RESEARCH ARTICLE



Invasive alien plant species dynamics in the Himalayan region under climate change

Pramod Lamsal 💿, Lalit Kumar 💿, Achyut Aryal, Kishor Atreya 💿

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Abstract Climate change will impact the dynamics of invasive alien plant species (IAPS). However, the ability of IAPS under changing climate to invade mountain ecosystems, particularly the Himalayan region, is less known. This study investigates the current and future habitat of five IAPS of the Himalayan region using MaxEnt and two representative concentration pathways (RCPs). Two invasive species, Ageratum conyzoides and Parthenium hysterophorus, will lose overall suitable area by 2070, while Ageratina adenophora, Chromolaena odorata and Lantana camara will gain suitable areas and all of them will retain most of the current habitat as stable. The southern Himalayan foothills will mostly conserve species ecological niches, while suitability of all the five species will decrease with increasing elevation. Such invasion dynamics in the Himalayan region could have impacts on numerous ecosystems and their biota, ecosystem services and human well-being. Transboundary response strategies suitable to the local context of the region could buffer some of the likely invasion impacts.

Keywords Climate change · Himalayas · Invasive species · MaxEnt · Niche modelling

INTRODUCTION

Almost one-sixth of the global land surface is currently highly vulnerable to invasion from alien species, including significant areas of developing economies and global biodiversity hotspots (Early et al. 2016). According to Masters and Norgrove (2010), Invasive alien plant species (IAPS) are "non-indigenous species that adversely affect, economically, environmentally or ecologically, habitats where they have been introduced, either accidentally or deliberately, outside their normal past or present distribution". Approximately, 0.5-0.7% of global tree and shrub species are currently invasive outside their natural range (Richardson and Rejmanek 2011). In India, Adhikari et al. (2015) reported nineteen out of forty-seven existing ecoregions harbour invasion hotspots. Both climate change and invasive species are the key drivers of biodiversity loss, and if acting together, they could exacerbate the impact on biodiversity and ecosystems as a whole (Mainka and Howard 2010). Many invasive plant populations, in the current context of climate change, are developing adaptations that could lead to exponential population growth in the future (Clements and Ditommaso 2011). IAPS are thus becoming a serious threat to biodiversity and ecosystems, and climate change may increase their distribution range.

Species that can withstand a wide range of environmental conditions show a broader physiological niche and are more likely to be invasive (Higgins and Richardson 2014). Pests and parasites are integral components of a natural ecosystem that help maintain healthy species populations. Torchin and Mitchell (2004) argued that escaping native natural biological enemies, such as pests from their area of origin, is one of the key mechanisms that makes introduced species more prone to proliferate in the novel environment and facilitate them to become a harsh invader. Similarly, Maron et al. (2004) found that adaptive evolution, apart from long-recognized phenotypic plasticity, facilitates the establishment and expansion of invasive species into broad environmental conditions of the invaded range. The high growth rate, wide climatic or

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environmental tolerance, short generation time, consistent reproduction, small seed size, high dispersal and high capacity for asexual reproduction are some of the specific traits of IAPS that undergo evolutionary change when they invade new areas (Whitney and Gabler 2008). In this context, four distinct pathways, such as transport, colonization, establishment and landscape spread, are essential for an invasive species to successfully complete an invasion (Hellmann et al. 2008).

The ongoing biotic invasion is modifying global natural communities and their ecological characteristics at an unprecedented rate and is being viewed as a major agent for human-driven global change, such as atmospheric and land use changes (Mack et al. 2000; Masters and Norgrove 2010). Disturbances to an ecosystem enhance the diversity and distribution of non-native plants; however, the strength of this enhancement relies on the disturbance type, especially grazing and anthropogenic activities for terrestrial ecosystems (Jauni et al. 2015). Invasive plants could directly exert an influence on the survival, productivity and activity of native biota along with changes in mineral and nutrient contents in plant tissues, and at the community level, to species richness, diversity and soil resources through the interaction between species traits and the biome invaded (Pysek et al. 2012). A recent study (Ren et al. 2017) in the Hindu Kush Himalaya (HKH) that overlaps most of the Himalayas and Tibetan Plateau region revealed a significant increasing trend of the annual mean surface air temperature during the last century. Jayanarayanan et al. (2017) projected an increment of seasonal warming up to 5.4 °C during the winter and 4.9 °C during the summer monsoon in the Karakoram and northwestern region of the Himalaya by the end of this century. Theoretically, greater expansion of the species adapted to low elevation is expected in such high elevation regions with the increasing trend of average temperature, including likely changes in the dynamism and impacts of hot climate plants such as invasive species. Dhar and Reshi (2015) observed invasive species promoting homogenization of the terrestrial ecosystem in Kashmir in the western Himalaya. Likewise, Privanka and Joshi (2013) reported that most of the southern and western regions of the western Himalaya will be climatically suitable in the future for the spread of Lantana camara due to increased warming. These invasive species have been spreading over the protected areas of the region and creating problems for wildlife habitat and their food availability (Murphy et al. 2013; Aryal et al. 2017). This suggests that the Himalayan region is equally vulnerable to species invasion because of past and future environmental change, such as increased warming.

Non-native invasive species are abundant at lower and mid-elevation regions in mountain ecosystems; however, it is likely that they will spread and become dominant at higher elevations because of ongoing climate change and anthropogenic activities (Alexander et al. 2016). An invasion of alien plant species is possible if the population growth continues in our mountainous areas under a warming climate (Marini et al. 2012). Haider et al. (2010) found that both climatic and habitat conditions affect altitudinal distribution of non-native plants, and hence, climate change can influence the occurrence of these plants directly and indirectly in such terrain conditions. On the other hand, it has also been acknowledged that regions at high elevations are less vulnerable to alien plant invasions with the existing conditions of energy constraints, low propagule pressure and disturbance, even if potential increases in temperature are considered (Marini et al. 2009). For instance, Zhang et al. (2015) reported a decrease in alien species richness with increasing elevation in the Tai and Lao mountain range, and Guo et al. (2017) found similar results in the high elevation protected areas (PAs) of China, which could be an influence of lower lethal temperature and other stressful abiotic environments, for instance, a lower propagule pressure or a less human mediated land use system (Lembrechts et al. 2014). It seems that high elevation landscapes could see more invasions from lowland invasive plants through likely moderate climate and increased human activities in the next few decades.

Some modelling studies on invasion potential are available in the Himalayas (Priyanka and Joshi 2013; Shrestha et al. 2015). However, there is a lack of a comprehensive study focusing on the broad Himalayan region as a whole on the current potential and future predicted distribution of major IAPS of the region. As the literature suggests, such an invasion expansion in mountain ecosystems and along its gradient is important to understand whether invasion phenomenon will occur in the Himalayan region considering the fragile ecosystems it has, the biodiversity therein and the continuing supplement of ecosystem services (ES) for human well-being. Invasive species are largely known to degrade the biota habitat in ecosystems by outcompeting native species through influence on availability of resources such as nutrients and space as well as modification of ecological processes (Grice 2006). The biodiversity-rich and vulnerable region, the Himalaya, is no exception from such invasion. Therefore, this study seeks to use maximum entropy (MaxEnt) (i) to model the invasion dynamics of five IAPS, viz. A. adenophora (Crofton weed), A. conyzoides (Billygoat weed), C. odorata (Siam weed), L. camara (Lantana) and P. hysterophorus (Famine weed), considering current and future (2070) time periods under the IPCC's RCP4.5 and RCP8.5; (ii) to understand how the five investigated IAPS respond along the altitudinal gradient of the Himalaya under future warming scenarios; and (iii) to see how the five investigated IAPS could affect ongoing conservation efforts, such as existing protected areas in the region. A brief introduction of the five IAPS in Nepal's context is provided in Supplementary Information S1.

MATERIALS AND METHODS

The ecological niches of the five IAPS that are found in the foothills of the Himalayas were modelled using maximum entropy (MaxEnt). MaxEnt is a robust model for invasive species modelling with high accuracy estimations of habitat suitability, even with a limited number of available field data (West et al. 2016), and it has higher stability (Duan et al. 2014). Global occurrence data representing both native and exotic ranges were collected from multiple sources, such as the Global Biodiversity Information Facility (GBIF), National Herbarium and Plant Laboratories (KATH), literature and a personal contact. A total of 23,193 occurrence data were used in the model: A. adenophora (2365), A. conyzoides (3005), C. odorata (3623), L. camara (11742) and P. hysterophorus (2458). An ecological niche model was first developed for each individual species at a global scale and then distributions specific to our study area (Fig. 1) were clipped. The idea was to create a global robust climatic envelop using the occurrence records of both native and non-native regions (Supplementary Information S2) and then narrow down a niche distribution analysis for the Himalayas. An ecological niche model calibrated on the data of the native region alone could provide a less reliable outcome on the current and future spread of invasive species compared to a model with the distribution data of the entire range (Beaumont et al. 2009). Similarly, Mainali et al. (2015) argued that model accuracy improved drastically if the dataset of all broader geographic space is used in model training rather than relying on data of a certain restricted region. Saurez-Mota et al. (2016) also recommended the use of global distribution records for niche modelling of invasive plants if the species in the target study region had an incipient presence or the record evidence was deemed not sufficient. Henceforth, we used a global dataset of the five IAPS with the assumption that models capture well the environmental and other variables of both native and exotic geographic ranges.

We downloaded 19 grid-based bioclimatic variables from the Worldclim dataset (www.worldclim.org) at 30 arc sec ($\sim 1 \text{ km}^2$) resolution (Supplementary Information S3). The use of such fine resolution climate data is appropriate for regions with complicated topography such as the Himalayas, where climatic conditions change over a short distance. Current global land cover data at 300 m spatial resolution for the study area were obtained from the European Space Agency (http://due.esrin.esa.int/page globcover.php), while elevation data with a similar resolution to that of bioclimatic variables were obtained from the global multi-resolution terrain elevation data 2010 (http://lta.cr.usgs.gov/GMTED2010). Slope and aspect rasters of the study area were derived from the elevation data, while a population density raster (30 arc sec) was obtained from the Socio-economic Data and Application Centre (http://sedac.ciesin.columbia.edu/data/set/gpw-v4population-density-adjusted-to-2015-unwpp-country-totals). We analysed a multicollinearity test of climatic (19 bioclimates), ecological (elevation, slope, aspect, land cover) and socio-economic (global population density) variables for each of the five species separately using a Pearson correlation in IBM SPSS Statistic Software version 21, removing all the variables with $R^2 \ge 0.75$ and keeping



Fig. 1 Study area showing the occurrence records of the five IAPS and the elevation gradient in the Himalaya

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variables below this threshold for the MaxEnt analysis. Strong collinearity between the variables in predictive modelling could influence the overall model outcome by placing high emphasis on one or two or more highly correlated variables (Baldwin 2009), resulting in misinterpretation. In this context, Dormann et al. (2012) viewed collinearity as a common feature of an ecological data set and often a problem for parameter estimation by inflating the variance of regression parameters that could lead to incorrect detection of relevant predictors in a statistical model, and therefore one needs to be sure that those environmental predictive variables are orthogonal or mutually independent of each other (Cruz-Cardenas et al. 2014). Binary habitat suitability maps for the present and future (2070) were prepared using the maximum training sensitivity plus the specificity logistic threshold in ArcGIS version 10.2 software package. Maximum training sensitivity plus a specificity threshold approach is a more restrictive and conservative approach to understand habitat suitability. This threshold approach is one of the best methods either for presence/absence data or for presence only data when random points are used (Liu et al. 2005a). Furthermore, a sound principle of threshold selection is based on three criteria, viz. objectivity, equality and discriminability, which is fully satisfied by this approach (Liu et al. 2013).

The MaxEnt model used a 20% random test, five replications and 1000 maximum iterations, whereas other parameters remained at default. These parameters are the software in-built features that a modeller adjusts to calibrate the model for achieving a better model output. The area under the curve (AUC) of the Receiver Operator Characteristic (ROC) plot that is available within MaxEnt was used to measure the discrimination ability of the model i.e. model's goodness of fit. AUC values range from 0 to 1 and the model with the highest AUC value is considered as the best performer. Of the total, 80% of the occurrence records were allocated to train the model, while 20% were allocated to test the model. The relative contribution of different bioclimatic predictors to the distribution model was evaluated through MaxEnt outcome using percent variable contribution and Jackknife procedures (Elith et al. 2011). The Jackknife procedure identifies the variables with the greatest influence to the overall model. As per Phillips et al. (2006), the Jackknife procedure is an in-built functionality of MaxEnt where each variable is excluded and a model is reconstructed with the remaining ones after which a new model is created using each variable in isolation. Data on existing protected areas (PAs) at the global scale that fell under the definition of the World Database on Protected Areas (WDPA) of UNEP-WCMC (www. protectedplanet.net) and classified and mapped accordingly were downloaded and clipped to study area to see how many PAs are currently and in the future could be invaded by either one or more of the five IAPS.

The Model for Interdisciplinary Research on Climate version 5 (MIROC5) of the global climate model (GCM) was selected to predict the distribution of the five IAPS. This GCM has better simulation of the mean climate, variability, and climate change due to anthropogenic radiative forcing than its past version (for details, please see Watanabe et al. 2010). Further, Mishra et al. (2014) and Sharmila et al. (2015) reported that MIROC5 captures various observed features of future climate very well, especially for the South Asian region, and some studies (Su et al. 2015; Aryal et al. 2016) used this GCM to model species distributions in the high elevation regions, such as the Himalaya and Tibetan Plateau. As per the IPCC (2013), RCP4.5 is the medium future emission scenario that peaks in approximately 2040, with total radiative forcing could reach almost + 4.5 W/m² (~ 650 ppm CO₂ equivalent) by the end of twenty first century and stabilizes thereafter. Similarly, RCP8.5 is an extreme carbon emission scenario that continues to rise throughout the twenty first century, with radiative forcing reaching almost $+ 8.5 \text{ W/m}^2$ (~ 935 ppm CO₂ equivalent).

After modelling each species separately, we calculated the likely changes in the suitability areas of each individual species for the future compared to current time period. We then overlaid all five species to see which areas would have impacts from all the five IAPS to show their dynamism in terms of expansion, reduction and stability under the future distribution. Likewise, we categorized the study area into six different elevation belts of 500-m intervals, i.e. B1 (<1500 m), B2 (1500-2000 m), B3 (2000-2500 m), B4 (2500–3000 m), B5 (3000–3500 m) and B6 (> 3500 m) to see how the five IAPS respond to climate change along the Himalaya gradient. Similarly, we overlaid existing PAs boundary over the merged IAPS suitability maps to look into the current and possible future invasion into PAs of the region. All of the analyses were carried out using spatial analysis tool available in the Environmental System Research Institute (ESRI) ArcGIS 10.2 software.

RESULTS

Distribution models

The four predictor variables with the highest contributions to the model were temperature seasonality (BIO4), annual mean temperature (BIO1), precipitation of coldest quarter (BIO19) and minimum temperature of coldest month (BIO6) for *A. adenophora*, accounting for 87.4% of the variance; temperature annual range (BIO7), annual precipitation (BIO12), annual mean temperature (BIO1) and

population density for A. convzoides, accounting for 91.8% of the variance; temperature annual range (BIO7), annual precipitation (BIO12), annual mean temperature (BIO1) and population density for C. odorata, accounting for 87.5% of the variance. Similarly, it was annual mean temperature (BIO1), temperature annual range (BIO7), annual precipitation (BIO12) and precipitation of coldest quarter (BIO19) for L. camara, accounting for 88.9% of the variance and annual mean temperature (BIO1), isothermality (BIO3), population density and precipitation of driest month (BIO14) for P. hysterophorus, accounting for 80.1% of the variance (Supplementary Information S4). Overall, BIO1 and BIO12 were common variables for all five IAPS, while the contribution of population density was found to be important for A. conyzoides, C. odorata and P. hysterophorus. The jackknife test also showed that the above variables are important to the model (Supplementary Information **S5**). Some selected response curves of all the species are presented in Supplementary Information S6, which showed how each environmental variable used for each individual species in the model responded to the predicted suitability of those species, which were found to be well within the ecological range. Similarly, the highest training and test area under the ROC curve (AUC) value as provided by the model for the investigated species were as follows: A. adenophora (0.920, 0.922), A. conyzoides (0.879, 0.879), C. odorata (0.866, 0.857), L. camara (0.749, 0.752) and P. hysterophorus (0.900, 0.899).

Current and future projection

The model shows that the suitable habitat of all the five IAPS will change both under RCP4.5 and RCP8.5 by 2070 compared to current distribution (Fig. 1, Table 1). Overall, three species, viz. *A. adenophora, C. odorata* and *L. camara*, will see increased suitable area under both RCP's by 2070, while *A. conyzoides* and *P. hysterophorus* will have decreased suitability. The average combined suitable area of all the five species is 578 908, 573 654 and

| Species | Suitable area (km ²) | | | | | | |
|---------------------|----------------------------------|------------------|-------------|------------------|-------------|--|--|
| | Current | RCP4.5 (2070) | % Change | RCP8.5 (2070) | % Change | | |
| A. adenophora | 353 986 | 426 496 | 20.48 | 431 439 | 21.88 | | |
| A. conyzoides | 770 549 | 639 544 | - 17 | 720 774 | - 6.45 | | |
| C. odorata | 391 386 | 441 639 | 12.84 | 416 016 | 6.29 | | |
| L. camara | 408 034 | 463 951 | 13.70 | 484 730 | 18.80 | | |
| P. hysterophorus | 970 589 | 896 641 | - 7.62 | 898 337 | - 7.44 | | |

590 259 km² for the current, RCP4.5 and RCP8.5 scenarios, respectively. Currently, *P. hysterophorus* occupies maximum suitable area (33.53% of the total suitable area) followed by *A. conyzoides* (26.62%), *L. camara* (14.10%) and *C. odorata* (13.52%), while *A. adenophora* occupied the least (12.22%). All the future changes in the suitability of the five species, either an increase or decrease, will be less than 22% for each species. The highest increase in suitability will be seen for *A. adenophora*, almost 21.88% under RCP8.5, while *A. conyzoides* will have the highest decrease in suitable area, almost -17% under RCP4.5 compared to current time (Table 1).

Suitability dynamics of individual species

Table 2 and Fig. 2 show how the five IAPS under investigation expand, decrease or remain stable under RCP4.5 and RCP8.5 by 2070 in the Himalayan region. All IAPS will have significant dynamism in terms of suitability with respect to future climate scenarios. The majority of suitable areas for all five species will remain stable under both RCPs compared to the present (Fig. 2). A. conyzoides and L. camara will lose the maximum (19.36%) and minimum (2.66%) of suitable areas, respectively, while A. adenophora and A. conyzoides will have the maximum (20.65%) and minimum (2.85%) gains in suitable area under RPC4.5 by 2070 (Table 2). Similarly, P. hysterophorus and L. camara will lose the maximum (14.66%) and minimum (1.67%) of their suitable area, respectively, while A. adenophora and P. hysterophorus will have the maximum (21.42%) and minimum (7.80%) gain in suitable area under RCP8.5 by 2070 (Table 2). Overall, A. adenophora will have the highest gain in suitability under both RCPs, whereas L. camara will have the smallest reduction in suitable area.

Ageratina adenophora will expand more in the western Himalaya, especially on the lower belts of Uttarakhand, Himachal Pradesh and Jammu and Kashmir along with some parts of northern Pakistan under RCP4.5 (Fig. 2a). Little expansion can be seen in the lower belt of the central Himalaya and eastern Himalaya in Assam. Minor expansion will occur in the whole northern belt, including the Tibetan Plateau and Yunnan Province of China. However, under RCP8.5 (Fig. 2b), more expansion can be expected in the lower belt of the central and eastern Himalaya, while less expansion in the western Himalaya is evident under RCP4.5. In RCP4.5, the species will have a minor northward expansion throughout the whole region, including Yunnan. For A. convzoides, some areas will become unsuitable under RCP4.5, especially the lower belt of the western Himalaya and northern India, while Yunnan will see expansion. A reduction of suitability can be seen under RCP8.5, but will also have more expansion both in the

| Species | Area under RCP4.5 (km ²) | | | Area under RCP8.5 (km ²) | | | |
|-----------------|--------------------------------------|------------------|-----------------|--------------------------------------|------------------|-----------------|--|
| | Reduction | Stable | Expansion | Reduction | Stable | Expansion | |
| A adenophora | 19 637 (4.40%) | 334 349 (74.94%) | 92 147 (20.65%) | 19 038 (4.25%) | 334 947 (74.35%) | 96 492 (21.42%) | |
| A conyzoides | 153 594 (19.36%) | 616 954 (77.79%) | 22 589 (2.85%) | 122 122 (14.49%) | 648 427 (76.93%) | 72 347 (8.58%) | |
| C odorata | 18 578 (4.04%) | 372 808 (81%) | 68 830 (14.96%) | 25 609 (5.80%) | 365 777 (82.82%) | 50 239 (11.37%) | |
| L camara | 12 694 (2.66%) | 395 339 (82.94%) | 68 612 (14.39%) | 8 236 (1.67%) | 399 798 (81.10%) | 84 932 (17.23%) | |
| P hysterophorus | 144 436 (13.87%) | 826 152 (79.35%) | 70 488 (6.77%) | 154 326 (14.66%) | 816 263 (77.54%) | 82 073 (7.80%) | |

Table 2 Stable, reduction and expansion suitable areas of the five IAPS by 2070 under RCP4.5 and RCP8.5

Note: The percentages in brackets denote the portion of the total distribution of a species

western Himalayas and Yunnan province (Fig. 2d). For C. odorata (Fig. 2e), some parts of Jammu and Kashmir will be more suitable, including the border between western Nepal and India as well as Yunnan, under RCP4.5. Northward expansion is visible and similar to that A. adenophora. However, expansion will be less under RCP8.5, though minor northward expansion is still evident. Likewise, L. camara (Fig. 2g) will expand into some parts of Afghanistan and Pakistan, including the lower belt of Himanchal State and Jammu and Kashmir of the western Himalaya, under RCP4.5. Northern India bordering central Nepal and Assam in the eastern Himalaya will see suitable areas for the expansion of L. camara, including the northern elevated range as well as in Yunnan Province. Similar phenomena could be expected for this species under RCP8.5 but with more climatically suitable areas in Yunnan Province. On the contrary, P. hysterophorus (Fig. 2i) will have less climatically suitable areas in the whole northern region at the highest elevations, including Yunnan, under both RCPs compared to the other four species. The southern belt of the Himalaya, mainly Punjab Province of both Pakistan and India, will have less expansion and more contraction in suitability. Northeast Afghanistan will gain some suitable areas under both RCPs, while northern Myanmar will see more unsuitable areas under RCP8.5 by 2070 (Fig. 2j).

Suitability along elevation belts

The percentage change in climatic suitability with respect to different elevation belts in the Himalayan region for the present and 2070 under RCP4.5 and RCP8.5 is provided in Table 3. On average, almost 78% of the current suitable habitats of the five IAPS lies below 1500 m (B1). Approximately 89% and 64% of the current suitable habitats of *C. odorata* and *A. adenophora* lie below 1500 m, respectively. From this, it is obvious that all the investigated species categorically belong to tropical and subtropical climates. However, there is a sharp decline in potential suitable areas with increasing elevation. *A. adenophora* and *L. camara* have almost 20% suitable area at B2 (1500–2000 m), while the remaining three species have only approximately 8% of suitability on average, and this suitability declines further at higher elevations. The future suitability of all the five IAPS under both RCPs follows the same pattern; however, they differ in the expansion and reduction of such suitability. For instance, the suitability of *A. adenophora* and *L. camara* continues to decline in both RCPs beyond B3 (2000–2500 m), while the rest of the species shows a mixed trend of both expansion and contraction. Such dynamism also differs if we consider the same elevation belts between the present and RCP4.5 and RCP8.5 in 2070.

Invasion of IAPS in the protected areas

A total of 493 protected areas (PAs), based on the classification and mapping of the World Database on Protected Areas (WDPA) of UNEP–WCMC, exist in the study area (Fig. 3). Our results show that no new PAs in the study area will be invaded by 2070 under both RCPs, since most of them (338 PAs, which is ~ 69%) are already being invaded in whole or part by either one or more of the five investigated IAPS. This includes almost all the PAs in Nepal and Bhutan, as well as one from Afghanistan, 78 from China, 114 from India, 5 from Myanmar and 83 from Pakistan. However, the areal extent of the five IAPS will either increase or decrease within the boundaries of the PAs in the future (under both RCPs by 2070).

For example, the future suitability expansion of *A. adenophora* will mostly be to PAs of north-western India, while *C. odorata* could affect some PAs of northern India (Figs. 2, 3). Similarly, the *L. camara* habitat expansion could invade PAs up to northern Pakistan and eastern India (Fig. 2, 3).

DISCUSSION

This study investigated current potential and future predicted habitat suitability of the five IAPS in the Himalayan region using the MaxEnt ecological niche modelling



Fig. 2 Projected distribution maps of five IAPS showing likely stable, expansion and reduction areas under RCP4.5 and RCP8.5 in 2070 with respect to the current time period (AF Afghanistan, TJ Tajikistan, PK Pakistan, IN India, NP Nepal, BT Bhutan, MM Myanmar and CN China)

| Elevation Belts (m) | CC scenario | < 1500 (B1) | 1500-2000 (B2) | 2000–2500 (B3) | 2500-3000 (B4) | 3000-3500 (B5) | > 3500 (B6) |
|---------------------|-------------------|-------------|----------------|----------------|----------------|----------------|-------------|
| A. adenophora | Current % | 63.897 | 22.449 | 11.966 | 1.588 | 0.082 | 0.018 |
| | RCP4.5 (% change) | 2.899 | - 2.705 | - 0.920 | 0.539 | 0.169 | 0.018 |
| | RCP8.5 (% change) | - 1.027 | - 2.002 | 1.036 | 1.523 | 0.423 | 0.048 |
| A. conyzoides | Current % | 72.084 | 11.253 | 9.410 | 4.461 | 2.646 | 0.146 |
| | RCP4.5 (% change) | - 3.372 | 1.979 | 0.889 | 0.612 | - 0.163 | 0.055 |
| | RCP8.5 (% change) | - 6.082 | 2.034 | 2.920 | 2.044 | - 0.969 | 0.052 |
| C. odorata | Current % | 89.485 | 8.477 | 1.570 | 0.429 | 0.032 | 0.006 |
| | RCP4.5 (% change) | - 2.252 | 0.261 | 1.329 | 0.648 | 0.015 | - 0.001 |
| | RCP8.5 (% change) | - 0.875 | 0.138 | 0.944 | - 0.191 | - 0.015 | -0.002 |
| L. camara | Current % | 75.640 | 18.705 | 5.434 | 0.190 | 0.027 | 0.004 |
| | RCP4.5 (% change) | - 1.181 | - 0.296 | 1.385 | 0.075 | 0.011 | 0.006 |
| | RCP8.5 (% change) | - 0.475 | - 0.780 | 1.117 | 0.123 | 0.011 | 0.005 |
| P. hysterophorus | Current % | 87.245 | 5.826 | 5.510 | 0.601 | 0.378 | 0.440 |
| | RCP4.5 (% change) | - 0.338 | 0.790 | - 0.474 | 0.569 | - 0.246 | - 0.301 |
| | RCP8.5 (% change) | 0.831 | 0.048 | - 1.432 | 1.150 | - 0.184 | - 0.413 |

Table 3 Percentage change in current and future suitability areas of the five IAPS with elevation belts and two emission scenarios

Note: Corresponding areas in km² with respect to elevation belts for each climate scenario are provided in Supplementary Information S7

software and also looked at possible impacts on biodiversity-rich PAs. The current potential habitat distribution of all five IAPS highly matched with the existing occurrence records used in the model analysis (Fig. 1) and supports the findings of Xu et al. (2012) and Chen et al. (2017), who also reported that the distribution of invasive species in China is highly concentrated in Yunnan, eastern and coastal provinces, while areas in western regions, such as the Tibetan Plateau, have the least. Our models obtained AUC values that ranged from almost 0.75 for L. camara to 0.92 for A. adenophora, which are within the acceptable range for models to be considered robust. Swets (1988), Pearce and Ferrier (2000) and Elith (2000) suggested that AUC values above 0.75 are potentially useful and acceptable for interpreting a niche model output. In this context, Evangelista et al. (2008) showed that predictive ecological niche models perform poorly for generalist plants such as invasive species that can withstand broad environmental conditions that are not easily defined by data, independent variables or model design compared to geographically restricted specialist plants. Thus, we considered our model performance sufficient for interpreting the overall result of the five IAPS in the Himalayas. The annual mean temperature and annual precipitation were found to be the most influential variables for most of the IAPS, along with population density, compared to topographical variables such as elevation, slope and aspect in describing their distribution. Zhu et al. (2007) reported temperature and precipitation as the major variables influencing the spread of A. adenophora in China. Human population density and economic activity were strongly

correlated with invasive species richness in 31 provinces of China (Liu et al. 2005b), which has been reported as a similar case to the central Himalaya (Bhattarai et al. 2014; Shrestha et al. 2015), suggesting that both of these factors are the keys behind the spread of invasion, as shown by our models.

Of the five species, three species, viz. A. adenophora, C. odorata and L. camara, will have overall increased suitability under both RCPs compared to the present, while A. convzoides and P. hysterophorus will have decreased suitability overall. This change in suitability in the future depends not only on the temperature or precipitation variables that the MaxEnt model used but also on many nonclimatic factors as well as the individual plant's morphological and physiological advancement and its ability to cope with an adverse climate. All five IAPS are characteristically known as broad ecological and environmentally tolerant species that possess the inherent features necessary to maintain their growth and survival in adverse conditions. It is for this reason that it is difficult for us to explain why some species will expand and others may contract their suitable areas in the next couple of decades. Bezeng et al. (2017), for instance, modelled 162 non-native trees and shrubs of South Africa and found that over half of them will have decreased climatic suitability by 2070. Fandohan et al. (2015) also reported a decrease in the suitability of C. odorata in the protected areas (PAs) of four West African countries by 2070. Similarly, the changes in either expansion or reduction of such suitable area are less than twenty two percent, while most of the area remains stable for all species (Table 2, Fig. 2). This suggests that all the







Fig. 3 Combined invasion of the five IAPS (grey coloured) for the present, RCP4.5 and RCP8.5 for the year 2070 and vulnerable protected areas (light brown coloured) in the study area

modelled IAPS will conserve most of their current ecological niche even with future changes in climate in the Himalayan region. Some species will expand towards the south, especially in the central and eastern foothills of the Himalaya. This is obvious, as Goncalves et al. (2014), citing spread of L. camara in India, reported that invasive species should not always be expected to conserve their strict niche, and therefore, areas in all directions may be at risk of a potential future invasion. Invasive species exhibit more phenotypic plasticity, an evolutionary mechanism, than native species occurring in the same region (Daehler 2003), signifying their ability to move into suitable climatic areas that enhance their growth and development. For instance, Zhao et al. (2012) reported that phenotypic plasticity is the only factor that helps the invasive weed A. adenophora to succeed in different climatic and geographic contexts in Yunnan, China. The southward expansion of L. camara in northern India on the border of Nepal and Assam shown by our model can be further justified because these areas are elevated terrain between 500 and 1300 m that could be under cold stress currently and whose climate may warm by 2070 to better suit the species requirement.

Our model shows less northward expansion overall from all of the five IAPS, with almost none towards the Tibetan Plateau, while there is some expansion towards the western Himalayan region (Fig. 2). As mentioned, it should be noted first that all the modelled species are of tropical and sub-tropical origin, with lower growth form that could not withstand the harsh climate of the high Himalaya and Tibetan Plateau, even though some climatic modification is projected there. For instance, alien invasive plants can have a strong response in the currently warm, urbanized and low elevation regions rather than the areas with cold and high elevations that have a low human population and less disturbance (Marini et al. 2009). In the case of China, Lin et al. (2007) argued that provinces located in southern China and the coastal areas of eastern China, which saw a major boost in economic activities in the last quarter of 20th century and are now more economically developed, have higher abundances of invasive species compared to provinces in inland and western China, such as our study area, that contributed as much to the expansion of invasive species as climatic factors.

Similarly, the B1 (< 1500 m) belt has high suitability for all the species, which tends to decrease with increasing elevation under both RCPs by 2070 (Table 3). McDougall et al. (2011) and Alexander et al. (2011) reiterated that invasion risk in the mountain ecosystem is comparatively less than other ecosystems. Low propagule availability, the absence of species exposed to wider environmental conditions, low anthropogenic disturbances and low invasibility of natural communities are reasons that the alpine ecosystem currently has a restricted number and intensity of invasive species (Alexander et al. 2016). Abiotic stressful areas, such as the Himalayas and Tibetan Plateau, are less prone to invasion than more moderate environments. Zefferman et al. (2015) explained the low invasibility of harsh areas through twin hypotheses: (i) propagule limitation hypothesis-suggests invasion on such sites is limited by the low arrival rates of propagules than in moderate habitat found at lower elevations; and (ii) invasion resistance hypothesis-suggests that such sites bear abiotic stressful conditions even in the future and also have increased biotic resistance from resident organisms. Our findings are consistent with (i) Andersen et al. (2015) and Averett et al. (2016), who reported a decreasing distribution of invasive species with increasing elevation in the Wallowa Mountains of the USA; (ii) Becker et al. (2005) and Seipel et al. (2016), for similar observations in the Swiss Alps; and (iii) Barni et al. (2012) in a mountain ecosystem in the Italian Alps. They argued that an invasion into such highlands will proceed at rather a slow pace due to the adverse climate in the context of future warming. Joshi et al. (2006) reported that lower winter temperatures or high frost levels constrained the vertical distribution of invasive plant species such as C. odorata towards the northern boundary of the Nepal Himalaya, mainly due to their impacts on photosynthetic activity.

The problems known so far as a result of the invasion of alien species should act as a lesson for us to take actions even before we are able to unearth all of their effects (McNeely 2001). Impacts from invasive species to ecosystems and their biota is pervasive at a global scale, which in turn affects ecosystem services (ES) upon which millions of people derive or sustain their livelihood. Our result shows the possible expansion of suitable areas of the five IAPS in different ecosystems ranging from tropical and sub-tropical to temperate in the elevated northern region (Fig. 2, Table 3). Similarly, Fig. 3 depicts that almost 69% of the PAs established within the study area are currently invaded and will remain so in the future by the five investigated IAPS that are capable of invading forests, shrub land, grassland, pasture and agroecosystems. This will have irreversible impacts on the habitat and food availability for many endangered wildlife species. The whole Himalayan region is a hotspot of biodiversity with numerous fragile ecosystems along the northern boundary. For instance, Chettri et al. (2008) reported that 32% of the PAs within the Hindu Kush Region fall under a global biodiversity hotspot, while 62% are under the Global 200 eco-regions. PAs in China occupy almost 15% of the total land area, with a high concentration found in the western region, including Tibet and Qinghai (Xu et al. 2017). Kannan et al. (2013) reported that the majority of PAs in India, i.e. 102 national parks and 515 wildlife sanctuaries spatially distributed from lowlands to highlands, are currently invaded by invasive species, notably with *Lantana* and *Eupatorium* spp., while future impacts are largely unknown. Even the southern tropical PAs are the critical habitat of numerous endangered species, such as rhinoceros, royal Bengal tiger and many indigenous flora, for which invasion is considered highly destructive. The provisioning ES, such as non-timber forest products (NTFPs) on which the livelihoods of mountain people depend, could be heavily hit from such invasions in the sub-temperate and temperate regions.

Similarly, as discussed, a niche model performs comparatively poorly for generalist plants, such as the ones that have been modelled in this paper. MaxEnt is based on climate, and many non-climatic factors such as biotic interactions, soil types, as well as dispersal mode and abilities that are also responsible for the future dynamism of invasive species by restricting or expanding their ranges are not included in the modelling process. Clements and Ditommaso (2011) argued that current modelling approaches should consider potential evolutionary changes to correctly predict the invasive range expansion because these plants are capable of rapid genetic changes to boost their invasive ability into newly invaded areas with a modified ecosystem. Urban et al. (2016) recently emphasized the use of biological mechanisms of species in the model to increase the prediction accuracy and make the model uncertainties explicit. There are uncertainties inherent in the existing model projection and future emission scenarios itself (Stott and Kettleborough 2002; Knutti and Sedlacek 2013). Similarly, Jones (2012) reported that high current niche model accuracy, especially in the case of invasive species, may not point to high future accuracy, mainly because they are not at equilibrium with the environment and therefore suggested to use it more cautiously.

The five IAPS investigated in this paper are of tropical origin, not temperate or alpine origin, and the growth form and physiological and morphological characteristics totally differ compared to plants from high elevations; therefore, we could not expect a massive northward and high elevation expansion with a future warming climate in the region, as suggested for cold-adapted plant species in other studies (Song et al. 2004; Benito et al. 2011; Xiaodan et al. 2011; Lamsal et al. 2017). Human activities, such as agriculture and urban development, might move upward in the mountain region under current global warming (Price 2006). Marini et al. (2012) reported human population pressure as a major driver of alien plant invasions in the European Alps in their distribution compared to climatic conditions. As the literature suggests, such activities in high lands cause areas to become suitable for invasion, which is also the case for the Himalayas. In addition, Zhang et al. (2015) found that the invasive species that reach higher elevation of mountain forests in Sangdong Province of China are those that have successfully invaded low elevations and filtered out to areas with successive worsening climate and decreasing anthropogenic propagule pressure. Similar findings have been reported from the Canary Islands of Spain (Haider et al. 2010), where most of the non-native plants of higher altitudinal ranges were the ones introduced in lowlands and preadapted to local climates. All the IAPS considered in this study were introduced and are currently well adapted to the lowlands of the Himalaya foothills and therefore are likely to expand along the high elevation gradient, though at a very low pace.

Invasive species pose a significant global problem, causing detrimental impacts to all states, to their ecosystems and diversity, and thus deserve a significant global response (McNeely 2001). IAPS in South Asia are a comparatively a less studied topic, though this region is highly vulnerable to invasion due to the high mosaic of biodiversity hotspots and low human response capacity. The fate of high elevation mountain ecosystems, such as the Himalayan region, is even unknown. Zhang et al. (2015) suggested that the monitoring and management of IAPS should first target low elevation areas to prevent their invasion into high elevation regions, which could be the case for the Himalayas. Likewise, Funk et al. (2014) reported the impact of IAPS on ecosystem services that directly hinders economic and ecological benefit to human beings. These effects should be considered in an intergovernmental policy dialogue to assure continuous and timely investment in control activities.

CONCLUSION

This study reveals that the five IAPS will mostly conserve their existing ecological niches in the future, with lesser expansion towards the northern high elevation regions of the Himalayas, because the high mountains and harsh climate could potentially serve as barriers. Therefore, our findings are timely and are thus expected to help resource managers, including those in PAs, in preparing a baseline database and initiating the formulation of future response strategies in the Himalayan region against anticipated invasion risks arising from these five IAPS. The newly identified areas at high risk as a result of transboundary scale IAPS expansion can be delineated for strategic control measures to prevent their spread. A good and realistic transboundary strategic response policy that is suitable to local context of each country, for example, indigenous biological and cultural weed control measures, could be a viable option to buffer against the current and future detrimental impacts of invasion into the fragile ecosystems of the region that harbour numerous endangered biota.

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AUTHOR BIOGRAPHIES

Pramod Lamsal (\boxtimes) is a Ph.D. candidate at The University of New England, Australia. His research interests include climate change impact and species distribution modelling, remote sensing, geo-spatial modelling and ecosystem services.

Address: School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia.

e-mail: plamsal@myune.edu.au; pramod_lamsal@yahoo.com

Lalit Kumar is a Professor at The University of New England, Australia. His research interests include climate change impacts on biodiversity and Small Island states, mainly in the Pacific and the Himalayan region, remote sensing, spatial modelling, spatial ecology and species distribution modelling.

Address: School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia. e-mail: lkumar@une.edu.au

Achyut Aryal is an honorary research fellow at The University of Sydney/Federation University of Australia, Australia; Toi Ohomai Institute of Technology, New Zealand, and research associate at Human-Wildlife Interaction Research Group, Massey University, New Zealand. His research interest includes conservation biology, wildlife ecology and climate change.

Address: Department of Forest and Resource Management, Toi Ohomai Institute of Technology, Rotorua 3046, New Zealand. e-mail: savefauna@gmail.com

Kishor Atreya is an agricultural and environmental health expert at Asia Network for Sustainable Agriculture and Bioresources (ANSAB), Nepal. His research interests include environment-human health/livelihood nexus; biodiversity, ecosystem services and climate change; health risk assessment; social cost–benefit analysis; and economic valuation of environmental resources/pollution.

Address: Asia Network for Sustainable Agriculture and Bioresources, Kathmandu, Nepal.

e-mail: k.atreya@gmail.com