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Climate change amplifies plant invasion hotspots in Nepal

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Abstract

Aim: Climate change has increased the risk of biological invasions, particularly by increasing the climatically suitable regions for invasive alien species. The distribution of many native and invasive species has been predicted to change under future climate. We performed species distribution modelling of invasive alien plants (IAPs) to identify hotspots under current and future climate scenarios in Nepal, a country ranked among the most vulnerable countries to biological invasions and climate change in the world.

Location: Nepal.

Methods: We predicted climatically suitable niches of 24 out of the total 26 reported IAPs in Nepal under current and future climate (2050 for RCP 6.0) using an ensemble of species distribution models. We also conducted hotspot analysis to highlight the geographic hotspots for IAPs in different climatic zones, land cover, ecoregions, physiography and federal states.

Results: Under future climate, climatically suitable regions for 75% of IAPs will expand in contrast to a contraction of the climatically suitable regions for the remaining 25% of the IAPs. A high proportion of the modelled suitable niches of IAPs occurred on agricultural lands followed by forests. In aggregation, both extent and intensity (invasion hotspots) of the climatically suitable regions for IAPs will increase in Nepal under future climate scenarios. The invasion hotspots will expand towards the high-elevation mountainous regions. In these regions, land use is rapidly transforming due to the development of infrastructure and expansion of tourism and trade.

Main conclusions: Negative impacts on livelihood, biodiversity and ecosystem services, as well as economic loss caused by IAPs in the future, may be amplified if preventive and control measures are not immediately initiated. Therefore, the management of IAPs in Nepal should account for the vulnerability of climate change-induced biological invasions into new areas, primarily in the mountains.

KEYWORDS
biological invasions, climate change, Himalaya, invasive species management, species distribution modelling

1 | INTRODUCTION

Biological invasions and climate change are two major drivers of biodiversity loss and ecosystem service change worldwide (Pecl et al., 2009; Urban, 2015; Vilà & Hulme, 2017; Walther et al., 2009). Invasive alien plants (IAPs; sensu Pyšek et al., 2014) pose the greatest threats to natural ecosystems, human health, economy, agriculture and fisheries (Pimentel, Zuniga, & Morrison, 2009; Vilà et al., 2010; Vilà & Hulme, 2017). The threat and loss constituted by invasive species are exacerbated by climate change through multiple mechanisms including the removal of climate barriers for establishment and the spread of many invasive species (Bradley, Blumenthal, Wilcove, & Ziska, 2010; Hellmann, Byers, Bierwagen, & Dukes, 2008). For example, Petitpierre et al. (2017) have shown that the upslope spread of the lowland IAPs to mountains is limited by low temperatures in the mountains. Yet, climate change will shift regions of optimal suitability for these IAPs from lowlands to highlands. Invasive species have a greater capacity to shift their niches more rapidly than native species, and they are more likely to adapt to new climatic conditions faster (Dukes & Mooney, 2004; Hellmann et al., 2008). The climatic niche shift has been demonstrated as one of the mechanisms used by IAPs to spread rapidly into introduced ranges (e.g., Treier et al., 2009; Gallagher, Beaumont, Hughes, & Leishman, 2017). Furthermore, the IAPs benefit from global warming and atmospheric CO_2 enrichment more than native plants (Liu et al., 2013; Verlinden & Nijs, 2010). Therefore, an integrated understanding of biological invasions and climate change is necessary for the management of IAPs.

Projected changes in climate in the future may influence the distribution of many native and invasive species (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Walther et al., 2009). At the species level, climate change causes range expansions of many invasive species and contraction to few (Bellard et al., 2013; Bradley et al., 2010). Therefore, these potential changes in distribution need to be incorporated into the management and conservation of ecosystems and biodiversity in the face of biological invasions and climate change (O'Donnell et al., 2012). A better understanding of threats and an ability to accurately predict the impacts of climate change on species distribution are necessary to make an informed decision for biodiversity conservation (Pimm et al., 2005). This will help to minimize the threat of invasive species into the future and support effective conservation efforts. Although the impact of climate change on the distribution of multiple invasive species is known in developed regions such as Australia, North America and Europe (Allen & Bradley, 2016; O'Donnell et al., 2012), little is known about how the distribution of invasive species will change with future climatic changes in developing countries such as Nepal.

With the estimated annual cost of US$ 1.4 billion, due to biological invasions to Nepal's agriculture sector, Nepal is ranked among the topmost countries (ranked 3rd out of 124 countries) in terms of invasion threats to agriculture sectors (Paini et al., 2016). The concentration of vertebrate species threatened by biological invasions is also high in the Indian subcontinent including Nepal (Bellard, Genovesi, & Jeschke, 2016). Currently, there are 241 alien plants and animals in Nepal and 45 of them are considered invasive (Shrestha, Budha, Wong, & Pagad, 2018). These invasive species can be found from lowland plains in the south to hills and mountains in the north. Globally, mountain ecosystems are generally less invaded compared to the surrounding lowlands (McDougall et al., 2011). However, the intensity of biological invasions is likely to increase in future with changing climate and increasing anthropogenic disturbances in the mountains (Pauchard et al., 2016; Petitpierre et al., 2017). In Nepal, most of the IAPs are found below 2,000 m in elevation (Shrestha, 2016) but recent studies based on field observations and models suggest that some of these IAPs are already expanding their ranges into new geographic locations at a higher elevation (Lamsal, Kumar, Aryal, & Atreya, 2012; Shrestha, Sharma, Devkota, Siwakoti, & Shrestha, 2018; Thapa, Chitale, Rijal, Bisht, & Shrestha, 2018).

The severity of threats to Nepal's economy and ecosystems from biological invasions is considered in national conservation policies and sectoral conservation strategies such as the Plant Protection Act (2007), National Biodiversity Strategy and Action Plan (2014), Forestry Sector Strategy (2016–2015) and National Ramsar Strategy and Action Plan (2018–2024). However, the implementation of these policies and strategies is very poor, partially because of the lack of scientific knowledge required to control invasive alien species (MFSC, 2014; Shrestha et al., 2015). National Biodiversity Strategy and Action Plan (2014–2020) has identified priorities of actions for the management of invasive alien species that includes, among others, research and prioritization of problematic IAPs (MFSC, 2014). To this end, this study is an important contribution to enhance the knowledge and understanding of invasive species by identifying potentially suitable niches for 24 IAPs (out of reported 26 species) in Nepal under current and future climate using an ensemble of species distribution models.

We also performed a hotspot analysis to identify areas suitable for a maximum number of IAPs. In biodiversity conservation, the concept of a biodiversity hotspot—an area with high species richness, endemism and threatened taxa—is well established (e.g., Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2003). Hotspot analysis provides a framework for cost-effective conservation programmes, thus helping to prioritize conservation efforts (Myers, 2004). Similarly, hotspot analysis can help streamline management efforts in a way to prevent, eradicate and control the maximum number of invasive species at the lowest cost possible (Adhikari, Tiwary, & Barik, 2015; O'Donnell et al., 2012). Attempts at applying the hotspot concept to biological invasions were made at a global scale (Drake & Lodge, 2013), according to country (Australia by O'Donnell et al., 2012, United States by Allen & Bradley, 2016, India by Adhikari et al., 2015) and according to the local scale (Corangamite Catchment in Australia by Catford, Vesk, White, & Wintle, 2011), using different tools and techniques. In this study, we used the invasion hotspot approach to identify regions with high concentrations of potentially
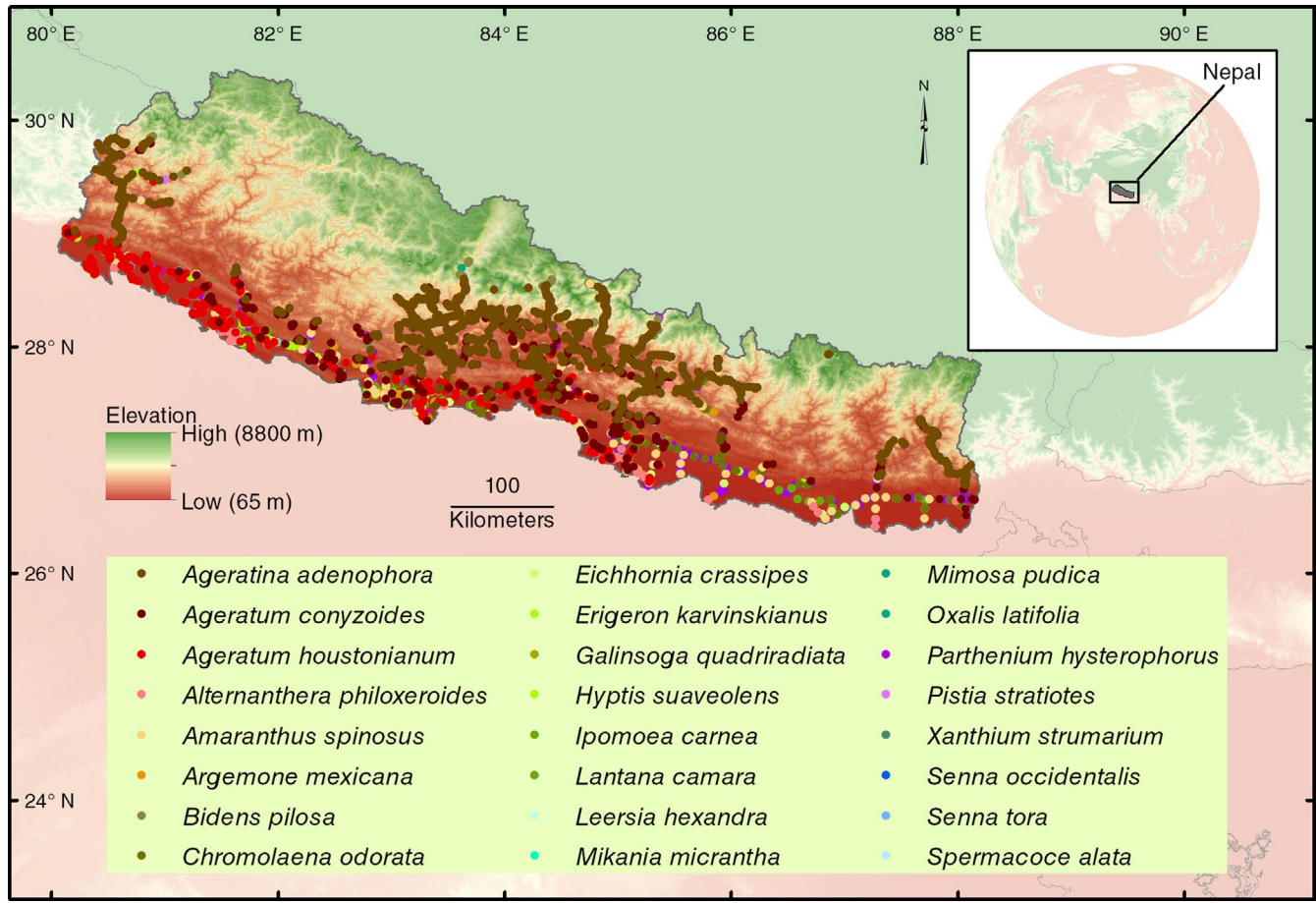
FIGURE 1 Occurrence of 24 invasive alien plants in Nepal. Each dot represents geographic coordinates of the species

suitable niches for multiple IAPs under current and future climate in Nepal. We also examined changes in invasion hotspots according to different land covers, climatic zones, physiographic regions, ecoregions and federal states. This study provides the first-ever comprehensive national-level assessment of biological invasions using occurrence data of most of the IAPs found in Nepal. By highlighting the geographic hotspots for IAPs, our results provide wide-ranging evidence of current and future risks constituted by IAPs at the national scale. The results of this study will be important when considering cost-effective strategies for managing IAPs and will support long-term biodiversity conservation and sustainable development goals in Nepal.

2 | METHODS

2.1 | Invasive alien plants' occurrence data

We selected 24 out of the total 26 species of IAPs reported in Nepal (Shrestha, 2016; Tiwari, Adhikari, Siwakoti, & Subedi, 2005) for the modelling exercise (Figure 1). Location information sufficient for the distribution modelling of the remaining two species (*Myriophyllum aquaticum* and *Spergula arvensis*) is not yet available. The description (name, family, native origin, functional group,

distribution range and mode of dispersal) of the selected species is given in Table 1. Four of the modelled species (*Chromolaena odorata*, *Eichhornia crassipes*, *Lantana camara* and *Mikania micrantha*) are among the 100 of the world's worst invasive species (Lowe, Browne, Boudjelas, & DePoorter, 2017). Sixteen of the modelled species are considered highly problematic species by the local people of Nepal due to their negative impacts on agriculture, local livelihood and natural ecosystems (Shrestha, Shrestha et al., 2018). Modelled species were introduced either deliberately for ornamental purpose (e.g., *L. camara*, *E. crassipes*) or accidentally (e.g., *Ageratina adenophora*, *Parthenium hysterophorus*) to Nepal at various times.

The occurrence data were collected through field surveys by experts in various localities of Nepal at different times from 2013 to 2018 (Shrestha, 2014; Shrestha, Joshi et al., 2018; Shrestha, Kokh, & Karki, 2016; Siwakoti et al., 2016). The number of occurrence locations for each species ranged from 25 (*Leersia hexandra*) to 1,910 (*Bidens pilosa*). Species distributional data often display spatial autocorrelation which has implications for predicting species occurrences under changing environmental conditions (Dormann, Grime, & Thompson, 2000; Dormann, 2007). We removed the multiple presence locations in the same grid of ~1 km^2 spatial resolution and retained only one unique record per grid by applying spatial filtering

TABLE 1 Characteristic features of the studied invasive alien plant species (Hara & Williams, 1979; Hara, Chater, & Williams, 1982; Shrestha, 2016; Tiwari et al., 2005)

Scientific name (family)	Common name	Growth form	Mode of reproduction	Native range	First year of report in Nepal
Ageratina adenophora (Spreng.) R.M.King & H.Rob. (Asteraceae)	Crofton weed	Shrub	Seed/vegetative	Mexico	1952
Ageratum conyzoides L. (Asteraceae)	Billygoat	Annual herb	Seed	Central and South America	1910
Ageratum houstonianum Mill. (Asteraceae)	Blue billygoat	Annual herb	Seed	Mexico to Central America	1929
Alternanthera philoxeroides (Mart.) Griseb. (Amaranthaceae)	Alligator weed	Perennial herb	Vegetative	South America	1994
Amaranthus spinosus L. (Amaranthaceae)	Spiny pigweed	Annual herb	Seed	Tropical Americas	1954
Argemone mexicana L. (Papaveraceae)	Mexican poppy	Annual herb	Seed	Tropical Americas	1910
Bidens pilosa L. (Asteraceae)	Black jack	Annual herb	Seed	Tropical Americas	1910
Chromolaena odorata (L.) R.M.King & H.Rob. (Asteraceae)	Siam weed	Shrub	Seed/vegetative	Mexico to South America	1825
Eichhornia crassipes (Mart.) Solms (Pontederiaceae)	Water hyacinth	Perennial herb	Seed/vegetative	South America	1966
Erigeron karvinskianus DC. (Asteraceae)	Karwinsky's fleabane	Perennial herb	Seed/vegetative	Mexico to Central America	1966
Galinsoga quadriradiata Ruiz & Pav. (Asteraceae)	Shaggy soldier	Annual herb	Seed	Mexico	1966
Hyptis suaveolens (L.) Poit. (Lamiaceae)	Bush mint	Annual herb	Seed	Tropical America	1956
Ipomoea carnea Jacq. (Convolvulaceae)	Bush morning glory	Shrub	Seed/vegetative	Mexico to South America	1966
Lantana camara L. (Verbenaceae)	Lantana	Shrub	Seed/vegetative	Central and South America	1848
Leersia hexandra Sw. (Poaceae)	Southern cut grass	Perennial herb	Seed/vegetative	Americas	1820
Mikania micrantha Kunth. (Asteraceae)	Mile-a-minute	Perennial vine	Seed/vegetative	Central and South America	1963
Mimosa pudica L. (Fabaceae)	Sensitive plant	Perennial herb	Seed	Mexico to South America	1910
Oxalis latifolia Kunth. (Oxalidaceae)	Purple wood sorrel	Perennial herb	Seed/vegetative	Central and South America	1954
Parthenium hysterophorus L. (Asteraceae)	Parthenium	Annual herb	Seed	Southern USA to South America	1967
Pistia stratiotes L. (Araceae)	Water lettuce	Perennial herb	Seed/vegetative	South America	1952
Senna occidentalis (L.) Link (Fabaceae)	Coffee senna	Subshrub	Seed	Tropical Americas	1910
Senna tora (L.) Roxb. (Fabaceae)	Sicklepod senna	Annual herb	Seed	Central America	1910
Spermacoce alata Aubl. (Rubiaceae)	Broadleaf buttonweed	Perennial herb	Seed/vegetative	West Indies and Tropical America	1966
Xanthium strumarium L. (Asteraceae)	Cocklebur	Annual herb	Seed	South America	1952

using SDMTOOLBOX 2.3 (Brown, 2014). We also checked differences in Moran's I index values after removing the multiple records using the APE package in R. This approach reduces spatial autocorrelation, which could lead to overfitting the models and therefore reduce model performance (Boria, Olson, Goodman, & Anderson, 2014). After spatial filtering, the total number of occurrence locations comprising 24 species was reduced from 17,682 records to 10,951, and these were then used for modelling.

2.2 | Environmental variables

We used nineteen bioclimatic variables with a spatial resolution of 30 arcsec (~1 × 1 km) downloaded from WORLDCLIM 2 (http://worldclim.org; Fick & Hijmans, 2009). The current bioclimatic variables were computed from monthly values of minimum, average and maximum temperature and monthly precipitation from 1970 to 2000 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2006). Pairwise diagnostic tools such as correlation

matrices and variance inflection factors (VIFs) can be used to detect multicollinearity in a set of bioclimatic variables (Dormann et al., 2000). Bioclimatic variables with high correlation (Pearson's correlation coefficients $r > 0.70$) were removed to reduce multicollinearity (Rogerson, 2001). The VIF values of the resulting predictor variables were less than 5. A VIF greater than 10 signals a collinearity problem (Chatterjee & Hadi, 2015). The remaining seven bioclimatic variables, namely annual mean temperature, mean diurnal range [mean of monthly (max temp-min temp)], isothermality, temperature annual range (max temperature of warmest month-min temperature of coldest month), precipitation in the driest month, precipitation in the warmest quarter and precipitation in the coldest quarter, were used as predictors to model the current distribution of the selected IAPs.

We also modelled distributions of the 24 IAPs for future climatic conditions. We used projected bioclimatic variables for the period 2050 for RCP 6.0 from the Coupled Model Intercomparison Project Phase 5 (CMIP5) as presented by the Intergovernmental Panel on Climate Change (Stocker et al., 2013) to model future distribution. Several groups around the world have been involved in climate model experiments, producing different global climate models (GCMs) which were submitted to the Couple Modelling Intercomparison Project (Taylor, Stouffer, & Meehl, 2012). The outputs of the GCMs for a range of time periods in the twenty-first century are used to produce gridded bioclimatic variables for future climate scenarios (Kriticos et al., 2005). GCMs mathematically represent physical processes in the atmosphere, ocean, cryosphere and land surface (McGuffie & Henderson-Sellers, 2011). Climate models capture the fundamental processes that respond to climate forcing such as concentrations of greenhouse gases, aerosols, surface albedo changes and solar irradiance. Therefore, GCMs are used to understand climate and forecast climate change. The same seven bioclimatic variables used for modelling current distribution were used to predict future distribution of the IAPs. We downloaded bioclimatic data of 12 global circulation models (GCMs): BCC-CSM1-1, CCSM4, GFDL-ESM2G, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3 and NorESM1-M from WorldClim (Fick & Hijmans, 2009). The details of the GCMs are provided in Table S1. Rather than relying on a single model, we created an ensemble of the twelve GCMs by taking average values and used the ensemble values as predictors. The multimodel ensemble average not only accounts for variability among different GCMs, but also yields results superior to individual models at global and regional scales (Aguirre-Gutiérrez, Treuren, Hoekstra, & Hintum, 2017; Murphy et al., 2005; Pierce, Barnett, Santer, & Gleckler, 2016). At a high greenhouse gas emission scenario, RCP 6.0 represents a target forcing of 6.0 W/m^2 above the pre-industrial baseline, predicted to occur by the end of the century (Clarke et al., 2007). According to this scenario, the projected average temperature will rise by about 1.3 and 2.2°C by mid- (2046–2065) and late 21st century (2081–2100), respectively. The average temperature is projected to stabilize after the 21st century by the employment of a range of technologies and strategies for reducing greenhouse gas emissions (Collins et al., 2013).

2.3 | Species distribution modelling

Species distribution modelling is an approach that predicts the distribution of a species across geographic space and time using the correlation between the geographic occurrence or abundance of a species and corresponding environmental conditions (Elith & Leathwick, 2010). This approach has been used in studies of biogeography, conservation biology, ecology, palaeoecology and wildlife management for more than a decade (Araújo & Guisan, 2006) and forecasts the range shifts of species under future climate change scenarios (Beaumont, Pitman, Poulsen, & Hughes, 2007; Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009) including invasive species (Bellard et al., 2013). Various species distribution modelling tools such as statistical regression, machine learning and geographic extrapolation are in current use to model species distribution (Elith et al., 1999). The performance of various algorithms available for species distribution modelling varies significantly (Elith, Kearney, & Phillips, 2006). An ensemble modelling of species distributions involves simulations across more than one set of initial conditions, model classes, model parameters and boundary conditions (Araújo & New, 2007). BIOMOD (BIOMOD2 package in R) is a platform for ensemble forecasting of species distributions (Thuiller, Lafourcade, Engler, & Araújo, 2009). The ensemble model accounts for the uncertainties in predictions of different algorithms and uses a wide range of approaches to test models (Aguirre-Gutiérrez et al., 2017; Thuiller et al., 2009). We used ensemble modelling as this consensus approach can perform better than a single modelling algorithm (Araújo & New, 2007; Thuiller et al., 2009). The analysis was conducted in R environment v 3.4.2 (R Core Team, 2016) using the BIOMOD2 package (Thuiller et al., 2009). The selected algorithms used to produce an ensemble model were as follows: three regression methods (GAM: general additive model; GLM: general linear model; and MARS: multivariate adaptive regression splines), three machine learning methods (ANN: artificial neural network; GBM: generalized boosting model; and RF: random forest) and two classification methods (CTA: classification tree analysis; FDA: flexible discriminant analysis).

As these models required background data (e.g., pseudo-absence) and the actual absence data were unavailable, we used 10,000 pseudo-absences selected randomly outside a buffer of 10 km from the presence points by following Barbet-Massin, Jiguet, Albert, and Thuiller (2012). The models were calibrated by using 70% of the occurrence points (presence and pseudo-absence) as training data and evaluated by using the remaining 30% as testing data (Araújo, Pearson, Thuiller, & Erhard, 2005). We repeated the process of pseudo-absence generation three times and three evaluation runs per species, resulting in a total of 72 models per species (eight models, three evaluation runs and three pseudo-absence selection procedures) under each climate scenario.

We used two evaluation measures of model validation and predictive performance namely the area under the curve (AUC) of receiver operating characteristics and true skills statistics (TSS). The AUC value represents the predictive power of a model (Allouche,

Tsoar, & Kadmon, 2006) although study suggested additional criteria (e.g., report of sensitivity and specificity) to assess the model performance (Lobo, Jiménez-Valverde, & Real, 2013). According to the AUC value, the model was graded as poor (if AUC = 0.6–0.7), fair (AUC = 0.7–0.8), good (AUC = 0.8–0.9) or excellent (AUC = 0.9–1.0) (Swets, 1988). TSS measure ranges from −1 to +1 where +1 indicates a perfect agreement, and a TSS value below 0.4 indicates poor model discrimination (Allouche et al., 2006; Beaumont et al., 2016). From the 72 models per species, we built ensemble models using a weighted-mean approach in which weights are awarded for each model proportionally to their evaluation metrics scores; hence, the discrimination is fair in this approach (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2000). Only the models with good predictive accuracy (TSS > 0.6 and AUC > 0.8) were used to build an ensemble from the projection outputs (Bellard et al., 2013; Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2010; Thuiller et al., 2009). Binary maps (suitable and unsuitable) were produced using the optimal threshold that maximizes the TSS score as a cut-off value, which then converted the projected occurrence probabilities during the cross-validation procedure (Allouche et al., 2006; Liu, White, & Newell, 2016; Marmion et al., 2000). This threshold is unaffected by the prevalence of species occurrence and favours sensitivity (the number of false positives) over specificity (the number of false negatives), which is considered superior for modelling invasive species (Gallardo & Aldridge, 2009). For all species, we built a minimum convex hull (MCH) around current locations of a species to determine the extent of their occurrence (IUCN, 2012; Wright, Hijmans, Schwartz, & Shaffer, 2015; Figure S1). For each species, we measured the size of their range as represented by the number of climatically suitable pixels within the convex hull for the designated period and calculated changes in the range sizes among two different periods (current and 2050). This allowed us to exclude the predicted suitable areas for future climate outside the convex hull where climatic conditions might not be analogous to present conditions. It also reduced the chances of overestimating the species niche (Capinha & Pateiro-López, 2014). We also computed the change in the total area of predicted niches within a MCH of currently occupied locations for each species under current and future climate (number of pixels suitable under future climate—number of pixels suitable under current)/number of pixels suitable under current).

2.4 | Invasion hotspot map

We conducted a hotspot analysis (e.g., O'donnell, 2011) to identify the regions potentially suitable for the maximum number of IAPs under current and future climate. We aggregated maps of climatically suitable niches for all species to generate species diversity (cells with a higher value indicating high species diversity) and extent maps (cells occupied by at least a single species). We calculated changes in the areas of both diversity and extent of potentially suitable regions under current and future climate. The species diversity map was later reclassified using the combined values greater than or equal to

the 25th percentile. The regions with potentially suitable niches for the top 25th percentile of the combined values were considered as "invasion hotspots" (Allen & Bradley, 2016; O'donnell et al., 2011). We calculated changes in the areas of so-called invasion hotspots under current and future climate with respect to climatic zones, land cover, ecoregions, physiographic regions and federal states. We used publicly available maps of ecoregions (Olson et al., 2012), land cover (Uddin et al., 2015), physiography and administrative units. A layer of climatic zones was created by using digital elevation model as tropical (<1,000 m asl), subtropical (1,000–2,000 m asl), temperate (2,000–3,000 m asl), subalpine (3,000–4,000 m asl) and alpine (>4,000 m asl) following Shrestha (2008).

3 | RESULTS

The model performance was evaluated by the scores of two (AUC and TSS) performance matrices (Figure S2). The average AUC values of the 24 studied IAPs ranged from 0.74 (*Leersia hexandra*) to 0.93 (*Erigeron karvinskianus*), indicating that the models have fair to excellent predictive accuracy. Likewise, the average TSS value ranged from 0.50 to 0.83 indicating good predictive accuracy. Moreover, we only used the model with the higher predictive accuracy (AUC > 0.8 and TSS > 0.6) to build an ensemble from the projection outputs.

Based on our species distribution models, areas of potentially suitable niches for the studied IAPs vary widely (Table 2; Figure S3). Out of the 24 species, 15 had potentially suitable areas that covered more than 10% of Nepal's land area under current climate. *Parthenium hysterophorus*, *Amaranthus spinosus*, *Senna tora*, *Ageratum houstonianum* and *Ageratum conyzoides* had a potentially widespread distribution, whereas *Pistia stratiotes*, *Leersia hexandra*, *Erigeron karvinskianus*, *Oxalis latifolia* and *Alternanthera philoxeroides* had a restricted distribution under the current climatic condition (Table 2). The predicted suitable niches for three species *Pistia stratiotes*, *Leersia hexandra* and *Erigeron karvinskianus* under the current climate covered less than 1% of the land area of the country.

We observed both expansion and contraction of suitable niches of the IAPs from current to future climate in Nepal (Table 2). Climatically suitable regions for 75% of the IAPs would increase in contrast to the decrease in the remaining 25%. The proportion of change in suitable niches was also greater for expanding than for contracting species. For example, a maximum increase in suitable niche was by 923% (*Pistia stratiotes*) while the maximum decrease in suitable niches was only by −36% (*Oxalis latifolia*). Therefore, climate change will create more areas suitable for the IAPs in Nepal in the future. However, for aquatic species as *Pistia stratiotes*, availability of water bodies will determine the actual expansion of species.

Climate change will increase both the extent and the intensity (invasion hotspots) of the climatically suitable regions for IAPs in Nepal (Figure 2). Under the current climate, around 59,700 km^2 (40%) of the country were predicted as suitable for IAPs, while 33,600 km^2

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(23%) were identified as invasion hotspots in Nepal. The niche extent and invasion hotspots will expand by 2% and 5%, respectively, suggesting an increase in the potential niche of IAPs from current to future climate.

Changes in the invasion hotspots were evident in different climatic zones, ecoregions, land covers, physiographic regions and federal states in Nepal (Figure 3). The maximum increase in the area of invasion hotspots was observed in the tropical zone, which is situated below 1,000 m (+2,747 pixels, 8%). Under the current climate, there were no invasion hotspots in the subalpine region (3,000–4,000 m asl); however, the hotspots will expand towards temperate and subalpine regions in the future, indicating an expansion towards higher elevation regions under future climate. Out of the ten ecoregions, eight coincided with the invasion hotspots. Terai-Duar savanna and grasslands had the highest area of invasion hotspots under the current climate. Both expansion and contraction in invasion hotspots were observed in the four ecoregions under future climate. However, the magnitude of expansion is higher than contraction. Himalayan subtropical broadleaf forests (+1,556 pixels, 8%) had the highest increase (+1,276 pixels, 7%) in climatically suitable region followed by the Terai-Duar savanna and grasslands. A decrease in the invasion hotspots was noticed in the Himalayan subtropical pine forests (–477 pixels, 7%) and Eastern Himalayan broadleaf forests (–110 pixels, 5%).

A higher level of overlap was seen between invasion hotspots and agricultural lands followed by forests under the current climate. The areas of invasion hotspots will increase in all land use types under the future climate, and the highest increase (+1,956 pixels, 10%) was predicted in forests while the lowest increase (+33 pixels, 6%) in built-up areas. Physiographically, under the current climate, Middle Mountains had the largest area of invasion hotspots followed by Terai. A maximum proportion of surge (+395 pixels, 41%) in the areas of invasion hotspots would occur in the High Mountain region, while Middle Mountains would lose some areas (–970 pixels, 5%) of the invasion hotspots under future climate. At the state level, State Five has the highest area of invasion hotspots while State Six has the lowest. With climate change projections, the highest proportion of increase in the area of invasion hotspots was found in State Six (+331 pixels, 61%) followed by State One (+751 pixels, 26%).

4 | DISCUSSION

To our knowledge, this study of modelling the distribution of 24 IAPs presents the most comprehensive analysis of biological invasions in Nepal. To date, most research either has focused on a handful of species (Shrestha, Sharma, et al., 2018) or has been limited to smaller geographic area of Nepal (Thapa et al., 2018). We identified the geographic areas with different land cover, ecoregions, physiography and climatic zones that are climatically suitable for invasions using a novel approach of invasion hotspots. As consistent with the previous studies (Shrestha, Sharma, et al., 2018; Thapa et al., 2018), our results show that changing climate will create additional climatically

TABLE 2 Change in the climatically suitable niches (km^2) of the invasive alien plant species

Species	Current	Future	% change
Ageratina adenophora	24,866	26,186	5.3
Ageratum conyzoides	26,664	25,611	−3.9
Ageratum houstonianum	26,776	30,406	13.6
Alternanthera philoxeroides	10,287	11,594	12.7
Amaranthus spinosus	28,337	18,913	−33.3
Argemone mexicana	13,807	10,924	−20.9
Bidens pilosa	23,409	20,931	−10.6
Chromolaena odorata	20,605	20,742	0.7
Eichhornia crassipes	12,160	10,400	−14.5
Erigeron karvinskianus	732	958	30.9
Galinsoga quadriradiata	14,234	14,245	0.1
Hyptis suaveolens	26,338	26,483	0.6
Ipomoea carnea	16,956	18,761	10.6
Lantana camara	19,606	27,231	38.9
Leersia hexandra	428	465	8.4
Mikania micrantha	12,447	12,779	2.7
Mimosa pudica	24,543	25,303	3.1
Oxalis latifolia	6,267	4,032	−35.7
Parthenium hysterophorus	30,915	34,437	11.4
Pistia stratiotes	198	2,024	922.8
Senna occidentalis	20,850	25,758	23.5
Senna tora	27,146	27,905	2.8
Spermacoce alata	16,883	18,185	7.7
Xanthium strumarium	18,413	19,824	7.7

Note: Areas of suitable region for each species were calculated within a minimum convex hull of its currently known localities within Nepal.

suitable areas for IAPs in Nepal in the future. This study provides baseline information for decision-makers for cost-effective management of IAPs by showing the areas which have suitable niches for a high number of IAPs. Our results will be helpful for the prevention and early detection of IAPs in their potentially suitable niches. Therefore, our research has important implications for the management and monitoring of biological invasions in Nepal and contributes to the growing global body of literature on the impacts of climate change on biological invasions. Our analysis also highlights the need of integrating biological invasions into Nepal's climate change policies and generally in the Himalayas.

The climatic condition of central Nepal, characterized by subtropical climate that is under cropping and forests, has the maximum suitable areas for a majority of IAPs under current climate. As the climate changes, a new suit of habitats will emerge that may be suitable for alien species (Hellmann et al., 2008). Climate change facilitates dispersal, introduction and naturalization of alien species as well as reduces the resilience of local ecosystems to alien species (Walther et al., 2009). Our models also predict that additional suitable areas for IAPs are expected to emerge in the higher elevation
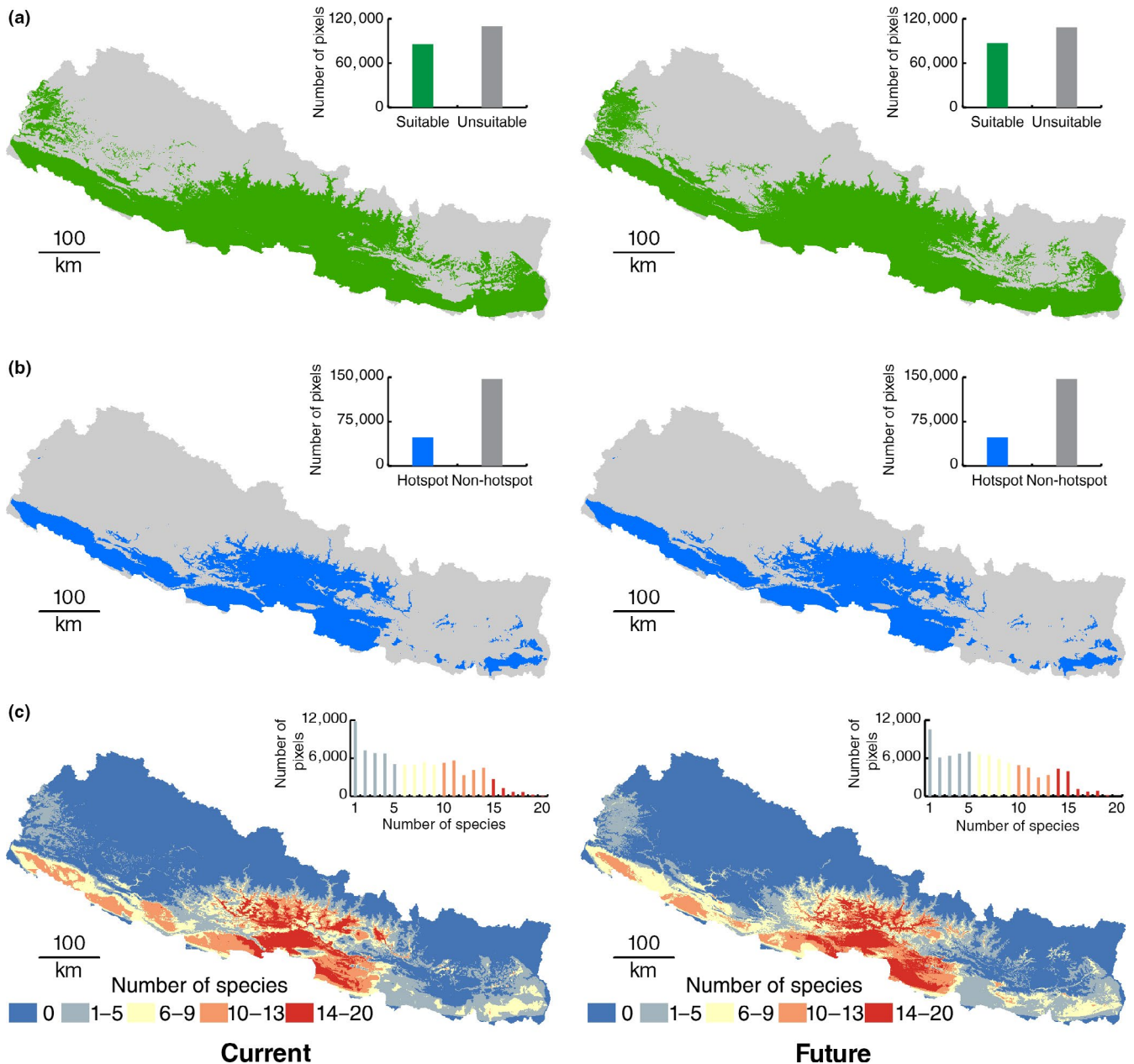
FIGURE 2 Extent and hotspot of predicted suitable niches of 24 invasive alien plants (IAPs) and their richness in these niches. (a) Combined extent of climatically suitable niches under current climate and future climate (for 2050 under RCP 6.0), (b) hotspot of suitable niches under current and future climate, (c) richness of suitable niches of IAPs under current and future climate. Inset graph shows the total number of pixels

zones of both the eastern and western regions of the country. At the species level, our results have broader similarities with the results of Shrestha, Sharma, et al. (2018) who found a consistent increase in the amount of climatically suitable regions for six IAPs of Nepal from current to future climate despite some variations in methods and data. However, the extent of suitable regions and percentages of changes in suitable regions are different. They found that the areas of potential niches under current climate for *Ageratum houstonianum*, *Hyptis suaveolens* and *Parthenium hysterophorus* are slightly smaller while *Chromolaena odorata*, *Lantana camara* and *Mikania micrantha* are greater than what we found. Although both expansion

and reduction of suitable niches of IAPs were observed at an individual species level, in aggregation, the extent and intensity of invasion hotspots are expected to increase in Nepal under future climate.

Globalization and climate change will likely increase the threat posed by invasive plants to high-elevation biodiversity, although high-elevation mountain ecosystems are still less invaded by IAPs as compared to lowland ecosystems (Pauchard et al., 2009). The invasion hotspots as predicted by our models will expand towards the higher elevation areas, especially in the temperate and subalpine regions, making these regions susceptible to biological invasions under future climate. The expansion on invasion hotspots will
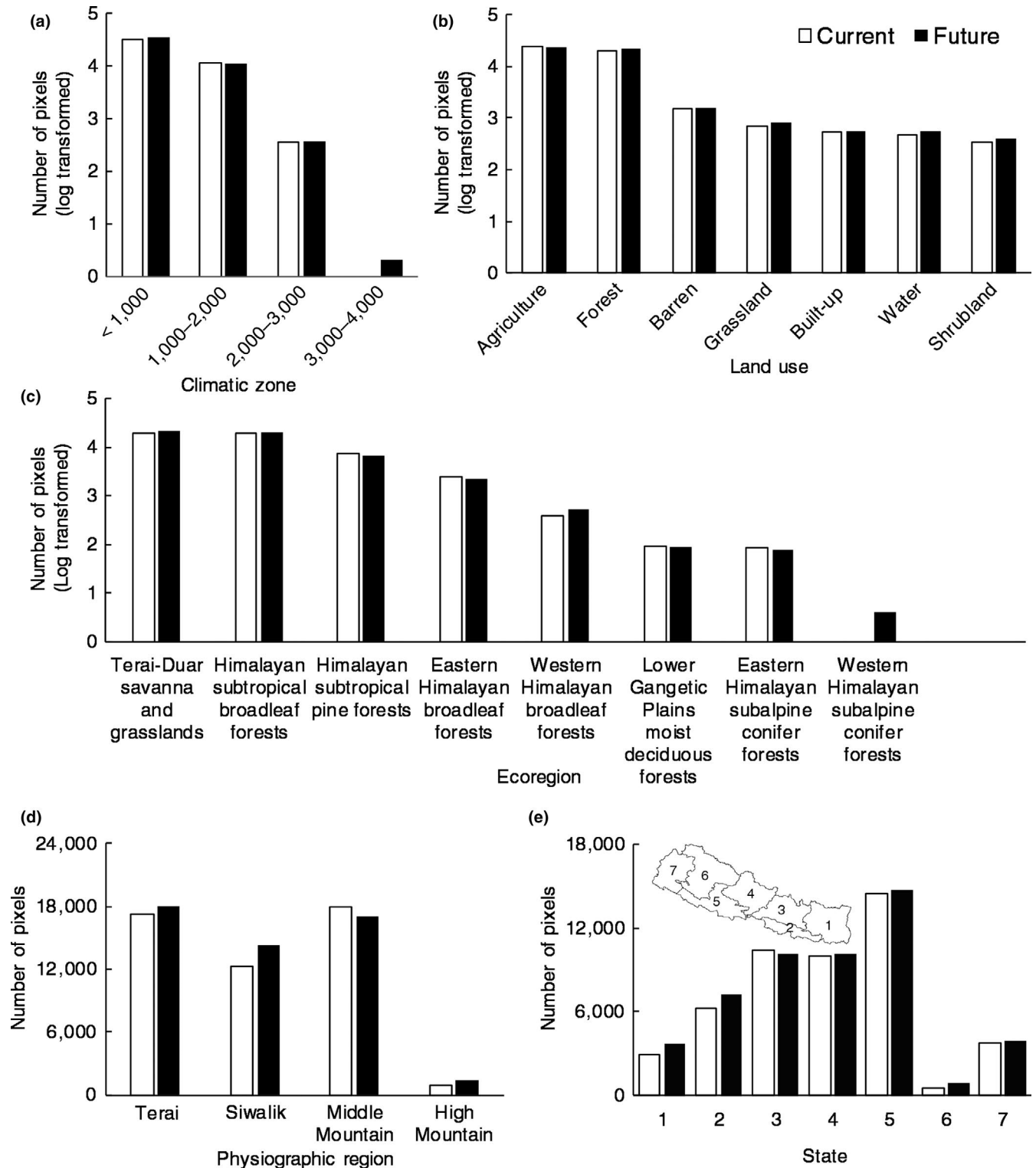
FIGURE 3 Change in the invasion hotspots for 24 invasive alien plants of Nepal between current and future climate (for 2050 under RCP 6.0). (a) Elevation bands, (b) land use types, (c) ecoregions, (d) physiographic regions and (e) federal states (Nepal has been recently divided into seven federal states and numbered from 1 (east) to 7 (west). Official names of the states have yet to be declared)

also be visible in the tropical region. Some field-based studies also showed that IAPs are currently invading higher elevation regions as compared to the past (Shrestha, Shabbir, & Adkins, 2015; Tiwari et al., 2005). At high-elevation regions, the impact of climate change is likely to be more severe than in low elevation, as the magnitude of temperature change is greater in those areas (Shrestha, Gautam, & Bawa, 2012). Our analysis showed that the maximum increase in the area of climatically suitable niches occurred at lower elevations

(below 2,000 m) while the proportion of change in suitable niches is greater at higher elevations (above 2,000 m). The creation of climatically suitable regions for IAPs in the high-elevation regions, which are already vulnerable to climate change and are currently experiencing its impact, will have severe consequences in the future. Therefore, biological invasions will add pressure and increase risks to the most vulnerable ecosystems in Nepal.

Along with climate change, anthropogenic disturbance is considered a major driver that promotes plant invasion in mountain ecosystems (Davis, Grime, & Thompson, 2014; Pauchard et al., 2016). Nepal has undergone a significant transformation due to infrastructure development, tourism and trade expansion (Lennartz, 2018; Nepal, 2000). In the mountain and lowland regions of Nepal, newly built roads destabilize slopes and trigger landslides, creating bare ground suitable for colonization by the IAPs (Lembrechts et al., 2012; Lennartz, 2018). Roads play an important role in the spread of alien species by facilitating dispersal pathways and by providing disturbed sites for percolation from roadsides into the natural adjacent vegetation (McDougall et al., 2018). With tourism industry predicted to be grown in the future, human mobility, trade and transport will increase significantly. This may promote the dispersal of IAPs from lowlands to high-elevation regions and to new areas in the lowlands. All of these socio-economic transformations favour the spread of IAPs, and climate change will open up suitable regions by reducing climatic barriers for them to invade higher elevation zones (Hellmann et al., 2008; Pauchard et al., 2009). However, the suitable regions identified may not be occupied by IAPs due to natural dispersal barriers in mountains, which are predominant physical features in Nepal. Therefore, monitoring and management of IAPs in Nepal should account for the vulnerability posed by climate change combined with an unprecedented increase in anthropogenic disturbances. The results of this study might be useful for taking a precautionary approach and encourage vigilance in these climatically suitable areas.

Currently, the maximum amount of suitable regions for IAPs is located in agricultural areas and areas with forest cover. The high suitability of agriculture and forest lands for IAPs will be a threat to the economy and local livelihoods. A global study roughly estimated that the total cost of IAPs to Nepal's agriculture was approximately US$ 1.4 billion per year (Paini et al., 2016). Local communities, who primarily rely on farming and forests for their livelihood and employment, have already been negatively impacted by IAPs, such as through increased labour input in weeding, reduced crop production, livestock poisoning, reduced supply of forage and negative impacts on forests (Shrestha, Shrestha et al., 2018). Future climate will increase the distribution of the IAPs that were ranked by local communities as the worst, such as *Ageratum houstonianum*, *Chromolaena odorata*, *Ageratina adenophora* and *Mikania micrantha* (Shrestha, Shrestha et al., 2018). Furthermore, the distribution of *Parthenium hysterophorus* and *Lantana camera*, which are considered the most troublesome weeds in the region (Thapa et al., 2018), will also increase in the future. Therefore, the economic loss and negative impacts caused by IAPs on food security, livelihood, biodiversity and ecosystem services in the future may be augmented if preventive and control measures are not immediately taken seriously.

The models developed from the current distribution are extrapolated in time and space to forecast potential IAP invasions under future climate and may not capture the issue of non-analogous climatic space (Fitzpatrick & Hargrove, 2007). Shifts in species range involve multiple ecological processes such as dispersal, demography, physiology, species interactions, population interactions and evolution operating at multiple scales (Urban et al., 2016). Furthermore, the correlation structure of future climatic conditions could be different from current conditions, thereby leading to errors in predictions. Therefore, SDMs do not explicitly consider these uncertainties caused by non-analogous climate space and ecological processes that affect the species (Elith & Leathwick, 2010). Limiting the areas within the current extent of occurrence (e.g., a MCH) in analysing the change in climatically suitable niches under current and future climate prevents severe changes in the total amount of suitable area (Wright et al., 2015). Furthermore, there are other potential issues such as modelling algorithm (Elith et al., 1999), the choices of environmental variables used (Synes & Osborne, 2011), for future climate, GCMs used (Steen, Sofaer, Skagen, Ray, & Noon, 2017), collinearity (Dormann et al., 2000), model complexity (Wright et al., 2015), model evaluation method (Lobo et al., 2013) and threshold values to produce binary maps (Liu et al., 2016) that can influence model outcomes. In addition, future land use change scenarios can also alter future species distributions (Martin, Dyck, Dendoncker, & Titeux, 2017). There is no agreement on optimal ecological modelling strategy, and such a strategy is unlikely to emerge due to the context-specific nature of the modelling process (Heikkinen et al., 1982; Wright et al., 2015). Despite the uncertainties, it was argued that some amount of model extrapolation for ecological management in a changing climate is essential for practice (Mahony, Cannon, Wang, & Aitken, 2008). Improvements of models are a crucial issue for enhancing the predictive accuracy of the models.

Despite global and local efforts to manage biological invasions, the number of alien species has been ever increasing across all taxonomic groups and geographic regions of the world (Seebens et al., 2017). Climate change has a potential to create more favourable regions in the future for IAPs as shown by this research and other studies (O'donnell et al., 2011; Shrestha, Sharma et al., 2018). By creating climatically suitable regions in the most vulnerable natural and agro-ecosystems that provide essential ecosystem services, climate change is likely to amplify the impacts on ecosystems and economy in the future by two major ways. First, climate change negatively affects ecosystems and native species by changing their distribution, composition and phenology (Walther et al., 2002) and hence reduces their resilience to biological invasions. Second, climate change facilitates the encroachment of invasive species by removing current climatic barriers (Hellmann et al., 2008). Cold temperatures limit invasion by many alien species in high-elevation regions (Alexander et al., 2011), but climate change will elevate this barrier to a higher elevation. The increase in biological invasions will have a serious consequence on

the country's economy and local livelihoods. Given that little attention is paid to biological invasions in biodiversity conservation and climate adaptation policies in Nepal, where the formulation of a national strategy for the management of invasive species is still underway, the result of this study as a precautionary note might be helpful to formulate such policies. With this result, we urge that early detection and preventive actions should focus on the mountainous areas of the country. Apart from distribution modelling, a better understanding of species traits, dispersal pathways and the mechanism of the natural filters that prevent colonization of invasive species, as well as the community perceptions and involvement in management, are necessary. Our results show a diverse response of IAPs to climate change; therefore, species-specific prioritization exercises may be helpful to better manage and monitor specific IAPs.

DATA ACCESSIBILITY

The occurrence data of the IAPs of Nepal used for analysis in this article are available at Dryad repository; https://doi.org/10.5061/dryad.27257r3.

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REFERENCES

Adhikari, D., Tiwary, R., & Barik, S. K. (2015). Modelling hotspots for invasive alien plants in India. *PLoS ONE*, *10*(7), e0134665. https://doi.org/10.1371/journal.pone.0134665

Aguirre-Gutiérrez, J., van Treuren, R., Hoekstra, R., & van Hintum, T. J. (2017). Crop wild relatives range shifts and conservation in Europe under climate change. *Diversity and Distributions*, *23*(7), 739–750. https://doi.org/10.1111/ddi.12573

Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T., & Miren Consortium. (2011). Assembly of non-native floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences*, *108*(2), 656–661. https://doi.org/10.1073/pnas.1013136108

Allen, J. M., & Bradley, B. A. (2016). Out of the weeds? Reduced plant invasion risk with climate change in the continental United States. *Biological Conservation*, *203*, 306–312. https://doi.org/10.1016/j.biocon.2016.09.015

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*(10), 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, *22*(1), 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, *11*(9), 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Beaumont, L. J., Graham, E., Duursma, D. E., Wilson, P. D., Cabrelli, A., Baumgartner, J. B., … VanDerWal, J. (2016). Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? *Ecological Modelling*, *342*, 135–146. https://doi.org/10.1016/j.ecolmodel.2016.10.004

Beaumont, L. J., Pitman, A. J., Poulsen, M., & Hughes, L. (2007). Where will species go? Incorporating new advances in climate modelling into projections of species distributions. *Global Change Biology*, *13*(7), 1368–1385. https://doi.org/10.1111/j.1365-2486.2007.01357.x

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bellard, C., Genovesi, P., & Jeschke, J. M. (2016). Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B*, *283*(1823), 20152454.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., & Courchamp, F. (2013). Will climate change promote future invasions? *Global Change Biology*, *19*(12), 3740–3748. https://doi.org/10.1111/gcb.12344

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, *275*, 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012

Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, *25*(5), 310–318. https://doi.org/10.1016/j.tree.2009.12.003

Brown, J. L. (2014). SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic, and species distribution model analyses. *Methods in Ecology and Evolution*, *5*, 694–700. https://doi.org/10.1111/2041-210X.12200

Capinha, C., & Pateiro-López, B. (2014). Predicting species distributions in new areas or time periods with alpha-shapes. *Ecological Informatics*, *24*, 231–237. https://doi.org/10.1016/j.ecoinf.2014.06.001

Catford, J. A., Vesk, P. A., White, M. D., & Wintle, B. A. (2011). Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. *Diversity and Distributions*, 17(6), 1099–1110. https://doi.org/10.1111/j.1472-4642.2011.00794.x

Chatterjee, S., & Hadi, A. S. (2015). *Regression analysis by example*. New Jersey, USA: John Wiley & Sons. Inc. Publication.

Clarke, L., Edmonds, J., Jacoby, H., Pitcher, H., Reilly, J., & Richels, R. (2007). *Scenarios of greenhouse gas emissions and atmospheric concentrations. Sub-report 2.1A of Synthesis and Assessment Product 2.1 by the US Climate Change Science Program and the Subcommittee on Global Change Research*. Washington, DC: Department of Energy, Office of Biological and Environmental Research.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J. L., Fichefet, T., Friedlingstein, P., & Shongwe, M. (2013). Long-term climate change: projections, commitments and irreversibility. In D. Stocker, G. K. Qin, M. Plattner, S. K. Tignor, J. Allen, & P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of Working Group I to the fifth assessment report of the intergovernmental panel on climate change*. New York, NY: Cambridge University Press.

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, 88(3), 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dormann, C. F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, 16(2), 129–138. https://doi.org/10.1111/j.1466-8238.2006.00279.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Drake, J. M., & Lodge, D. M. (2004). Global hot spots of biological invasions: evaluating options for ballast–water management. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(1539), 575–580.

Dukes, J. S., & Mooney, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, 14(4), 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., … Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30, 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. https://doi.org/10.1002/joc.5086

Fitzpatrick, M. C., & Hargrove, W. W. (2009). The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation*, 18(8), 2255–2261. https://doi.org/10.1007/s10531-009-9584-8

Gallagher, R. V., Beaumont, L. J., Hughes, L., & Leishman, M. R. (2010). Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology*, 98(4), 790–799. https://doi.org/10.1111/j.1365-2745.2010.01677.x

Gallardo, B., & Aldridge, D. C. (2013). Evaluating the combined threat of climate change and biological invasions on endangered species. *Biological Conservation*, 160, 225–233. https://doi.org/10.1016/j.biocon.2013.02.001

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models–how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, 21(11), 1126–1136. https://doi.org/10.1111/j.1466-8238.2012.00768.x

Hara, H., Chater, A. O., & Williams, L. H. J. (1982). *An enumeration of the flowering plants of Nepal, volume II*. London, UK: Trustees of the British Museum (Natural History).

Hara, H., & Williams, L. H. J. (1979). *An enumeration of the flowering plants of Nepal, volume II*. London, UK: Trustees of the British Museum (Natural History).

Heikkinen, R. K., Luoto, M., Araújo, M. B., Virkkala, R., Thuiller, W., & Sykes, M. T. (2006). Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, 30(6), 751–777. https://doi.org/10.1177/0309133306071957

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology*, 22(3), 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 25(15), 1965–1978. https://doi.org/10.1002/joc.1276

IUCN. (2012). *IUCN red list categories and criteria: version 3.1*, 2nd ed. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32 pp.

Kriticos, D. J., Webber, B. L., Leriche, A., Ota, N., Macadam, I., Bathols, J., & Scott, J. K. (2012). CliMond: Global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, 3(1), 53–64. https://doi.org/10.1111/j.2041-210X.2011.00134.x

Lamsal, P., Kumar, L., Aryal, A., & Atreya, K. (2018). Invasive alien plant species dynamics in the Himalayan region under climate change. *Ambio*, 47, 697–710. https://doi.org/10.1007/s13280-018-1017-z

Lembrechts, J. J., Pauchard, A., Lenoir, J., Nuñez, M. A., Geron, C., Ven, A., … Milbau, A. (2016). Disturbance is the key to plant invasions in cold environments. *Proceedings of the National Academy of Sciences*, 113(49), 14061–14066. https://doi.org/10.1073/pnas.1608980113

Lennartz, T. (2013). Constructing roads—constructing risks? Settlement decisions in view of landslide risk and economic opportunities in Western Nepal. *Mountain Research and Development*, 33(4), 364–371. https://doi.org/10.1659/MRD-JOURNAL-D-13-00048.1

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, 40(4), 778–789. https://doi.org/10.1111/jbi.12058

Liu, Y., Oduor, A. M., Zhang, Z., Manea, A., Tooth, I. M., Leishman, M. R., … Van Kleunen, M. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology*, 23(8), 3363–3370. https://doi.org/10.1111/gcb.13579

Lobo, J. M., Jiménez-Valverde, A., & Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17(2), 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x

Lowe, S., Browne, M., Boudjelas, S., & DePoorter, M. (2000). *100 of the world's worst invasive alien species: A selection from the global invasive species database*, vol. 12. Auckland, New Zealand: Invasive Species Specialist Group.

Mahony, C. R., Cannon, A. J., Wang, T., & Aitken, S. N. (2017). A closer look at novel climates: New methods and insights at continental to landscape scales. *Global Change Biology*, 23(9), 3934–3955. https://doi.org/10.1111/gcb.13645

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation of consensus methods in predictive

species distribution modelling. *Diversity and Distributions*, *15*(1), 59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x

Martin, Y., Van Dyck, H., Dendoncker, N., & Titeux, N. (2013). Testing instead of assuming the importance of land use change scenarios to model species distributions under climate change. *Global Ecology and Biogeography*, *22*(11), 1204–1216. https://doi.org/10.1111/geb.12087

McDougall, K. L., Alexander, J. M., Haider, S., Pauchard, A., Walsh, N. G., & Kueffer, C. (2011). Alien flora of mountains: Global comparisons for the development of local preventive measures against plant invasions. *Diversity and Distributions*, *17*(1), 103–111. https://doi.org/10.1111/j.1472-4642.2010.00713.x

McDougall, K. L., Lembrechts, J., Rew, L. J., Haider, S., Cavieres, L. A., Kueffer, C., … Alexander, J. M. (2018). Running off the road: Roadside non-native plants invading mountain vegetation. *Biological Invasions*, *20*, 3461–3473. https://doi.org/10.1007/s10530-018-1787-z

McGuffie, K., & Henderson-Sellers, A. (2005). *A climate modelling primer*. New Jersey, USA: John Wiley & Sons, Inc., Publication.

MFSC. (2014). *Nepal National Biodiversity Strategy and Action Plan 2014–2020*. Kathmandu, Nepal: Ministry of Forests and Soil Conservation (MFSC).

Murphy, J. M., Sexton, D. M., Barnett, D. N., Jones, G. S., Webb, M. J., Collins, M., & Stainforth, D. A. (2004). Quantification of modelling uncertainties in a large ensemble of climate change simulations. *Nature*, *430*(7001), 768–772.

Myers, N. (2003). Biodiversity hotspots revisited. *BioScience*, *53*(10), 916–917. https://doi.org/10.1641/0006-3568(2003)053[0916:BHR]2.0.CO;2

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858.

Nepal, S. K. (2011). Mountain tourism and climate change: Implications for the Nepal Himalaya. *Nepal Tourism and Development Review*, *1*(1), 1–14. https://doi.org/10.3126/ntdr.v1i1.7367

O'Donnell, J., Gallagher, R. V., Wilson, P. D., Downey, P. O., Hughes, L., & Leishman, M. R. (2012). Invasion hotspots for non-native plants in Australia under current and future climates. *Global Change Biology*, *18*(2), 617–629. https://doi.org/10.1111/j.1365-2486.2011.02537.x

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., … Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Paini, D. R., Sheppard, A. W., Cook, D. C., De Barro, P. J., Worner, S. P., & Thomas, M. B. (2016). Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences*, *113*(27), 7575–7579. https://doi.org/10.1073/pnas.1602205113

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., … Seipel, T. (2009). Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, *7*(9), 479–486. https://doi.org/10.1890/080072

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Petitpierre, B., McDougall, K., Seipel, T., Broennimann, O., Guisan, A., & Kueffer, C. (2016). Will climate change increase the risk of plant invasions into mountains? *Ecological Applications*, *26*(2), 530–544. https://doi.org/10.1890/14-1871

Pierce, D. W., Barnett, T. P., Santer, B. D., & Gleckler, P. J. (2009). Selecting global climate models for regional climate change studies. *Proceedings of the National Academy of Sciences*, *106*(21), 8441–8446. https://doi.org/10.1073/pnas.0900094106

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3), 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., … Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M., & Kirschner, J. (2004). Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon*, *53*(1), 131–143. https://doi.org/10.2307/4135498

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rogerson, P. (2001). *Statistical methods for geography*. London, UK: Sage.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Shrestha, B. B. (2014). *Distribution of Alien Invasive Weed* Parthenium hysterophorus *and its Biological Control Agent in Nepal. A research report submitted to*. Sweden: International Foundation for Science, Unpublished.

Shrestha, B. B. (2016). Invasive alien plant species in Nepal. In P. K. Jha, M. Siwakoti, & S. Rajbhandary (Eds.), *Frontiers of botany* (pp. 269–284). Kathmandu, Nepal: Central Department of Botany, Tribhuvan University.

Shrestha, B. B., Budha, P. B., Wong, L. J., & Pagad, S. (2018). *Global register of introduced and invasive species- Nepal. Version 2.3. Invasive Species Specialist Group ISSG*. Checklist dataset doi: https://doi.org/10.15468/4r0kkr accessed via GBIF.org on 2018-10-15.

Shrestha, B. B., Joshi, S., Bisht, N., Yi, S., Kotru, R., Chaudhary, R. P., & Wu, N. (2018). *Inventory and impact assessment of invasive alien plant species in Kailash Sacred Landscape, Working Paper 2018/3*. Kathmandu, Nepal: International Centre for Integrated Mountain Development (ICIMOD).

Shrestha, B. B., Kokh, M., & Karki, J. B. (2016). *Mapping of invasive alien plant species in Tarai Arc Landscape (TAL) and Chitwan-Annapurna Landscape (CHAL), Nepal*. A Report Submitted to National Trust for Nature Conservation (NTNC), Kathmandu, Nepal (Unpublished).

Shrestha, B. B., Shabbir, A., & Adkins, S. W. (2015). *Parthenium hysterophorus* in Nepal: A review of its weed status and possibilities for management. *Weed Research*, *55*(2), 132–144.

Shrestha, B. B., Shrestha, U. B., Sharma, K. P., Thapa-Parajuli, R. B., Devkota, A., & Siwakoti, M. (2018). Community perception and prioritization of invasive alien plants in Chitwan-Annapurna Landscape, Nepal. *Journal of Environmental Management*, *229*, 38–47. https://doi.org/10.1016/j.jenvman.2018.06.034

Shrestha, T. B. (2008). Classification of Nepalese forests and their distribution in protected areas. *The Initiation*, *2*(1), 1–9. https://doi.org/10.3126/init.v2i1.2512

Shrestha, U. B., Gautam, S., & Bawa, K. S. (2012). Widespread climate change in the Himalayas and associated changes in local ecosystems. *PLoS ONE*, *7*(5), e36741. https://doi.org/10.1371/journal.pone.0036741

Shrestha, U. B., Sharma, K. P., Devkota, A., Siwakoti, M., & Shrestha, B. B. (2018). Potential impact of climate change on the distribution of six invasive alien plants in Nepal. *Ecological Indicators*, *95*, 99–107. https://doi.org/10.1016/j.ecolind.2018.07.009

Siwakoti, M., Shrestha, B. B., Devkota, A., Shrestha, U. B., Thapaparajuli, R. B., & Sharma, K. P. (2016). Assessment of the effects of climate change on the distribution of invasive alien plant species in Nepal. In D. R. Bhuju, K. McLaughlin, J. Sijapati, B. D. Devkota, N. Shrestha, G. P. Ghimire, & P. K. Neupane (Eds.), *Building knowledge for climate resilience in Nepal: Research Brief* (pp. 5–8). Kathmandu, Nepal: Nepal Academy of Science and Technology.

Steen, V., Sofaer, H. R., Skagen, S. K., Ray, A. J., & Noon, B. R. (2017). Projecting species' vulnerability to climate change: Which uncertainty sources matter most and extrapolate best? *Ecology and Evolution*, 7(21), 8841–8851. https://doi.org/10.1002/ece3.3403

Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M., Allen, S. K., Boschung, J., & Midgley, P. M. (2013). *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*, 1535.

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240(4857), 1285–1293.

Synes, N. W., & Osborne, P. E. (2011). Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Global Ecology and Biogeography*, 20(6), 904–914. https://doi.org/10.1111/j.1466-8238.2010.00635.x

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, 93(4), 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

Thapa, S., Chitale, V., Rijal, S. J., Bisht, N., & Shrestha, B. B. (2018). Understanding the dynamics in distribution of invasive alien plant species under predicted climate change in Western Himalaya. *PLoS ONE*, 13(4), e0195752. https://doi.org/10.1371/journal.pone.0195752

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography*, 32(3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Tiwari, S., Adhikari, B., Siwakoti, M., & Subedi, K. (2005). *An inventory and assessment of invasive alien plant species of Nepal*. Kathmandu, Nepal: IUCN Nepal.

Treier, U. A., Broennimann, O., Normand, S., Guisan, A., Schaffner, U., Steinger, T., & Müller-Schärer, H. (2009). Shift in cytotype frequency and niche space in the invasive plant *Centaurea maculosa*. *Ecology*, 90(5), 1366–1377.

Uddin, K., Shrestha, H. L., Murthy, M., Bajracharya, B., Shrestha, B., Gilani, H., … Dangol, B. (2015). Development of 2010 national land cover database for the Nepal. *Journal of Environmental Management*, 148, 82–90. https://doi.org/10.1016/j.jenvman.2014.07.047

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234), 571–573.

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Peer, G., Singer, A., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353, aad8466. https://doi.org/10.1126/science.aad8466

Verlinden, M., & Nijs, I. (2010). Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. *Biological Invasions*, 12(8), 2777–2787. https://doi.org/10.1007/s10530-009-9683-1

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., … Hulme, P. E. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8(3), 135–144. https://doi.org/10.1890/080083

M. Vilà, & P. E. Hulme (Eds.). (2017). *Impact of biological invasions on ecosystem services (invading nature- springer series in invasion ecology*, Vol. 12). Switzerland: Springer.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389–395.

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., … Bugmann, H. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, 24(12), 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*, 106(Supplement 2), 19729–19736. https://doi.org/10.1073/pnas.0901639106

Wright, A. N., Hijmans, R. J., Schwartz, M. W., & Shaffer, H. B. (2015). Multiple sources of uncertainty affect metrics for ranking conservation risk under climate change. *Diversity and Distributions*, 21(1), 111–122. https://doi.org/10.1111/ddi.12257

BIOSKETCHES

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SUPPORTING INFORMATION

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