Distributions of Alien Invasive Weeds under Climate Change Scenarios in Mountainous Bhutan

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Abstract: Climate change is viewed as a cause in accelerating the rate of invasion by alien species in addition to the globalization of anthropogenic activities. Ecological niche modeling has become an instrument in predicting invasion from natural or invaded ranges to uninvaded ranges based on the presence records of organisms and environmental parameters. This study explored the changes in the distributions of globally noxious alien species (Aegratina adenophora, Ageratum conyzoides, Chromolaena odorata, Lantana camara, Mikania micrantha, and Parthenium hysterophorus) in Bhutan, to provide evidence that even a mountain environment is under the threat of invasion given the change in climatic conditions. With fairly high accuracy, the model results suggest that there will be a potential increase in the areas of invasion among most of the species, except Parthenium hysterophorus, which will experience a northerly shift and decline in distribution. The results also indicate changes in patterns of invasion, some becoming more concentrated toward a given direction, while others become more dispersed over time. This study provides a framework that can be used in the strategic control of the species, future detection surveys, and further research.

Keywords: climate change; directional distributions; ecological niche modelling; Maxent; predicted invasion; partial area under curve

1. Introduction

There is abundant evidence that climate change may profoundly affect the geographic distribution of organisms [1–8]. Global warming may result in the expansion in the habitat range of invasive species and the contraction or displacement of the habitat range of indigenous species [6–10]. The invasion risk remains very high given the current rate of global warming (0.8–1.2 °C per decade according to the Intergovernmental Panel on Climate Change (IPCC) [11].) There is also a strong concordance that most invasive species are phenotypically plastic to novel environments [12–14]. Climate change is a catalyst in facilitating the hybridization and introgression of invasive species establishment [15, 16]. Through hybrid vigor, invasion success has been predicted to enhance the evolutionary potential within populations [17], as in the case of a cosmopolitan weed, Silene vulgaris.

Mountain ecosystems are theoretically less vulnerable to invasions due to indomitable barriers of steep slopes and inhospitable environmental conditions that prevent the dispersal of propagules [18]. However, shifts in land management and economic activities such as the development of hiking trails,
recreational amenities for ecotourism, deforestation, and upland agriculture adoption [19], compounded by climatic change, have exposed vulnerable mountains to disturbance [20–24]. The warming climate has resulted in an altitudinal upward shifting of cold-temperate species (e.g., *Fagus sylvatica*) and Mediterranean species (*Quercus ilex*) in Catalina, Spain [25]. In Bhutan, farmers have reported that due to climate change, invasive plants have started to colonize highland pasture, preventing the regeneration of fodder grasses [26]. Given a change in climatic conditions, adjacent lowland flora heavily influence species composition in mountain communities [27]. Mountain environments are rated as highly sensitive to climate change due to a short growing season and limited niches for resident species [28–32]. Human activities and climate change has led to invasions in mountainous areas in Europe, Australia, South Africa, Kashmir, Hawaii, the United States Pacific Northwest, and Chile [20]. Furthermore, alien invasive weeds are habitat generalists, with high plasticity to adapt to wide ranges of climatic conditions [33–37]. Species tolerant of wider environmental conditions are frequently associated with the following physiological traits: an efficient use of nutrients in low nutrient soils, higher root–shoot ratio in arid systems and a lower root–shoot ratio in light-limited systems for resource acquisition, lower leaf construction costs and higher photosynthetic energy use efficiency as well as early phenology in arid systems [38,39].

With its inhospitable terrain and strong conservation strategies (maintaining 60% or more forest cover, with more than 51% designated as protected areas and with a rigid forest management rule of one-third annual allowable cut [40]), can Bhutan thwart invasion from alien species? No scientific evidence exists to corroborate the effectiveness of such strategies, especially in ecologically sensitive areas such as Bhutan and alpine regions [24,31]. Already, more than 46 alien plant species have been recorded in Bhutan [41,42]. Invasive species such as *Ageratina adenophora*, *Ageratum conyzoides*, *Chromolaena odorata*, *Lantana camara*, *Mikania micrantha*, and *Parthenium hysterophorus* were selected as target species of study in Bhutan (Figure A1 and Table 1).

<table>
<thead>
<tr>
<th>Species</th>
<th>Native Range</th>
<th>Invaded Area in Bhutan</th>
<th>Impact</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ageratina adenophora</em></td>
<td>Mexico</td>
<td>Punakha, Trongsa, Samtse, Wangdue, and Phuentsholing</td>
<td>Toxic to animal health, and displaces native vegetation</td>
<td>Grierson and Long [43]</td>
</tr>
<tr>
<td><em>Ageratum conyzoides</em></td>
<td>Central America and South America</td>
<td>Mongar, Sarpang, and Wangdue</td>
<td>Causes liver cancer in humans and inhibits the growth of other plants</td>
<td>Parker [44]</td>
</tr>
<tr>
<td><em>Chromolaena odorata</em></td>
<td>Southeastern USA, Mexico, and South America</td>
<td>Punakha, Trongsa, Wangdue, Mongar, and Phuentsholing</td>
<td>Toxic to animal health and causes asthma in humans</td>
<td>Bhutan Biodiversity Portal [45]</td>
</tr>
<tr>
<td><em>Lantana camara</em></td>
<td>Mexico, Central America, the Caribbean, and tropical South America</td>
<td>Wangdue and Phuentsholing</td>
<td>Causes allergic rhinitis, a type of child cirrhosis via pollen-contaminated milk</td>
<td>Bhutan Biodiversity Portal [45]</td>
</tr>
<tr>
<td><em>Mikania micrantha</em></td>
<td>Mexico, Central America, the Caribbean, and tropical South America</td>
<td>Chhukha, Mongar, Samtse, and Sarpang</td>
<td>Can damage perennial crops by twinning and entanglement, and reduces biodiversity through competition</td>
<td>Parker [44]</td>
</tr>
<tr>
<td><em>Parthenium hysterophorus</em></td>
<td>Mexico, Central America, the Caribbean, and South America</td>
<td>Mongar, Tashigang, Tengsa, and Wangdi</td>
<td>Causes severe allergic illness in adult human males, when in contact with the pollen.</td>
<td>Parker [44]</td>
</tr>
</tbody>
</table>

In Bhutan, although information on the impacts of these species are lacking, most have been reported to reduce crop productivity, and some of them have been described as encroaching the forest understory, particularly, *A. adenophora*, *C. odorata*, and *M. micrantha* [46]. Given the negative impacts of these species on the economy, biodiversity, and society, it is not only crucial to predict potential invasions in new areas, but more so in a climate change scenario. In general, models predict that climate change will not only redistribute species, but also move them poleward in latitudes and upward in altitudes [47,48].
Ecological niche modeling (ENM) is now widely used in predicting the distributions of species due to ample species records in museums, on paper maps, online e.g., Global Biodiversity Information Facility, etc., and adequate environmental data in the form of raster/grid-cells due to advances in geographic information systems (GIS) and satellite-based remote sensing [49–53]. Ecological niche modeling uses computerized algorithms to predict the distributions of a species across a geographical space and time, based on observed distributions of a species as a function of environmental conditions [54]. In particular, the presence only correlative modeling has gained in popularity over presence–absence modeling as the locational records of species are amassed mostly in the form of presence only, and not presence–absence localities [21,55–57]. Additionally, the absence records are dubious in their affirmation as they can be affected by many factors including the inaccessibility of the site, not being detected during the survey, or may have experienced local extinction due to disturbances [58]. Maxent has often performed better than other approaches such as artificial neural network, Bioclim, Domain, ENFA, GAM, GARP etc., [59,60] because it can cope with sparse, irregularly sampled data and minor location errors [61]. Additionally, it has the advantages that it (1) requires only presence data, (2) can handle both continuous and categorical variables, and (3) can converge to optimal probability [62]. Maxent works based on Gibbs probability distributions of the maximum entropy given the constraints.

\[ q_\lambda(x) = e^{\lambda \cdot f(x)}, \]  

where \( x \) is pixel in the study area, \( \lambda \) is vector of coefficients (feature weights), and \( f \) is vector of all features.

This study tested the theory of alien invasive species being highly adaptable to a wide variety of environmental conditions by using a topographically variable landscape (ranging from 100 to >7500 m.a.s.l.) and highly heterogeneous ecoregions (ranging from alpine to tropical climatic zones). Two different climatic scenarios, the average of 1960 to 1990 (hereafter referred to as current) and the average of 2041 to 2060 (hereafter referred to as future) were used to model current and future spatial distributions of the species. The objectives were to (1) compare the model evaluation techniques of partial area under curve (\( \text{PAUC} \)) and full area under the curve (\( \text{FAUC} \)) in the current and future climatic scenarios, (2) assess the predicted distributional change under two climatic conditions, and (3) test the statistical significance of change.

2. Materials and Methods

2.1. Defining Survey Site and Species Record Sampling

The study was conducted in Bhutan, located on the southern slopes of the Himalayan Mountains between 26°45’00” N and 92°10’00” E, with altitudes ranging from 100 m on the Indian border to 7500 m bordering Tibet [63]. The country encompasses 38,394 km² [42]. Suitable survey sites were defined within the species’ altitudinal range, below a 45° slope, outside human settlements, roads, and rivers by using extraction and clip tools in ArcGIS 10.1. Then, we drew polygon grids of 1 km × 1 km, each containing a point using the fishnet tool in ArcGIS 10.1. The total points within the fishnet polygons were considered as the pseudo-population of the species. From these, 30% were randomly sampled and uploaded onto GPS units for ground surveys (candidates/presurvey points, Table 2). After every 1 km along the road within the survey sites, a species search was conducted up to approximately 250 m on either side of the road. Recordings (field records/post survey points, Table 2) were conducted only if the species cover was ≥5% within a 10 × 10 m² plot to avoid source–sink population errors [64].

Samples from easily accessible areas such as roadside or nearby settlements were found to be biased and autocorrelated [61]. Autocorrelation was mediated in SDMTools v2.3 [65] by using the following procedures: (1) Principal component analysis to construct climatic heterogeneity surface, (2) Calculation of climatic heterogeneity using the percent of eigenvalues from the principal components, and (3) Rarefaction of occurrence data using the spatially rarely occurrence data tool. The resulting
climate heterogeneity surface is shown in Figure S1 and the number of records after rarefication is shown in the last column of Table 2.

**Table 2.** Number of candidates (pre-survey), field detected records (post-survey), and rarefied records for five species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pre-Survey</th>
<th>Post-Survey</th>
<th>Rarefied Record</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ageratina adenophora</em></td>
<td>132</td>
<td>336</td>
<td>48</td>
</tr>
<tr>
<td><em>Ageratum conyzoides</em></td>
<td>170</td>
<td>172</td>
<td>27</td>
</tr>
<tr>
<td><em>Chromolaena odorata</em></td>
<td>200</td>
<td>89</td>
<td>30</td>
</tr>
<tr>
<td><em>Lantana camara</em></td>
<td>200</td>
<td>71</td>
<td>18</td>
</tr>
<tr>
<td><em>Mikania micrantha</em></td>
<td>200</td>
<td>147</td>
<td>26</td>
</tr>
<tr>
<td><em>Parthenium hysterophorus</em></td>
<td>282</td>
<td>167</td>
<td>20</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>1184</strong></td>
<td><strong>982</strong></td>
<td><strong>169</strong></td>
</tr>
</tbody>
</table>

2.2. Environmental Data Processing

The current and future bioclimatic variables comprising a total of 19 temperature and precipitation parameters were collated from worldclim.org [66] (Table A1). Following Ashraf et al. [60], the multicollinearity of current bioclimatic variables was evaluated using the Pearson correlation in SDMTools [65]. Bioclimatic variables with an average (Avg) Pearson’s $r \geq 0.9$ were removed (with the exception of annual mean temperature, since it is considered as a proximal and important climatic variable). Isothermality, maximum temperature of the warmest month, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of warmest quarter, and precipitation of the coldest quarter were used for modeling (the boldface values in Table 3 indicate the selected variables).
Table 3. Pearson’s correlation matrix indicating the above and below threshold correlations. Variables corresponding to the boldface values were selected for ecological niche modeling (ENM).

| Bio | 1   | 2   | 3   | 4   | 5   | 6   | 7   | 8   | 9   | 10  | 11  | 12  | 13  | 14  | 15  | 16  | 17  | 18  | 19  | Avg |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1   | 0.9 | 0.3 | 0.1 | 0.9 | 1   | 0.1 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.3 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 |
| 2   | 0.3 | 1   | 1   | 0.2 | 1   | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 |
| 3   | 0.1 | 0.9 | 0.9 | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 4   | 1   | 1   | 1   | 0.9 | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 5   | 0.9 | 1   | 0.9 | 1   | 0.9 | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 6   | 1   | 1   | 1   | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 7   | 1   | 1   | 1   | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 8   | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.3 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 9   | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.3 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 10  | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.3 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 11  | 1   | 1   | 1   | 0.9 | 0.9 | 0.9 | 0.3 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 12  | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 13  | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 14  | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 15  | 1   | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 16  | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 17  | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 | 0.9 |
| 18  | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 |
| 19  | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 |
2.3. Model Calibration

Maxent 3.3.3k [67] was downloaded using http://www.cs.princeton.edu/~schapire/maxent. After feeding Maxent with the species records (rarefied) and climatic variables (current and future), ENM was calibrated as follows: feature types = linear, quadratic, product, and threshold; regularization multiplier = 2; maximum number of background points = 10,000; replicates per species = 10; maximum iteration per species per replicate = 500; convergence threshold = 0.001. Replicated run type = 10-fold cross validation. The remaining parameters were maintained at their default values.

In addition to the $F_{AUC}$ (defined as the full spectrum of areal predictions, ranging from 0–1) of the receiver-operating characteristic (ROC), $P_{AUC}$ (defined as the subset of full spectrum of areal predictions) was used to evaluate the performance of the model (AUC is a statistical test defined by the sensitivity along Y-axis and 1 – specificity along the X-axis). $P_{AUC}$ is known to avoid some omission errors, which are common in $F_{AUC}$ [58,60]. Using the online tools at http://shiny.conabio.gob.mx:3838/nichetoolb2/, $P_{AUC}$ was calibrated with an omission error threshold of $E = 10$ and 500 replicates with 50% bootstrap resampling. Direct count of the proportion of replicate analyses with an AUC ratio $\leq 1.0$ was used to test the significance of the partial ROCs [60]. Departure of AUC ratio from unity (i.e., >1) indicated a good performance of the model.

2.4. Statistical Testing of Model Predicted Areas of Invasion

To carry out the significance test in areas of predicted invasion change between the current and future climatic conditions, ENM outputs from Maxent were converted into binary suitability (0 = unsuitable and 1 = suitable as shown in Figure A2) using the 10-percentile threshold and computed the difference in areas of predicted invasion using ArcGIS 10.1. The differences obtained as cell values were then converted into polygons to compute the areas and enable statistical analysis of the mean area comparisons between increase, decrease, and no change. For visual illustration, hexagonal binning was used (Figure 1). The statistical significance of change in the invasion areas of increase and decrease between the current and future climatic conditions was tested using the Wilcoxon Signed Rank Test for each species. A Mann–Whitney U test was used for an overall comparison between the increase and decrease in areas of predicted invasion with all species combined.

2.5. Tracking Directional Distributions between Two Climatic Conditions

Using the spatial statistic tool in ArcGIS 10.1, directional distribution (standard deviational ellipse) was computed (see Equations (2)–(5)) for the predicted areas of invasion for each species, under each climatic condition. The standard deviational ellipse tool can capture the directional distributions by the angle of rotation (the angle from north clockwise to the axis), the deviation along the major axis (the longer one), and the deviation along the minor axis (the shorter one) [68]. The ellipse was calibrated at one standard deviation with the area of polygons as the weight to the mean centroid of the polygons. This method provides directional distribution patterns with xy distances and angle of rotation.

Calculate the mean center of the polygons:

$$\left(\bar{x}_{mc}, \bar{y}_{mc}\right) = \left(\frac{\sum_{i=1}^{n} x_i}{n}, \frac{\sum_{i=1}^{n} y_i}{n}\right).$$

(2)

where:

- $\bar{x}_{mc}, \bar{y}_{mc} =$ coordinates of the mean center,
- $x_i, y_i =$ coordinates of polygon $i$,
- $n =$ number of polygons.

In order to calculate the angle of rotation and deviational ellipse in Equation (4) and (5), respectively, the coordinates $((x_i, y_i)$ of the mean center were transformed as shown in Equation (3).
Transform the coordinates of the mean center:

\[ x'_i = x_i - x_{mc}, y'_i = y_i - y_{mc}. \]  

Calculate the angle of rotation:

\[
\tan \theta = \frac{\left( \sum_{i=1}^{n} x_i^2 - \sum_{i=1}^{n} y_i^2 \right) + \sqrt{\left( \sum_{i=1}^{n} x_i^2 - \sum_{i=1}^{n} y_i^2 \right)^2 + 4\left( \sum_{i=1}^{n} x_i^2 \sum_{i=1}^{n} y_i^2 \right)}}{2\left( \sum_{i=1}^{n} x_i^2 \sum_{i=1}^{n} y_i^2 \right)}.
\]

Calculate the deviational ellipse along the \(x\) and \(y\) axes:

\[
\delta_x = \sqrt{\frac{\sum_{i=1}^{n} \left( x_i \cos \theta - y_i \sin \theta \right)^2}{n}}, \quad \delta_y = \sqrt{\frac{\sum_{i=1}^{n} \left( x_i \sin \theta - y_i \cos \theta \right)^2}{n}}.
\]

3. Results and Discussion

3.1. Model Evaluation

The model yielded predictions of invasion that were statistically significant \((p < 0.05)\) from a random chance in all species and in both climatic conditions. The AUC ratios \(AUC_c = AUC\) current and \(AUC_f = AUC\) future) were well departed from \(\leq 1\) in both climate scenarios. However, the AUC ratios and mean \(p\) AUCs decreased from current to future scenarios across all species (Table 4). This concurs with the axiom that the accuracy of any model decays with extrapolation both temporally and spatially [69]. Model evaluation using the \(p\) AUC approach improved its performance over the \(F\) AUC since \(pAUC_c > pAUC_f\) across all species, as shown in Table 4. This improvement suggests that the Maxent prediction along a restricted range (region of interest) of ROC is more useful than its entire length, as found by Peterson et al. [58]. *Lantana camara* and *P. hysterophorus* performed better than the rest of the species in all scenarios, consistent with the premise that species with restricted climatic ranges require \(p\) AUC as a model evaluation technique. Mean partial AUCs were not highly deviant between the current and future scenarios, indicating the Maxent’s high accuracy in model transfer for the target species and the landscape.

Table 4. Model performance based on area under curve (AUC) ratios and mean partial AUCs at \(\alpha = 0.05\).

<table>
<thead>
<tr>
<th>Species</th>
<th>(N)</th>
<th>Ratio (AUC_c)</th>
<th>Ratio (AUC_f)</th>
<th>(pAUC_c)</th>
<th>(pAUC_f)</th>
<th>(F)AUCc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ageratina adenophora</td>
<td>48</td>
<td>1.76 ± 0.05</td>
<td>1.71 ± 0.07</td>
<td>0.88</td>
<td>0.86</td>
<td>0.79</td>
</tr>
<tr>
<td>Ageratum conyzoides</td>
<td>27</td>
<td>1.76 ± 0.08</td>
<td>1.74 ± 0.08</td>
<td>0.88</td>
<td>0.87</td>
<td>0.77</td>
</tr>
<tr>
<td>Chromolaena odorata</td>
<td>30</td>
<td>1.82 ± 0.09</td>
<td>1.76 ± 0.09</td>
<td>0.91</td>
<td>0.88</td>
<td>0.83</td>
</tr>
<tr>
<td>Lantana camara</td>
<td>18</td>
<td>1.93 ± 0.04</td>
<td>1.92 ± 0.04</td>
<td>0.97</td>
<td>0.96</td>
<td>0.86</td>
</tr>
<tr>
<td>Mikania micrantha</td>
<td>26</td>
<td>1.85 ± 0.05</td>
<td>1.81 ± 0.04</td>
<td>0.93</td>
<td>0.90</td>
<td>0.81</td>
</tr>
<tr>
<td>Parthenium hysteranthra</td>
<td>20</td>
<td>1.94 ± 0.03</td>
<td>1.92 ± 0.03</td>
<td>0.97</td>
<td>0.96</td>
<td>0.93</td>
</tr>
</tbody>
</table>

3.2. Spatial Change Analysis

For *P. hysterophorus*, the area of expansion (0.55%) was much less than its area of contraction (5.26%) under the future climatic condition (Figure 1a) when compared with the other species (Figure S2). In terms of absolute change, the area of invasion increased in the case of *A. conyzoides* (Ac), *C. odorata* (Co), *L. camara* (Lc), and *M. micrantha* (Mm), while it decreased for *A. adenophora* \((Aa = 27.07\%\) to 26.85\%) and *P. hysterophorus* \((Ph = 8.36\%\) to 4.15\%) (Figure 1b). *Ageratina adenophora* and *A. conyzoides* appeared to be the most gregarious species (Figure S2), while *P. hysterophorus* appeared to be the most intolerant to changes in climatic conditions. According to Wan et al. [70], *A. adenophora* exhibits morphological and structural plasticity to adapt to the environment in invaded areas through genetic
diversification. Furthermore, He et al. [71] reported a positive correlation between the stomatal density and altitude, thus attributing A. adenophora’s adaptability to higher temperature and lower humidity in high altitude areas. Similar to the report by Lamsal et al. [21], the spread of P. hysterophorus decreased in this study, which could be because this species thrives mostly in agroecosystems and grasslands [22], and in Bhutan, the land cover is dominated by forests, as high as 71%. Parthenium hysterophorus is also very sensitive to photoperiodic fluxes and temperature changes [72], which are very common in Bhutan due to its high topographical variability [73,74]. In contrast, A. adenophora, A. conyzoides, C. odorata, L. camara, and M. micrantha are characterized as forest understory invaders with a high dispersal mobility [22].

![Map of Parthenium hysterophorus](image)

**Figure 1.** (a) Hexagonally binned-map illustrating the rate of change in areas of distribution of P. hysterophorus across the study area. Contraction = decrease in rate, Expansion = increase in rate, and No Change = neither a decrease nor increase in rate with respect to the future climate scenario. (b) Percent of predicted invasion by areas in the current and future climatic scenarios. Aa = A. adenophora, Ac = A. conyzoides, Co = C. odorata, Lc = L. camara, Mm = M. micrantha, and Ph = P. hysterophorus.
3.3. Testing the Statistical Significance of Changes

The model predictions of decrease and increase in areas of invasion in the future climatic scenario were tested using Wilcoxon Signed-Ranks Tests. The decrease in area (4.15%) was significant for \( P. \) hysterophorus \((Z = 2.766, p = 0.006)\), and the decrease in area (26.85%) was non-significant for \( A. \) adenophora \((Z = 0.371, p = 0.711)\). The increase in area (17.59%) was significant for \( C. \) odorata \((Z = 2.785, p = 0.005)\), while the increase in areas (25.82%, 8.44%, and 17.15%) were non-significant for \( A. \) conyzoides \((Z = 1.063, p = 0.288)\), \( L. \) camara \((Z = 0.642, p = 0.521)\), and \( M. \) micrantha \((Z = 0.751, p = 0.453)\), respectively. Therefore, \( P. \) hysterophorus can be characterized as intolerant, and \( C. \) odorata is adaptable to changing climate (see the rate of change in Figure S2 and standard ellipse in Figure S3). However, \( P. \) hysterophorus was predicted to be highly invasive under future climatic scenarios in the landscape of Nepal [22]. This difference could be attributed to the fact that Bhutan is predominantly covered by forests [75,76], which act as natural barriers to the mobility of the species. \( Parthenium \) hysterophorus seeds are mainly dispersed by vehicular movements and are found in disturbed areas such as agricultural lands, roadsides, river banks, and wastelands [22].

A Mann–Whitney U test showed that there was no significant difference \((U = 6413057, p = 0.645)\) between the increase in area of predicted invasion compared to the decrease in area of predicted invasion when all species were combined across the study area (Figure 2). This underscores the fact that Bhutan has primarily intact forests, of which 52% are totally protected as national parks, wildlife sanctuaries, and biological corridors [76]. Furthermore, the species in question more or less prefer habitats along roadsides, degraded lands, pastures, and agricultural fields.

![Figure 2](image-url)  
**Figure 2.** Showing the differences in the mean ranks of increase and decrease in areas of invasion between the two climate scenarios.

3.4. Cardinal Directions of Distributions

The directional distribution in the current climatic scenario (blue ellipse) followed angles of rotation from 87.06° to 89.73° northeast and 92.22° to 92.88° southeast, while in the future (orange ellipse) it followed from 78.74° to 89.99° northeast and 90.41° to 93.04° southeast (see Supplementary Material Figure S3). The directional distribution of \( A. \) conyzoides became almost a perfect circle in the
future climatic scenario, which according to the algorithm of standard deviational ellipse represents a dispersion in distribution. There was also a notable northward shift in the distribution of *P. hysterophorus* from the current to the future scenario as seen in Figure 3. Such observations are in accordance with the findings that climate change can disrupt species distributional patterns [64,77–80] by the process of colonization and removal of local species through competition.

![Figure 3. Predicted directional distributions of *P. hysterophorus* in the two climatic conditions.](image_url)

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3.5. Limitations and Caveats of the Model

As in the case of any correlative modeling, Maxent modeling has its limitations. Maxent assumes that the sampling effort is uniform across the entire area of interest and that the prevalence of occurrence is 50% or more, while in practice, the models are developed from the occurrence records of accessible areas, thus tending toward a spatial bias [61,81]. Furthermore, the interpretation of the results should be treated from an inductive rather than deductive perspective, which means that such models are to build rather than test the hypothesis. As such, models demand several iterations to account for the effects of sample sizes [82,83], the spatial scales of the area of interest, the spatial resolutions of the predictors [84], the selection of biologically meaningful environmental predictors [85], and different filtering levels of autocorrelations of occurrence records [86] to enhance model fidelity and consistency.

To circumvent the limitations above, this study undertook measures such as planning the sampling design by considering the population viability within the plots and reduction of spatial autocorrelation. Furthermore, the multicollinearity of predictor variables was removed and their biological usefulness considered. This study, therefore, remains fairly robust, relative to those that have resorted to using secondary data from museums, herbaria, or online databases (e.g., GBIF) that have been collected on an ad hoc basis.

4. Conclusions

Our model predictions conformed to the established theory that invasion is facilitated by climate change since areas of predicted invasion increased during future climate scenarios. One notable indication of this study was that the projection of current to future predictions could lead to weaker
power of the Maxent model (partial AUC values decreased from current to future climate scenarios). This occurs when the correlation between the response and predictors may only be adequate over a narrow range of spatial and temporal scales. Among the six species, *C. odorata* could become more prevalent over time, while *P. hysterophorus* may be very sensitive to climate change, as indicated by its northward shift with a decrease in extent. Despite expansion in areas under the future climatic condition, most species appear to limit their invasion to the southern region (S2: 26°52′30″ N to 27°18′0″ N) of the country. *Lantana camara* turned out to be the most stable species to change in climatic conditions (No change = 97.49%), in contrast to *P. hysterophorus*, which was the most unstable species to climate change (No change = 94.19%). Statistical non-significance of the Mann–Whitney U test reinforced that overall, there is no significant impact of climatic change on invasion. Such a unique result could be due to the country’s strong policies on environmental protection such as the delimitation of protected areas, banning slash and burn agriculture practices, and the plant quarantine act. However, the ruggedness of the mountain terrain cannot be overruled as a limiting factor. This study not only points out which species are more likely to respond positively and negatively to changes in climatic conditions, but also provides the directions of potential spread in the geographical space. This approach can serve as the basis for strategic control (e.g., plant quarantine policy implementation using transborder screening) of the species in question as well as further studies into these species such as detection surveys.

**Supplementary Materials:** The following are available online at [http://www.mdpi.com/2073-4395/9/8/442/s1](http://www.mdpi.com/2073-4395/9/8/442/s1), Figure S1: Sample rarefaction using climatic heterogeneity; Figure S2: Change maps of six species between the current and future climatic scenarios; Figure S3: Species wise directional distributions between current and future climatic scenarios.


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**Conflicts of Interest:** The authors declare no conflicts of interest.

**Appendix A**

![Photos of alien invasive weeds from the sampling sites.](http://www.mdpi.com/2073-4395/9/8/442/s1)
Table A1. Bioclimatic variables derived from temperature and precipitation with the definitions of the abbreviation, scaling factor, and measurement unit.

<table>
<thead>
<tr>
<th>Label</th>
<th>Variable</th>
<th>Scaling Factor</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIO1</td>
<td>Annual mean Temperature</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO2</td>
<td>Mean Diurnal Range (Mean of monthly (max temp-min temp))</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO3</td>
<td>Isothermality (BIO2/BIO7)</td>
<td>100</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO4</td>
<td>Temperature seasonality (standard deviation)</td>
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<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO5</td>
<td>Max Temperature of Warmest Month</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO6</td>
<td>Min Temperature of Coldest Month</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO7</td>
<td>Temperature annual Range (BIO5-BIO6)</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO8</td>
<td>Mean Temperature of Wettest Quarter</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
<td>BIO9</td>
<td>Mean Temperature of Driest Quarter</td>
<td>10</td>
<td>Degree Celsius</td>
</tr>
<tr>
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<td>Mean Temperature of Warmest Quarter</td>
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<td>Degree Celsius</td>
</tr>
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<td>Mean Temperature of Coldest Quarter</td>
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</tr>
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<td>BIO12</td>
<td>Annual Precipitation</td>
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<td>Millimetres</td>
</tr>
<tr>
<td>BIO13</td>
<td>Precipitation of Wettest Month</td>
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<td>Millimetres</td>
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<td>Precipitation Seasonality (Coefficient of variation)</td>
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<td>Precipitation of Wettest Quarter</td>
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<td>BIO18</td>
<td>Precipitation of Warmest Quarter</td>
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<tr>
<td>BIO19</td>
<td>Precipitation of Coldest Quarter</td>
<td>1</td>
<td>Millimetres</td>
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</tbody>
</table>

Figure A2. Binary suitability maps for the current and future climatic conditions using the 10-percentile threshold (green = predicted as potential invasion or 1, and brown = predicted as non-invasion or 0).

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