 BHRs, the UR area decreased under the future climate change scenarios with respect to under current conditions, and the largest average decrease occurred in the Mesoamerica BHR (319,824.90 km^2). Increases in UR area were observed in only six BHRs: California Floristic Province, Cape Floristic Region, Chilean Winter Rainfall and Valdivian Forests, Maputaland-Pondoland-Albany, Mountains of Southwest China, and New Zealand. As shown in Figure 7, obvious increasing trends in UR area can be observed in the Chilean Winter Rainfall and Valdivian Forests, New Zealand, and Mountains of Southwest China BHRs; the UR areas in the California Floristic Province and Cape Floristic Region BHRs remained relatively flat. Among the BHRs, the largest increase (increased by 115.21%) in UR area was found in the Maputaland-Pondoland-Albany BHR under RCP8.5 in 2070.

3.4 *A. Adenophora* distribution characteristics with elevation under current conditions and climate change scenarios

Under current conditions, the UR regions are mainly distributed at elevations below 2500 m; these regions account for approximately 96.46% of the total UR area, with areas at elevations under 500 m accounting for 35.51% (Table 4). The areas classified as LR, MR, and HR show similar distributions with elevation; these areas are primarily distributed in low-elevation regions, and the distribution probability of *A. adenophora* decreases with increasing elevation. Regions with elevations below 2500 m are also the main distribution areas of *A. Adenophora* under the eight RCPs. UR areas at elevations below 2500 m decreased under all RCPs compared to under current conditions, except for regions at elevations between 2000 and 2500 m under RCP 6.0 in 2050. The UR areas at elevations between 500 and 1000 m is currently around 1,191,096.03 km^2; this value decreased by an average of 55.07% under the eight RCPs, with the largest decrease (65.91%) occurring under RCP8.5 in 2070. The URs at elevations between 1000 and 1500 m decreased by an average of 42.78% under the eight RCPs. The URs at elevations between 1500 and 2000 m decreased by an average of 21.99 % under all RCPs compared to under current conditions. This decreasing trend is getting small with the elevation rise up. For example, UR areas at elevations between 2000 and 2500 m decreased by only an average of 1.84 % under eight RCPs.

However, increasing trend was observed in UR areas above 2500m. The UR areas with elevations between 2500 and 3000 m increased by an average of 41.84% under the eight RCPs. This value increased to 143.20% when UR areas with elevations between 3,000 and 3,500 m. When the UR areas are at an altitude of more than 3500 m, it only take no more than 3% of the total UR areas. The same phenomenon was observed in the areas classified as LR, MR, and HR. Under current climate conditions, the areas classified as LR, MR, and HR are primarily distributed in regions with elevations below 500 m (36.33%, 29.93%, and 48.61%, respectively). Under all RCPs, LR, MR and LR areas with elevations below 2500 m decreased compared to under current conditions, except for HR areas with elevations between 3500 to 4000m under RCP 2.6 in 2050 and 2070, while the opposite trend was observed for elevations from 2500 to 4000 m.

A further analysis about the *A. Adenophora* distribution along with the elevation was depicted in Figure 8, compared to under current conditions, the percentages of UR areas at elevations less than 1500 m clearly decreased under future climate scenarios, while the opposite trend was observed for UR areas at elevations above 1500 m. For example, under RCP 8.5 in 2070, the percentage of UR areas at elevations between 3000 and 3500 m (3.58 %) is nearly fivefold higher than that under current climate conditions. Thus, *A. Adenophora* tended to move toward higher elevations under the climate change scenarios.

4 Discussion

IAS have caused enormous economic losses and threaten biodiversity globally. The continental accumulation of IAS is predicted to increase by 36% from 2005 to 2050 (Seebens et al., 2020). The most effective way to prevent damages caused by IAS is to predict their potential distributions and take measures to limit their spread to new areas (Fournier et al., 2019). *A. adenophora* has proven to be a very aggressive invasive species in some parts of the world, including China, Australia, Mexico, and South Africa. These regions have enacted costly measures to control the spread of *A. adenophora*. Therefore, it is of great significance to predict the potential distribution patterns of *A. adenophora* under current climate conditions and future climate change scenarios.

SDMs have been widely applied to predict the potential distributions of IAS based on niche conservatism, which assumes that an IAS will retain a similar niche in the native and introduced regions (Ahmad et al., 2019; Graham, 2005). Recent research has indicated that niche expansion of IAS is very limited in the native and introduced ranges, suggesting that niche models can be used to predict IAS responses to climate change (Datta, Schweiger, & Kühn, 2019; Liu, Wolter, Xian, & Jeschke, 2020). The MaxEnt model has been shown to outperform the other available SDMs (Hernandez, Graham, Master, & Albert, 2006; Li, Chang, Liu, & Zhang, 2019; Merow, Smith, & Silander, 2013). In this study, we built nine MaxEnt models according to the species occurrence data and climate data under current and future scenarios (four RCPs for two time periods, 2050 and 2070) together with terrain factors, soil conditions, and land cover data. To avoid overfitting, Spearman's rank correlation was used to examine the cross-correlation of all variables and remove the highly correlated variables (Spearman's coefficient > 0.75) (Hu & Liu, 2014). We also applied spatial thinning to remove the spatial autocorrelation and sampling bias of the occurrence data for *A. Adenophora* (Ahmad et al., 2019). The AUC value of the model was 0.972, indicating excellent model performance (Phillips et al., 2006). The predicted distribution shows the same spatial pattern as the current global distribution of *A. adenophora*. To the best of our knowledge, this is the first study to model the potential distribution of *A. adenophora* at a global scale under both current and future climate scenarios.

4.1 Effect of temperature change on the distribution of *A. adenophora*

Previous studies have shown that *A. adenophora* is invasive in tropical and subtropical regions, including Asia (China, India, and Nepal), Oceania (eastern Australia and New Zealand), Africa, and North America (Cronk & Fuller, 1995; Del Guacchio, 2013; Kluge, 1991b; Tererai & Wood, 2014; Wang & Wang, 2006). According to our results, the potentially suitable habitats for *A. adenophora* invasion under current climate conditions are mainly distributed in Mexico and the southeastern United States in North America; the southern part of Chile and the central parts of Peru and Bolivia in South America; the southern coastal part of South Africa, Ethiopia, and Madagascar in Africa; the eastern coastal part of Australia in Oceania; the central Himalaya in India and Nepal, the southwestern region of China and most of Taiwan, eastern Myanmar, most parts of Laos and the Korean peninsula, and large parts of Japan in Asia. This concurs with previous findings. Furthermore, we found that over 70% of the UR areas are distributed in the 36 BHRs, which are distributed in tropical and subtropical regions. Previous studies have shown that the expansion of IAS might become apparent later in invasion events and consequently have extensive negative effects on native species and the overall stability of native ecosystems (Adams et al., 2015; Mainali et al., 2015; Pyšek et al., 2012; Roger et al., 2015; Vicente et al., 2013). From this point of view, the invasion of *A. adenophora* may have serious consequences in these regions.

According to the growth environment of this weed and previous studies, the temperature is major factor controlling the distribution of *A. adenophora*. A study by Wang et al., (2017) found that the temperature during winter is the most influential factor affecting the distribution of *A. adenophora* in China. The research results of Thapa et al., (2018) showed that the Minimum Temperature of Coldest Month is the most significant variable in the western Himalaya. Among environmental factors, temperature, particularly the low temperature, is the main factor governing the distribution of *A. adenophora* (Li, Qiang, & Qian, 2008b; Wang et al., 2017). The abovementioned studies support our finding that Mean Temperature of Coldest Quarter (Bio11) was the most important factor (47.5% contribution to the model) governing the distribution of *A. adenophora*. In general, areas with warm temperatures and moist conditions are climatically suitable for invasion by *A. adenophora*, which prefers temperatures in the range of 10°C–25°C (Tererai & Wood, 2014). Thus, changes in temperature will significantly affect the distribution of *A. adenophora*. He et al., (2012) demonstrated that experimental warming increase the biomass production and canopy of *A. adenophora* and reduced mortality in comparison with its native neighbours. This means that global warming may create favourable conditions for the invasions of *A. adenophora* by promoting its growth and environmental tolerance (Poudel, Jha, Shrestha, & Muniappan, 2019b). Based on the four RCPs used in this study, global warming will continue for some decades. In theory, climatically suitable areas of *A. adenophora* in the future would expand to other regions under the background of climate warming. Chong et al., (2017) predicted that the suitable habitat of *A. adenophora* would expand in southwest China under climate warming scenarios. A similar expansion is also expected in the western Himalaya under future global warming (Lamsal, Kumar, Aryal, & Atreya, 2018). However, we found that the suitable habitat for *A. adenophora* decreases obviously on a global scale under the four RCPs in 2050 and 2070 compared to under current conditions. A likely explanation is that *A. adenophora* will shift upslope under future climate conditions and thus face consistent reductions in the area that this species can occupy (Liang et al., 2018).

4.2 *A. adenophora* will shift toward higher elevation under future climate change scenarios

Under global warming, some species will migrate to higher latitudes or higher elevations to adapt to climate change (Bertrand et al., 2011; Hackett et al., 2008; Root et al., 2003), especially in mountain ecosystems (Felde, Kapfer, & Grytnes, 2012). Under current climate conditions, the distribution of *A. adenophora* with respect to elevation is similar in native and introduced regions. *A. adenophora* is distributed in areas with elevations ranging from 520 to 3200 m in its native range (Mexico) (Sang et al., 2010), while it is found at elevations between 330 and 2500 m in China (Wang & Wang, 2006) and between 400 and 3280 m in Nepal (Shrestha, Sharma, Devkota, Siwakoti, & Shrestha, 2018). According to Sunil et al., (2018), *A. adenophora* is expected to move to elevations up to 3547 m a.s.l. by 2070. Our results show that the spatial pattern and altitudinal distribution of this weed change under future climate change scenarios. In the altitude range of 500–1500 m, UR areas decreased under the eight RCPs, while the opposite trend was observed for elevations exceeding 1500 m. To explore the response of *A. adenophora* to climate change in mountain ecosystems, we further analysed the change in altitudinal distribution in the Hengduan Mountainous BHR, which has suffered severe damage due to the invasion of *A. adenophora*.

Interestingly, we found that the distribution of *A. adenophora* moved toward higher elevation in the Hengduan Mountainous BHR under the future climate change scenarios (Figure 9 andFigure 10), with areas at elevations of 2500–3000 m accounting for the largest proportion of UR areas (average of 26.46%) under all RCPs except RCP 2.6 2070. It is worth noting that the UR areas at elevations below 2000 m decreased under all RCPs compared to under current conditions. For example, UR areas with elevations below 2000 m account for 42.41% of all UR regions under current conditions; this percentage decreased to 27.65% under RCP8.5 2070. Nevertheless, UR areas with elevations between 2000 and 3500 m increased under all RCPs. Under current climate conditions, the UR areas are primarily distributed at elevations of 2000–2500. However, under RCP8.5 2070, the UR areas are primarily found at elevations of 2500–3000 m. This phenomenon was also observed in the Himalayas (Figure 11). As shown in Figure 11, *A. adenophora* shows an obvious trend of expansion into higher altitudes in the Himalayan region.

Biological invasions are considered to be the second most severe threat affecting biodiversity (Fournier et al., 2019). Montane ecosystems, which have high biodiversity and are sensitive to climate change, are of particular concern under climate warming (Dullinger et al., 2012). Among terrestrial ecosystems, mountain ecosystems and particularly high mountains are often considered to be at low risk of invasion (Pauchard et al., 2009). However, the invasion process is driven by a combination of climate change and human activities (Alexander et al., 2016). Increasing anthropogenic activities offer more opportunities for the invasion of non-native species, and road networks are regarded as the major pathway for IAS invasion. There will be at least 25 million kilometres of new roads anticipated by

2050, with developing countries accounting for 90% of this increase.(Laurance et al., 2014). This will provide opportunities for the establishment of non-native species and conduits for their dispersal (Becker, Dietz, Billeter, Buschmann, & Edwards, 2005); roads and trails are recognized as major pathways for invasion into mountains (Fuentes, Ugarte, Kühn, & Klotz, 2010; Lembrechts J J, 2014; Pauchard & Alaback, 2004). Hence, a detailed assessment of the effects of road infrastructure on biodiversity is needed given the rapid expansion of road networks.

4.3 Uncertainty

The limitations of this study can be summarized as follows. Since MaxEnt is an ecological niche model, only the abiotic factors were taken into consideration (Ahmad et al., 2019; Xu et al., 2019). As indicated by the "BAM" (abiotic factors, biotic factors, and movement) diagram (Pauchard & Alaback, 2004), the distribution of a species is governed not only by abiotic factors, but also biotic factors including interactions between species and dispersal ability. In this study, the land cover conditions along with climate variables were used as input to the model; however, we assumed that the land cover conditions would remain unchanged in the future. Climate factors were considered to be the principal factors in other global- or country-scale studies of species distribution. To better understand the influence of climate change on species distribution, the intraspecific interactions and changes in land cover should be taken into consideration. Furthermore, the current climate conditions in this study are not "current" for the current climate data derived from interpolations of observed data (representative of 1960–2000). During the past two decades, the world climate has changed greatly, which may affect the accuracy of the model (Wang et al., 2018). Finally, although we have determined the regions of native occurrence from all records, the artificial introduction of *A. adenophora* was not taken into consideration. This may explain why the occurrence of *A. adenophora* is always near Urban/Built-up regions.

5 Conclusions

Detecting the potential suitable regions for species invasion is of great significance for preventing IAS invasion. Based on the MaxEnt model, the potential invasion ranges of *A. adenophora* under current and future climate conditions were evaluated. Our results show that the potential invasion range of *A. adenophora* is mainly distributed in subtropical and warmer temperate regions, including southwestern America, Chile, the Himalayas, southwestern China, and southeastern Australia. Among environmental factors, the Mean Temperature of Coldest Quarter contributes the most to the model, and the optimal temperature range for this species is 8°C–16°C. Although the invasion range of *A. adenophora* will shrink globally under all RCPs, the invasion risk will increase in six biodiversity hotspot regions (BHRs), such as the Hengduan Mountainous region, with a clear trend toward higher elevations under future climate scenarios. The findings provide reference information for developing appropriate management strategies to prevent the establishment and further spread of *A. adenophora* across the globe, especially in BHRs.

6 Tables

Table 1 Environmental variables used in the MaxEnt model

Code	Description
bio-2	Mean Diurnal Range
bio-10	Mean Temperature of Warmest Quarter
bio-11	Mean Temperature of Coldest Quarter
bio-15	Precipitation Seasonality
bio-17	Precipitation of Driest Quarter
bio-18	Precipitation of Warmest Quarter
bio-19	Precipitation of Coldest Quarter
BLDFIE_M_sl3_1km_ll	Bulk density (fine earth, oven dry) in kg / cubic-meter
CECSOL_M_sl3_1km_ll	Cation exchange capacity of soil in cmolc/kg
CLYPPT_M_sl3_1km_ll	Clay content (0-2 micro meter) mass fraction in %
CRFVOL_M_sl3_1km_ll	Coarse fragments volumetric in %
OCDENS_M_sl3_1km_ll	Soil organic carbon density in kg per cubic-m
ORCDRC_M_sl3_1km_ll	Soil organic carbon content (fine earth fraction) in g per kg
PHIHOX_M_sl3_1km_ll	Soil pH x 10 in H2O
PHIKCL_M_sl3_1km_ll	Soil pH x 10 in KCl
SLTPPT_M_sl3_1km_ll	Silt content (2-50 micro meter) mass fraction in %
consensus_full_class_1	Evergreen/Deciduous Needleleaf Trees
consensus_full_class_2	Evergreen Broadleaf Trees
consensus_full_class_3	Deciduous Broadleaf Trees
consensus_full_class_4	Mixed/Other Trees
consensus_full_class_5	Shrubs
consensus_full_class_6	Herbaceous Vegetation
consensus_full_class_7	Cultivated and Managed Vegetation
consensus_full_class_8	Regularly Flooded Vegetation
consensus_full_class_9	Urban/Built-up
consensus_full_class_10	Snow/Ice
consensus_full_class_11	Barren
consensus_full_class_12	Open Water
elevation	————

slope	————
aspect	————

Table 2 Main variables in the MaxEnt model of *A. adenophora* under current climate conditions

Variable	**Percent contribution**	**Permutation importance**
bio_11	47.5	47.5
consensus_full_class_2	22.9	70.4
consensus_full_class_9	6.5	76.9
consensus_full_class_11	5.8	82.7
bio_10	2.8	85.5
cecsol_m_sl3_1km_ll	2.2	87.7
phihox_m_sl3_1km_ll	1.4	89.1
crfvol_m_sl3_1km_ll	1.3	90.4
bio_15	1.1	91.5

Table 3 Area in square kilometres (km^2) and rate of changes in the areas classified as different risk rank under future climatic scenarios for two time periods (2050 and 2070).

Risk rank	Current (km^2)	RCP2.6 (%)		RCP4.5 (%)		RCP6.0 (%)		RCP8.5 (%)	
		2050	2070	2050	2070	2050	2070	2050	2070
NR	125,115,100.00	1.23	1.21	1.32	1.38	1.24	1.39	1.51	1.71
LR	3,786,904.74	-30.44	-30.11	-33.94	-35.40	-32.72	-37.42	-39.12	-45.64
MR	1,271,142.83	-23.20	-22.84	-23.37	-23.97	-20.11	-21.43	-25.26	-26.94
HR	306,172.76	-29.87	-28.98	-23.75	-26.13	-19.86	-14.51	-26.74	-21.49
UR	5,364,220.33	-28.69	-28.32	-30.85	-32.16	-29.00	-32.33	-35.13	-39.83

Table 4. Distributions of UR regions in different elevation ranges under current conditions and the eight RCPs

Elevation (m)	Current (km^2)	RCP2.6 2050(%)	RCP2.6 2070(%)	RCP4.5 2050(%)	RCP4.5 2070(%)	RCP6.0 2050(%)	RCP6.0 2070(%)	RCP8.5 2050(%)	RCP8.5 2070(%)
<500	1,908,804.21	-30.35	-29.57	-32.76	-32.89	-31.69	-34.88	-36.63	-39.66
500−1000	1,191,096.03	-49.13	-48.80	-53.76	-56.00	-51.42	-56.25	-59.32	-65.91
1000−1500	964,855.44	-35.72	-35.41	-39.77	-43.30	-37.09	-43.39	-47.61	-59.95
1500−2000	685,939.53	-18.47	-17.83	-20.15	-22.36	-17.94	-21.38	-25.34	-32.49
2000−2500	434,080.22	-1.21	-1.73	-0.94	-1.70	1.29	-0.33	-2.75	-7.36
2500−3000	143,383.84	34.01	32.19	41.74	41.94	42.98	47.00	45.51	49.39

3000−3500	35,553.71	97.03	93.62	133.14	141.62	131.68	161.94	161.03	225.52
3500−4000	9,017.92	193.78	190.10	297.71	371.85	290.50	424.33	429.01	745.04
4000−4500	1,858.92	-46.97	-48.34	23.60	113.55	11.23	158.24	177.20	1002.21
>4500	266.77	-66.05	-62.60	-38.73	-34.75	-43.77	-13.79	-20.95	99.73

7 Figures:

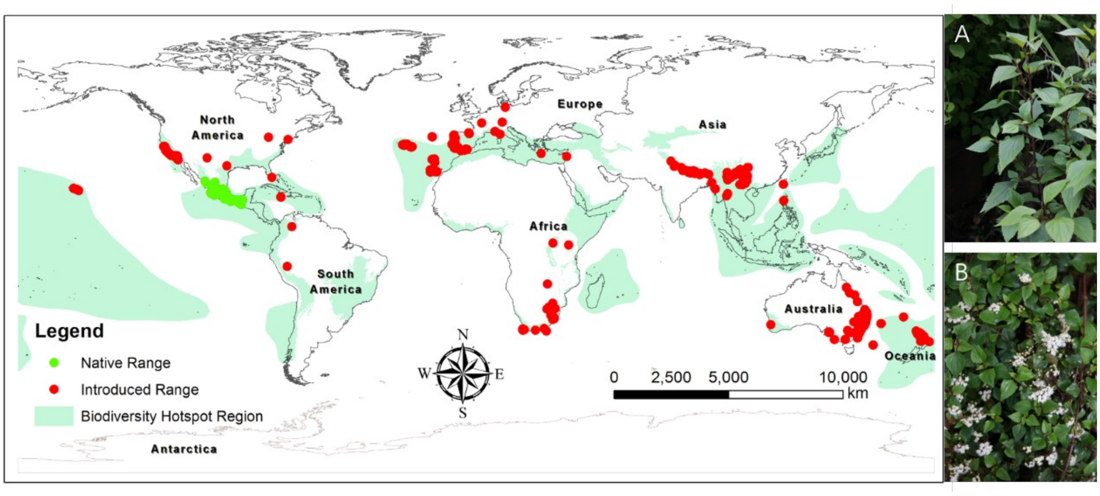


Figure 1. Spatial distribution of *A. adenophora* occurrence. Green points denote native regions, while red points denote introduced or invasive regions. Photos A and B show *A. adenophora*. The purple-coloured regions show BHRs, which are Earth's most biologically rich and threatened terrestrial regions (Myers, Mittermeier, Mittermeier, Da, & Kent, 2000).

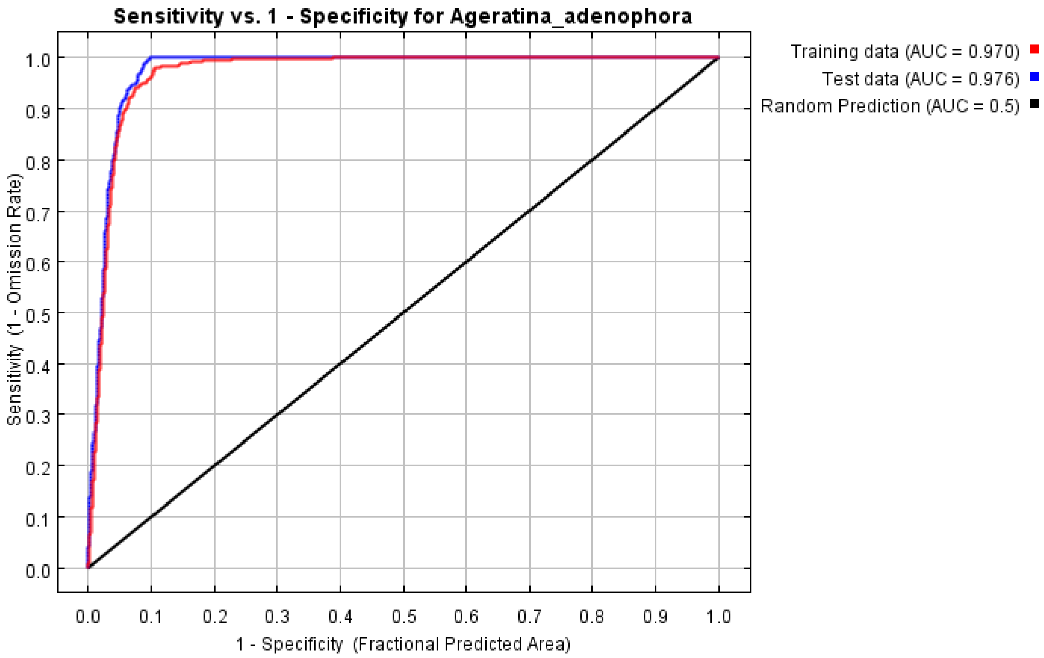


Figure 2 ROC curve and AUC value under current climate conditions

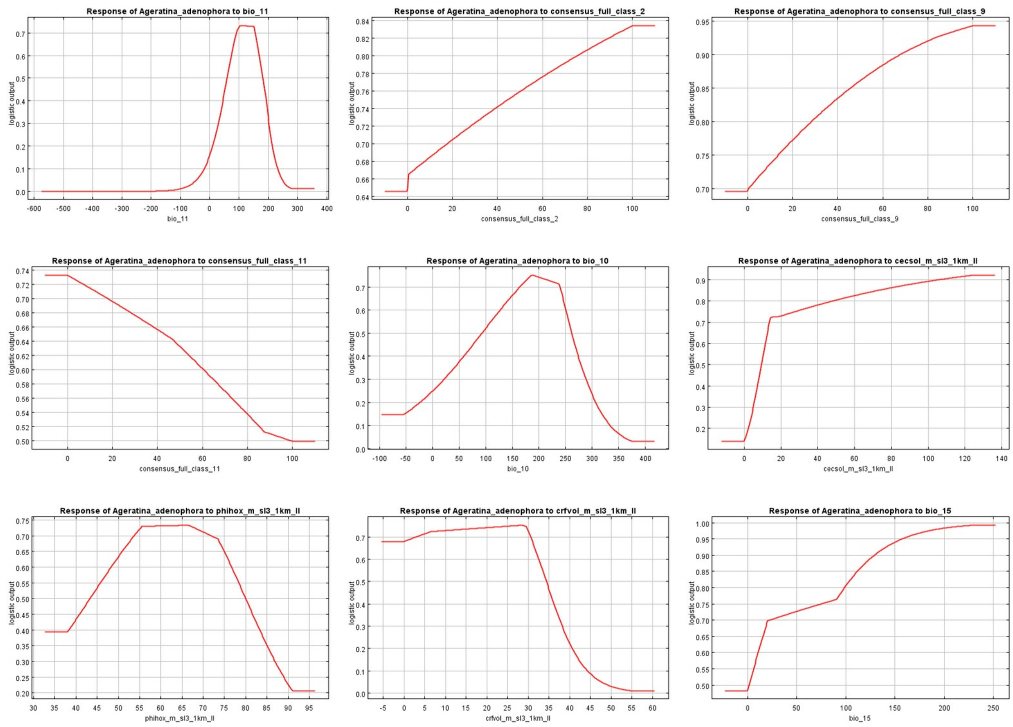


Figure 3 Response curves for the eight main environmental variables affecting the potential distribution of *A. adenophora*. The thresholds of suitability were set as existence probability greater than 0.2.

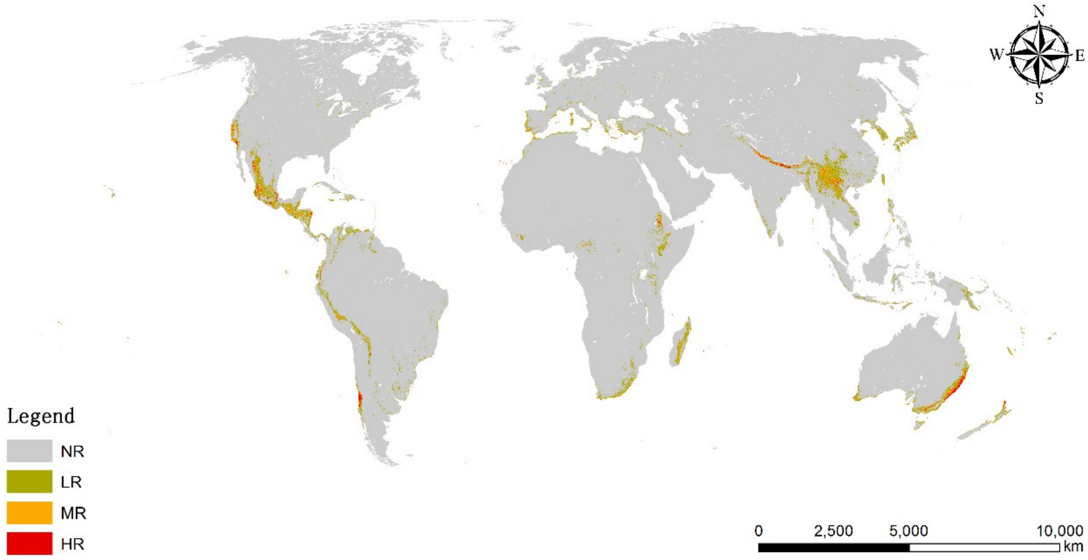


Figure 4 Potential spatial distribution of *A. adenophora* under current climate conditions. NR, LR, MR, and HR denotes No Risk, Low Risk, Moderate Risk, and High Risk, respectively.

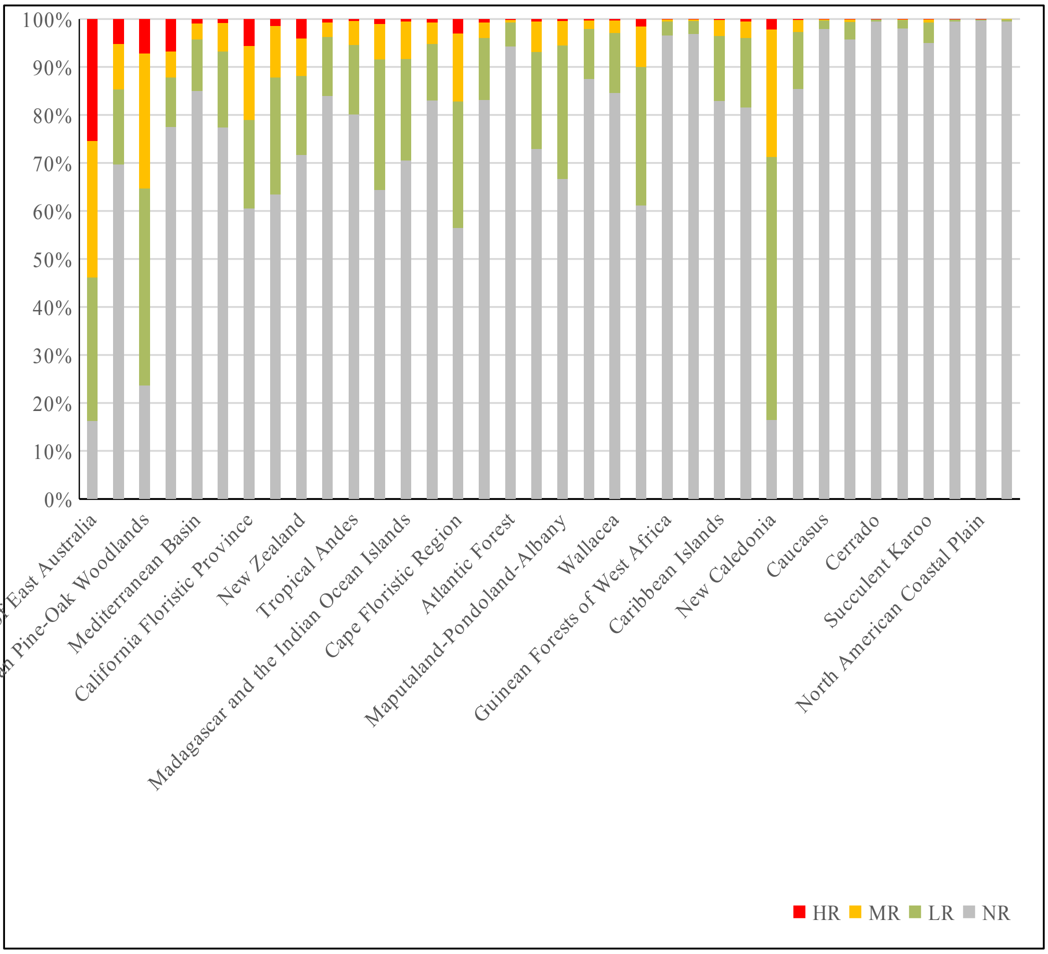


Figure 5 Potential invasion areas within BHRs under current climate conditions. NR, LR, MR, and HR denotes No Risk, Low Risk, Moderate Risk, and High Risk, respectively.

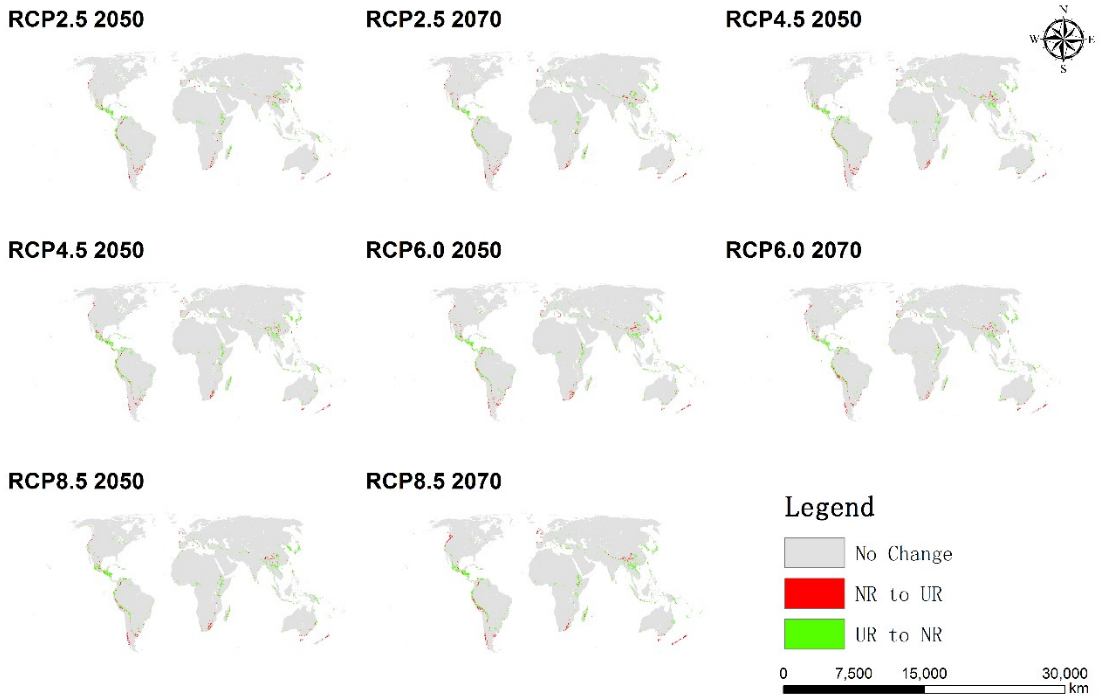
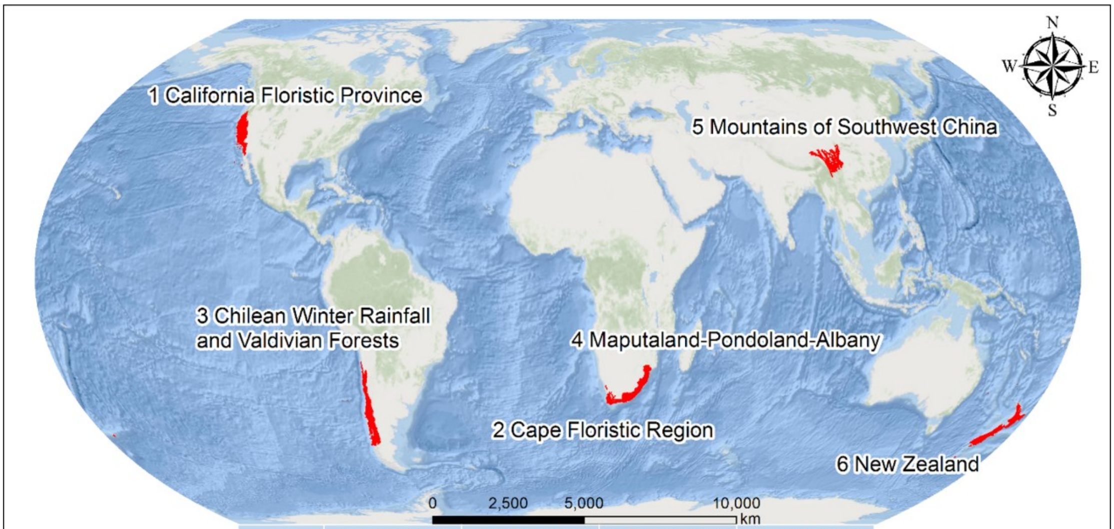


Figure 6. Potential spatial distributions of *A. adenophora* under the eight RCPs. Gray denotes no risk, green denotes regions converted from UR to NR, red denotes regions converted from NR to UR..



ID	RCP2.6(%)		RCP4.5(%)		RCP6.0(%)		RCP8.5(%)	
	2050	2070	2050	2070	2050	2070	2050	2070
1	6.65	7.92	9.08	8.43	8.61	7.93	6.08	7.26
2	7.19	9.31	7.32	9.86	10.84	9.36	8.07	9.02
3	67.21	65.96	79.60	83.18	75.92	87.62	83.43	104.51
4	34.99	34.00	27.50	25.21	27.19	19.73	20.91	-0.27
5	2.47	2.61	15.11	18.89	16.76	29.26	29.28	48.83
6	56.68	62.70	69.77	80.65	67.90	87.34	85.76	115.21

Figure 7 Changes in UR area in seven BHRs under the eight RCPs. 1, California Floristic Province Cape Floristic Region; 2, Chilean Winter Rainfall and Valdivian Forests; 3, Maputaland-Pondoland-Albany; 4, Mountains of Southwest China; 5, New Zealand; 6, North American Coastal Plain

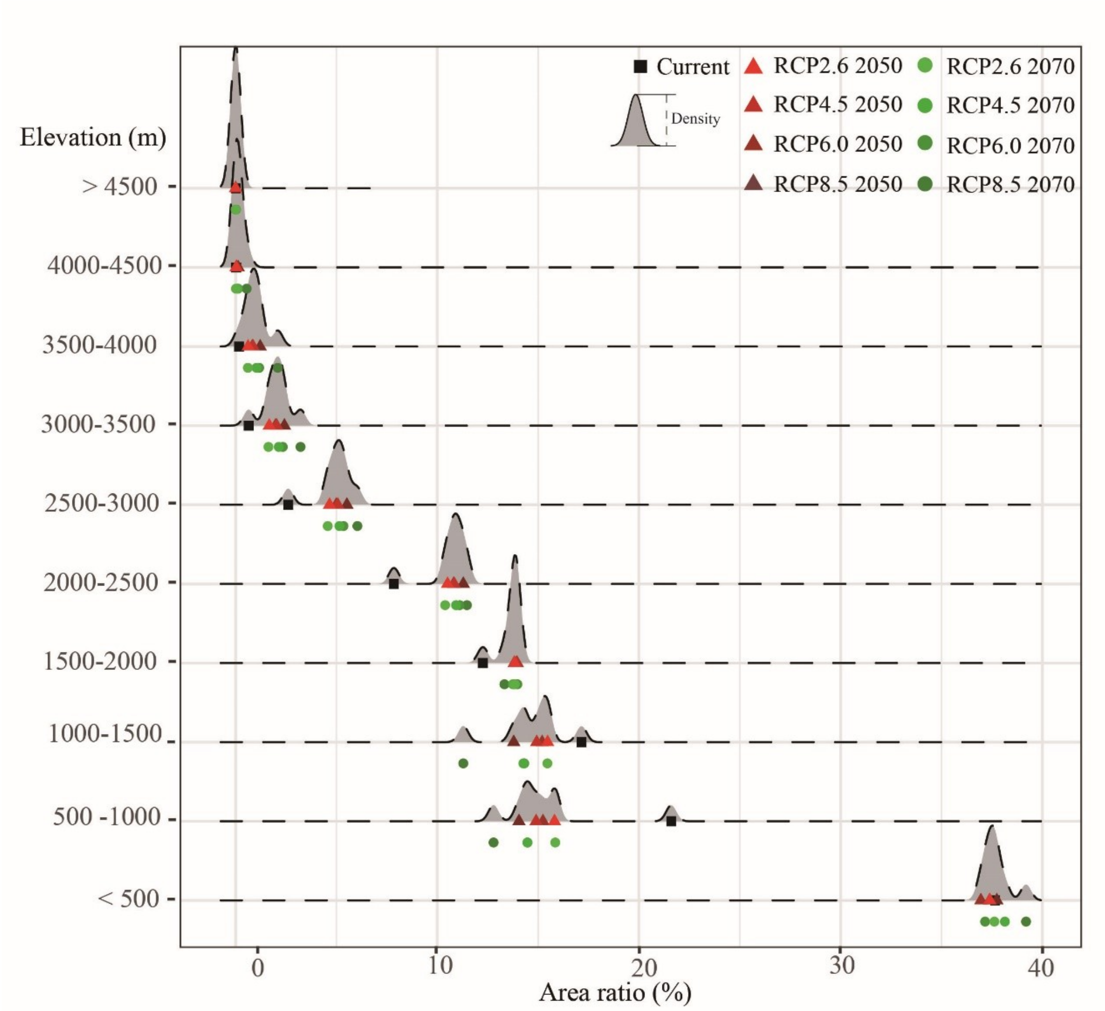


Figure 8. Distributions of UR regions for *A. adenophora* within different elevation ranges. Red triangles denote the four RCPs in 2050, while the green dots represent the four RCPs in 2070. To improve the visibility of differences between the RCPs for 2050 and 2070, the four RCPs for 2070 are located beneath the four RCPs for 2050.

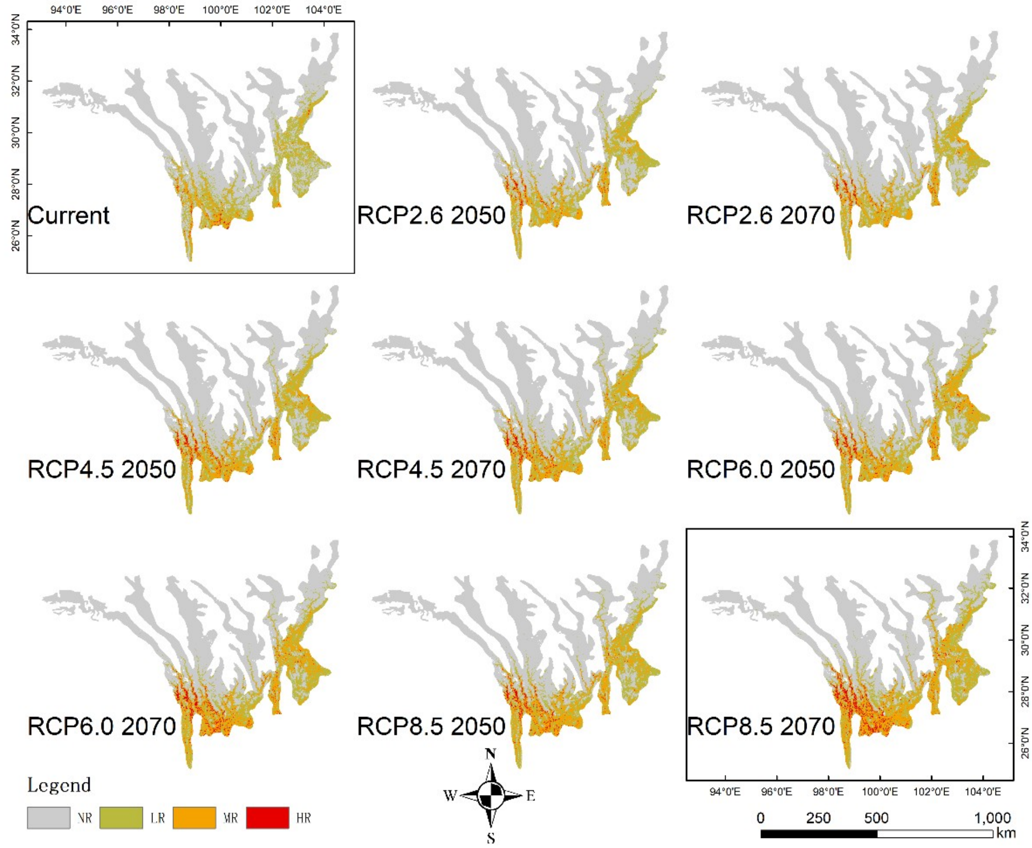


Figure 9. Potential invasion range of *A. adenophora* in the Mountains of Southwest China BHR under current and future climate change scenarios. The trend in *A. adenophora* invasion range in this BHR is opposite the global trend.

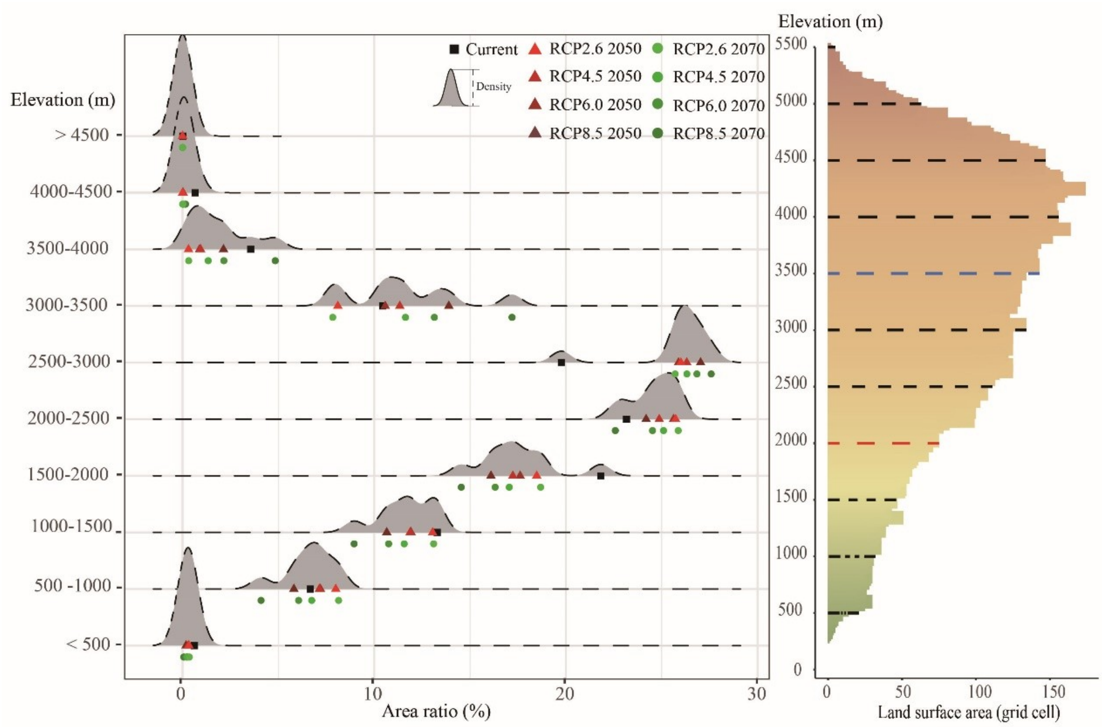


Figure 10. Distributions of *A. adenophora* UR regions in different elevation ranges within the Mountains of Southwest China BHR.

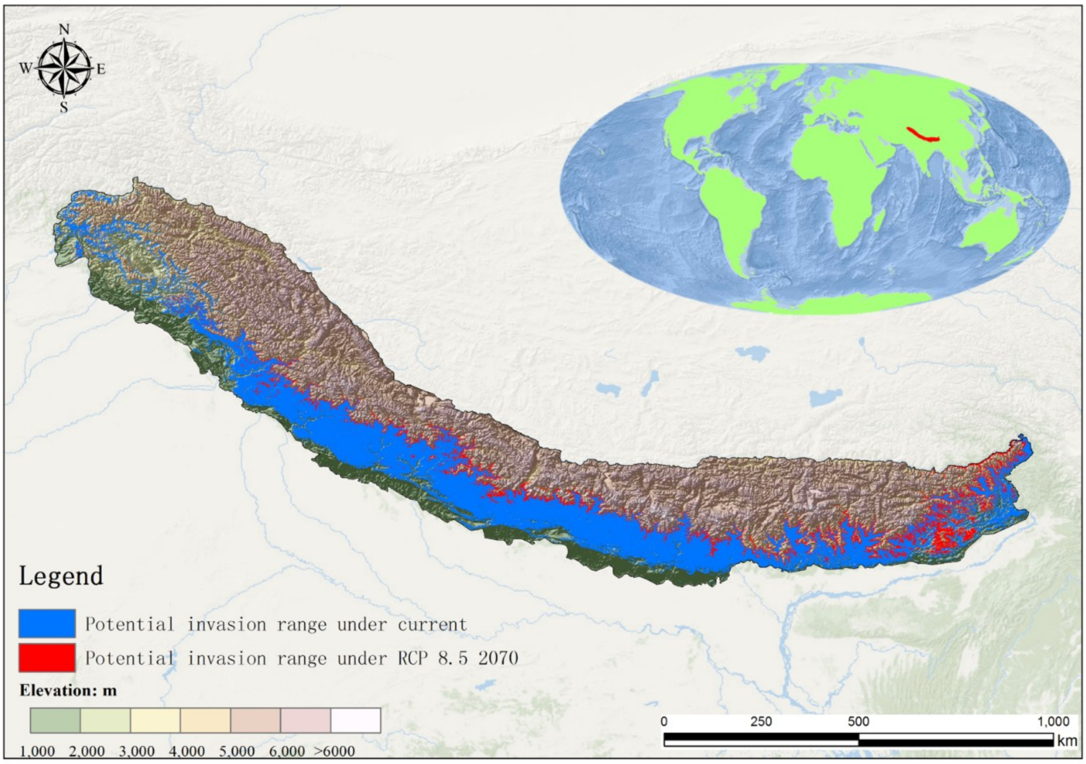


Figure 11. Distributions of *A. adenophora* UR regions in the Himalayas under current conditions and a future climate change scenario (RCP8.5 2070)

8 Data availability statement

Data on spatial distribution of *A. adenophora* occurrence, potential distribution of A.adenophora under 8 RCPs, Distributions of *A. adenophora* UR regions in different elevation ranges within the Mountains of Southwest China BHR are available from datadryad, and Distributions of *A. adenophora* UR regions in the Himalayas under current conditions and a future climate change scenario (RCP8.5 2070) (https://datadryad.org/stash/share/gl0QaDZj9T8dRdTuNJvrj2dt0G9ZZvsdhsNueE07Wt8)

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10 Biosketch:

Gu Changjun is is a PhD candidate in Institute of Geographic Sciences and Natural Resources Research, CAS. He is specifically interested in exploring potential distribution of invasive alien species and their response to climate change at large scale. This research is part of his PhD project and his work is primarily focused on the application of machine learning methods in biogeography.

Author contributions: C.G., Y.T., L.L., and Y.Z.conceived the ideas; Y.T., X.W. and Y.Z. conducted the fieldwork; C.G., B.W., and B.H. analysed the data; and C.G. led the writing with assistance from B.Z. and B.C..

11 Significance Statement

Invasive alien species (IAS) are a troublesome problem worldwide. IAS pose great threats to local ecosystems along with enormous economic loss. Unfortunately, we do not have effective ways to control the spread of most IAS. Predicting suitable distributions of IAS is an effective way to prevent their further expansion. *Ageratina adenophora* is a typical vicious invasive weed in more than 30 countries located in tropical and subtropical regions. However, little is known about its potential distribution globally and its response to future climate change. In this study, we attempted to address these gaps in knowledge. We hope that this study provides valuable reference information for preventing invasion by *A. adenophora.*