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ORIGINAL ARTICLE

Climate change induced elevational range shifts of Himalayan tree species

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Abstract

Global warming may force montane species to shift upward to keep pace with their shifting climate niche. How species differences in such distribution shifts depend on their elevational positions, elevation-dependent warming rates, and other environmental constraints, or plant functional traits is poorly understood. Here, we analyzed for 137 Himalayan tree species how distribution shifts vary with elevational niche positions, environmental constraints, and their functional traits. We developed ecological niche models using MaxEnt by combining species survey and botanical collections data with 19 environmental predictors. Species distributions were projected to 1985 and 2050 conditions, and elevational range parameters and distribution areas were derived. Under the worst-case RCP 8.5 scenario, species are predicted to shift, on average, 3 m/year in optimum elevation, and have 33% increase in distribution area. Highland species showed faster predicted elevational shifts than lowland species. Lowland and highland species are predicted to expand in distribution area in contrast to mid-elevation species. Tree species for which species distribution models are driven by responses to temperature, aridity, or soil clay content showed the strongest predicted upslope shifts. Tree species with conservative trait values that enable them to survive resource poor conditions (i.e., narrow conduits) showed larger predicted upslope shifts than species with wide conduits. The predicted average upslope shift in maximum elevation (8 m/year) is >2 times faster than the current observations indicating that many species will not be able to track climate change and potentially go extinct, unless they are supported by active conservation measures, such as assisted migration.

Abstract in Nepali is available with online material

KEYWORDS
assisted migration, climate change velocity, elevation dependent warming, elevational gradient, MaxEnt, Nepal, plant functional traits, species distribution modeling

1 | INTRODUCTION

The global climate is changing at an unprecedented rate, with adverse effects on species, their interactions, and entire ecosystems (IPCC, 2014; Nunez et al., 2019). Species are expected to track their preferred climatic niches and shift their distribution ranges (i.e., climate change induced species range shift, Bellard et al., 2012; Lenoir & Svenning, 2015; Tingley et al., 2009). With rising temperatures, species are bound to shift either upslope to higher elevations or poleward to higher latitudes (Lenoir et al., 2008; Morueta-Holme et al., 2015). Studies from the Himalayas (He et al., 2019), Andes (Feeley et al., 2011), Alps (Geppert et al., 2020), and Pyrenees (Marshall et al., 2020) have shown that many species are indeed shifting upslope to cooler elevations in response to rising temperatures. However, relatively few studies have assessed how shifts in distribution ranges of species vary with their niche positions along the elevational gradient and whether this is associated with plant functional traits (Estrada et al., 2016; Pacifici et al., 2017; Zu et al., 2021). Understanding the influence of species niche positions and traits on species elevational range shift potentials will be crucial to predict the future of species under climate change and to design appropriate conservation and climate adaptation measures.

With rising temperatures, species survival ultimately will depend on species' ability to keep pace with their shifting climate niche. To represent an instantaneous local velocity along Earth's surface needed to keep pace with rising temperatures, Loarie et al. (2009) introduced a new index called “the velocity of temperature change” or more generally “the velocity of climate change.” It is calculated by dividing temporal change in temperature (°C/year) by spatial change in temperature (°C/km) and is expressed in km/year. Available observations below 5000 m a.s.l. elevation suggest that high elevation areas of some mountain regions are experiencing faster temporal rates of warming (0.05 °C/year) than their low elevation areas (0.02 °C/year), the phenomenon called “elevation-dependent warming (EDW)” (Gao et al., 2018; Luitel et al., 2020; Pepin et al., 2015). Studies have indicated that EDW occurs partly because of increase in downward longwave radiation at higher elevations in response to increased water vapor and partly because of increase in surface absorption of solar radiation at higher elevations in response to reduced snow cover (Minder et al., 2018; Rangwala et al., 2013). This implies that the velocity of temperature change may change with elevation. However, since upslope movements along steep slopes result in rapid changes in temperature, it is likely that small geographic displacements will be enough to keep pace with climate warming in the highlands despite the EDW. In contrast, in flatter areas such as valleys and lowland plains, larger geographic displacements will be required to track temperature increase. Mamantov et al. (2021), in a meta-analysis from 16 montane regions world-wide including Eastern Himalayas, showed that rates of species range shift indeed decrease with increase in elevation.

Plant functional traits are important to understand and predict species potential responses to climate change. Plant functional traits are defined as morphological, physiological, or phenological characteristics that affect plant physiological performance and their spatial distribution (Poorter & Bongers, 2006; Violle et al., 2007). Although plant traits can reflect the ability of species to disperse, establish, grow, and colonize new sites (Estrada et al., 2016), little is known about how the variation in plant traits with elevation affect the capacity of species to shift their elevational ranges. Neither is there a consensus on how different plant traits contribute to species range shifts (MacLean & Beissinger, 2017). For instance, higher competitive ability may facilitate establishment and proliferation, and in plants, competitive ability is regulated by leaf-economic traits (Estrada et al., 2016). In the Himalayas, traits related to plant size, hydraulic efficiency, and light competition determine species distribution along the elevational gradient (Maharjan et al., 2021). These traits that are advantageous in closed vegetations associated with warm low elevations (Maharjan et al., 2021) may also be important to colonize new sites that become available because of increased warming, as a large stature, wide conductive conduits and large leaf area per xylem area may allow plant to be competitive, acquire more resources, and attain a faster growth (cf. Estrada et al., 2016; Maharjan et al., 2021). Here, we ask whether such simple, easy to measure traits can serve as proxies to predict temperature-induced range shifts.

The Himalayas in Nepal provide an excellent opportunity to investigate the effects of climate change on plant species distribution because within a 200 km distance elevation increases from ca. 60 m a.s.l. in the south to >8 km in the north (HMGN/MFSC, 2002). Along this gradient, the vegetation changes from wet and warm tropical forests in the lowland plains, via temperate and sub-alpine forests to dry and cold alpine meadows above the treeline (Lillesø et al., 2005). The Himalayas experience substantial warming (0.2 °C/decade from 1951–2014, Ren et al., 2017), particularly at higher elevations (0.5 °C/decade, Gao et al., 2018; Luitel et al., 2020; Pepin et al., 2015) and climatic projections suggest that by 2050 the average temperature will increase with 2–5°C (Rajbhandari et al., 2016; Shrestha, Agrawal, et al., 2015; Shrestha, Hofgaard, & Vandvik, 2015). Average annual precipitation in the Himalayas is predicted to increase by 2–6% by 2030 and by 8–12% by 2050 (MoFE, 2019). Predicted climate warming and increase in precipitation should therefore have a pronounced effect on the distribution of Himalayan plant species and empirical studies show that species are shifting their upper elevation limits upslope at a rate as high as 27 m/decade (Bhatta et al., 2018; Gaire et al., 2014; Suwal et al., 2016; Telwala et al., 2013).

In this study, we assessed the potential effects of rising temperature on the distribution of 137 common tree species that partition the elevational gradient of the Himalayas in Nepal. We focused on the common tree species in the study area because they contribute most to the forest biomass and ecosystem functioning and because we believe if common tree species are impacted by global warming it is likely that endemic and rare species are impacted even more. For each of these species, we compared near current (1985) climatic niche models (as quantified using MaxEnt) with future climatic projections for 2050 and relate that to traits that are considered to be important for shaping tree species distribution ranges in the Himalayas. We addressed the following four research questions and corresponding hypotheses:

First, how does climate warming affect the elevational range shift of low and high elevation species? Because in montane landscapes, upslope movements along steep slope result in large changes in temperature on short spatial distance, it is likely that small geographic displacements will be enough to keep pace with climate warming in the highlands despite the elevation dependent warming, whereas in flatter areas such as valleys and lowland plains, larger geographic displacements will be required to compensate for temperature increase. Mamantov et al. (2021), in a meta-analysis from 16 montane regions world-wide including Eastern Himalayas, showed that rates of species range shift indeed decrease with increase in elevation. Here, we tested whether the same relationship holds for the (Central) Himalayan elevational gradient, meaning that species with an optimum at low elevation shift their geographic ranges upslope at faster rates than species with an optimum at high elevation to track the environmental changes.

Second, how does climate warming affect the distribution area of low and high elevation species? Because climate warming is expected to force species to shift their distribution ranges to smaller upslope surface areas, we hypothesized that all species will have a reduced distribution area under future climatic conditions, and that species with an optimum at low elevation show the largest predicted reductions in distribution area.

Third, which environmental variable controls the species range shifts? Because the Himalayas are already experiencing substantial warming and are predicted to experience even faster rates of warming in the future, particularly at higher elevations (Luitel et al., 2020; Rajbhandari et al., 2016; Shrestha, Agrawal, et al., 2015; Shrestha, Hofgaard, & Vandvik, 2015) additional to predicted increase in precipitation throughout the Himalayas (MoFE, 2019), we hypothesized that species for which species distribution models are driven by responses to temperature and precipitation will show upslope shifts in their optimum elevation resulting in a reduction of their distribution area.

Fourth, can plant traits predict species range shifts and changes in distribution area? Because acquisitive trait values (e.g., wide conductive conduits) allow species to acquire resources faster and attain faster growth, that is, to be more competitive (Estrada et al., 2016; Maharjan et al., 2021), they may easily colonize novel climate niches that becomes available as a result of climate change, we hypothesized that species with acquisitive trait values have large predicted range shifts and changes in distribution area.

2 | METHODS

2.1 | Study area

Our research focused on the Himalayan elevational gradient in Nepal (Figure 1a). Within a horizontal span of 200 km, elevation increases from ca. 60 m a.s.l. in the south to >8 km a.s.l. in the north (HMGN/MFSC, 2002; Figure 1a). In the south of the gradient, is the Gangetic plain called Terai (60–300 m a.s.l.) and north of this plain is the range of round hills called the Siwalik Hills (300–1500 m a.s.l.). North of the Siwalik Hills is the Lesser Himalayas or the Mahabharat range (1500–2700 m a.s.l.) with some valleys in-between called Inner Terai. North of the Mahabharat range is the Himalayas (> 4000 m a.s.l.) with some valleys in-between called Midlands (600–3500 m a.s.l.). Amid the Himalayas are several inner Himalayan valleys (valleys at elevations >3600 m a.s.l.). Finally, north of the Himalayas are plateaus that are part of the Tibetan Plateau (HMGN/MFSC, 2002; Figure 1a). Because of this unique topography, a rapid decline in surface area with small increase between 4000 and 5000 m a.s.l. can be observed as one climbs up from the Terai toward the Himalayas (Figure 1a) and the majority of surface area falls under slope class 20–30 degrees (Figure 1b). Along this gradient, temperature approximately decreases linearly (Table S1a), precipitation peaks around 1000 m a.s.l. and then decreases rapidly (Table S1e), and aridity (Table S1h) follows the inverse precipitation patterns. Cloud cover increases with increasing elevation (Table S1i, j). Soils become dry (Table S1k) and coarse (Table S1l-n), with increase in elevation with exception for intermountain valleys. Soil organic carbon content increases with increasing elevation (Table S1o). The soils in the Trans-Himalayan valleys are slightly alkaline while the rest of the country has neutral to acidic soils (Table S1p). Vegetation follows changes in temperature and precipitation patterns and changes from wet (1738 mm/year) and warm (24.1 °C) Tropical Deciduous *Shorea robusta* Forests to intermediate Temperate Moist Forests of Oaks and Conifers to comparatively drier (1132 mm/year) and colder (6.9 °C) Sub-alpine Forests of Birchs, Rhododendrons and Junipers (HMGN/MFSC, 2002; Lillesø et al., 2005; Shrestha, Agrawal, et al., 2015; Shrestha, Hofgaard, & Vandvik, 2015).

2.2 | Study species

To show how species responses to climate change may vary with climatic niche, we selected 137 common tree species that occupy different elevational zones along the Himalayas (a subset of 277 plant species used in Maharjan et al. (2022) (Table S2)).

2.3 | Near current environmental conditions

To model the near current (1970–2000) distributions of the study species, we initially selected 53 environmental variables: climate variables from WorldClim (http://worldclim.org/version2, Fick & Hijmans, 2017), irradiance variables from EarthEnv (http://www.earthenv.org/cloud, Wilson & Jetz, 2016), soil related variables from ISRIC-SoilGrids (ftp://ftp.soilgrids.org/data/aggregated/1km/, Hengl et al., 2017), topographic variables from CGIAR-CSI (https://cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1/), river network data from HydroSHEDS (http://www.hydrosheds.org/), and global lakes and wetlands

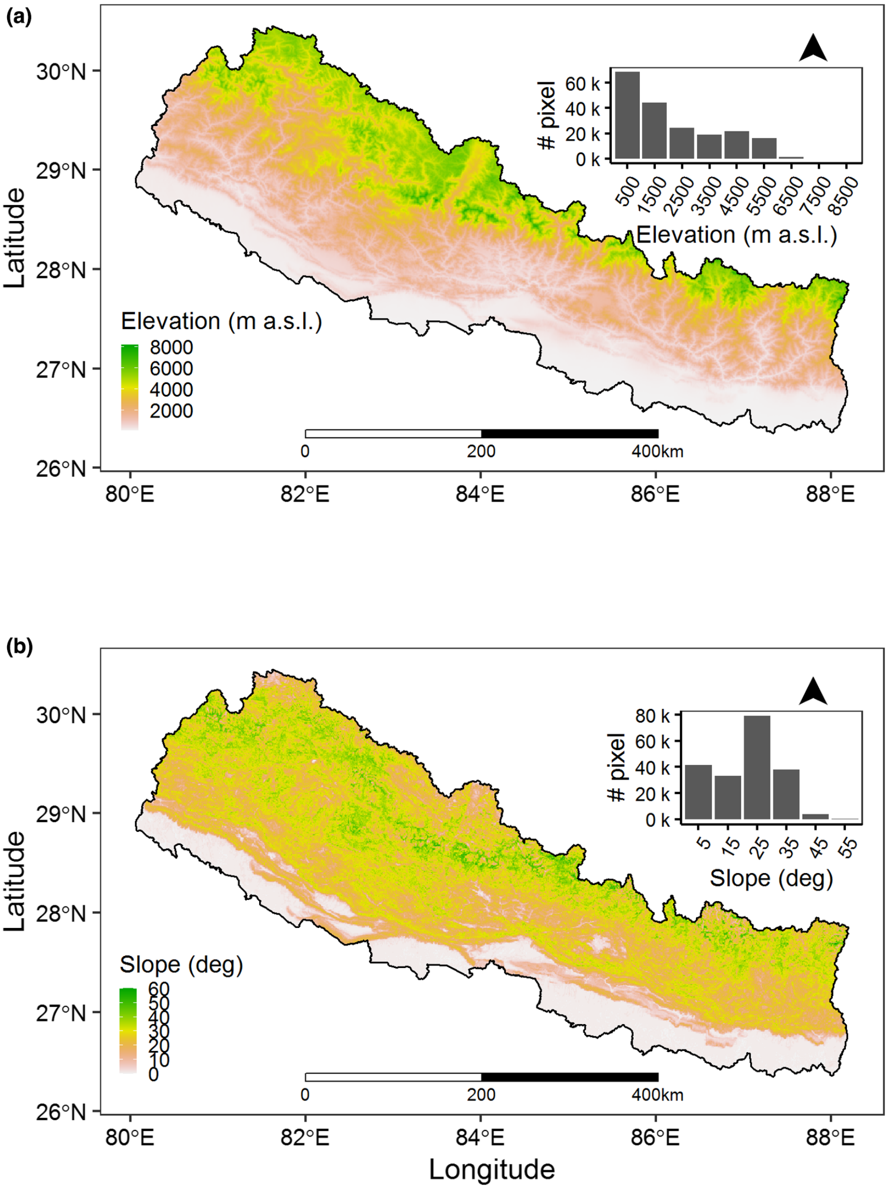


FIGURE 1 Map of the study area. (a) Elevation and (b) slope map of the study area. Pixel count per 1000 m elevation class in case of elevation map and that per 10 degree slope class in case of slope map are shown in the insets. The black line indicates national boundary of Nepal. The government of Nepal published on May 20, 2020, a new political map including Kalapani, Lipulekh, and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories.

data from WWF (https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database) that are known to potentially affect species distributions (Table S3; for details see also Maharjan et al., 2022). To meet statistical assumptions and to avoid multicollinearity, we selected 19 environmental variables that were least correlated ($r < 0.7$, Dormann et al., 2013; Table S3). The variables were related to temperature (mean annual temperature, isothermality, temperature diurnal range, and temperature annual range), water availability (annual precipitation, precipitation of driest quarter, precipitation seasonality, and [Thornthwaite's] aridity index), irradiance (cloud cover seasonality and mean annual cloud frequency), topography (slope, aspect, and distance to water (i.e., perennial water sources, Sarvade et al., 2016; Tsheboeng, 2018)), soil texture (clay content, coarse fragments content and silt content), and soil conditions (organic carbon content, pH, and available water capacity until wilting point). The spatial maps of these near current environmental variables are presented in Table S1.

2.4 | Future environmental conditions

To correctly predict the effects of predicted climate change on plant species in the Himalayas, it is essential that the Global Climate Models (GCMs) that are used represent the monsoonal climate. A study by Jourdain et al. (2013) reported that five Coupled Model Intercomparison Project Phase 5 (CMIP5) GCMs best reflect the monsoon in South Asia, namely, CCSM4, HadGEM2-AO, HadGEM2-ES, MIROC5, and NorESM1-M.

GCMs simulate weather in different layers of the atmosphere for small time steps and they are numerically complex. To allow for relatively fast computations, the world is divided into a rather limited number of spatial units (grid cells), typically in the order of 2 to 3 degrees (one degree of longitude is ~111 km at the equator). This is problematic for studies considering variation at much higher spatial resolution, which is addressed by downscaling GCM outputs. The approach for downscaling taken by Worldclim is to compute the absolute, or relative, difference between the output of the GCM run for the baseline year ("near present") and the future target year (e.g., 2050). This difference is then interpolated to a grid with the desired high spatial resolution. Subsequently, the future (or past) difference is applied to the high-resolution data for the present conditions based on actual weather station data, the WorldClim dataset. WorldClim refers to this step as the "calibration." Calibration is a necessary step because GCMs do not accurately predict the current climate in all places. For that reason, it is not recommended to directly compare observed current climate with predicted future (or past) climate (for more details on downscaling, see https://www.worldclim.org/data/downscaling.html).

At present, WorldClim version 2 (WC2) does not include future predictions for the five selected CMIP5 GCMs. Therefore, we adapted the approach for downscaling taken by WorldClim to construct our future data. For this, we used the WorldClim version 1.4 (WC1.4) data that have both near present and future datasets. We subtracted the near present WC1.4 data (average for 1960–1990) from the future WC1.4 data (average for 2041–2060) for the best-case representative concentration pathway (RCP) 2.6 and the worst-case RCP 8.5 scenarios to derive the predicted differences between present and future for monthly minimum, maximum, and mean temperature, and monthly precipitation for each of the five selected CMIP5 GCMs. The future differences for the five CMIP5 GCMs were then averaged to obtain multi-model monthly mean differences for minimum, maximum, and mean temperature, and monthly precipitation. These multi-model mean differences were then added to near present monthly climate data of WC2 to construct WC2 future monthly climate data for the best-case RCP 2.6 and the worst-case RCP 8.5 scenarios. The mean multi-model monthly datasets for minimum, maximum, and mean temperature, and monthly precipitation were used as input data to calculate the 19 future bioclimatic variables using the function "biovars" from the R-package DISMO (Hijmans et al., 2017). Future aridity (Thornthwaite's aridity index), climatic moisture index, growing degree days (base temperature = 10°C), and potential evapotranspiration (annual PET, PET extremes, and PET seasonality) were computed using future WC2 monthly minimum, maximum, and mean temperature, and monthly precipitation data using ENVIREM R-package (Title & Bemmels, 2018). Future maximum climatic water deficit (MCWD) was computed using future WC2 monthly precipitation data based on (Malhi et al., 2009; see also Maharjan et al., 2022). The spatial maps of the calculated future environmental variables for the worst-case RCP 8.5 scenario are presented in Table S1.

Studies such as Bobrowski et al. (2021) and Bobrowski and Udo (2017) have suggested that more recent CHELSA climatic data (Karger et al., 2017) and their future projections are more suitable for distribution modeling than WorldClim climatic data in complex topographical regions like the Himalaya. However, provided our study is a follow-up on Maharjan et al. (2022), where we used WorldClim version 2 climatic data for building species distribution models, provided WorldClim version 1.4 has future projections available for five CMIP5 GCMs reported to best reflect the monsoon in South Asia (Jourdain et al., 2013), provided WorldClim climatic data are reported to perform substantially better that CHELSA climatic data in transferring species distribution models beyond the calibration range (Datta et al., 2020), and, above all, provided comparison between WorldClim version 2 and CHELSA version 1.2 data showed highly significant correlations (Table S4) and comparable spatial maps (Table S5) for the bioclimatic variables, we chose to use WorldClim climatic data for the current study. Nonetheless, we would like to acknowledge that the use of CHELSA data may change the results to some extent but not completely as we chose to use equally good, if not better, WorldClim climatic data and we used the established method to calculate the future climatic data.

2.5 | Modeling near current and future species distributions

Our study is a follow-up on Maharjan et al. (2022). For this study, we selected 137 common tree species (a subset of 277 species used in Maharjan et al. (2022)). For the selected species, we used the species distribution models developed in Maharjan et al. (2022) to project their spatial distributions using "near current" (1985) and future (2050) predicted environmental conditions. In Maharjan et al. (2022), the near current (1970–2000) species distribution models for 277 species were developed using "samples with data (SWD)" (in our case occurrence data combined with 19 climatic, soil, and topographic predictor variables) format of MaxEnt version 3.3.3 k (Phillips, 2010) within the R-package DISMO (Hijmans et al., 2017). To comply with the ecological theory that species responses to environmental gradients are often unimodal (Austin, 2007), MaxEnt was restricted to use only linear and quadratic features (Boucher-Lalonde et al., 2012; Merow et al., 2013), where linear features represent one side of a unimodal response due to partial representation of the entire gradient. The study area was defined by the country border of Nepal plus a 200 km buffer surrounding the Nepalese border to avoid truncated niche predictions (Raes, 2012). We used 10,775 spatially unique observed species presence records at 30 arc seconds (~1 km) raster resolution from forest inventories, online floral databases (Global Biodiversity Information Facility: http://www.gbif.org, Integrated Digitized Biocollections: http://www.idigbio.org and iNaturalist: http://www.inaturalist.org) and supplementary fieldwork (undertaken in Oct-Dec 2017) for the modeling (for details on sources of collection, processing, and cleaning of species presence records, and MaxEnt modeling see Maharjan et al., 2022).

For each of our 137 tree species, we prepared near current and future probability of occurrence maps by projecting the near current "species.lambdas" files to the near current and the future environmental conditions, respectively, using MaxEnt's "density.Project" function. Since collection localities cover the entire gradient of Nepal, species were interpolated for the near current projections whereas they were allowed to be extrapolated to non-analog or novel future climatic conditions for the future projections. Since future projections for irradiance (i.e., cloud cover seasonality, mean annual cloud frequency) were not available, these were kept unchanged. As topographic variables (i.e., aspect, slope, and distance to water) and edaphic variables (i.e., soil organic carbon content, soil pH, available soil water capacity until wilting point, soil clay content, soil coarse fragments content, soil silt content) change little with time, these were also kept unchanged. For the further analyses, all near current and future probability of occurrence maps were cropped to the country border of Nepal. Then, we prepared discrete presence-absence maps, that is, species distribution maps by thresholding probability of occurrence maps using "10 percentile training presence logistic threshold" (one of the most conservative and absence independent thresholds for presence-only species distribution models, Liu et al., 2011).

2.6 | Data analysis

To evaluate whether climate warming results into different rates of elevational range shift among low and high elevation species, we compared the near current (1970–2000 i.e., "1985") minimum, maximum, and optimum elevations of species with their future (2041–2060 i.e., "2050") values using linear regression. For this, we used the near current and the future species distribution maps to compute respective species' minimum, maximum, and optimum elevations. We used 5th and 95th percentile elevation values as conservative estimates of species' minimum and maximum elevations. To quantify species' optimum elevation, we used the mid-value of the 100 m elevation band with the highest proportion of pixels predicted to be occupied. This procedure effectively corrects for the smaller available surface area at higher elevational bins (also see Maharjan et al., 2022).

To evaluate whether climate warming results in differential changes in distribution area among low and high-elevation species, we regressed percentage changes in species distribution area relative to the near current distribution against the optimum elevation of the species using linear regression. For this, we used the abovementioned species distribution maps to compute species distributions areas for period 1985 and 2050. Then, we calculated percentage changes in species distribution area relative to the near current distribution as the species distribution area for 2050 minus the species distribution area for 1985 divided by species distribution area for 1985 whole multiplied by 100.

To evaluate which environmental variable controls the species range shifts, we grouped the species by the environmental variables contributing the most to the species distribution models (variables with the highest relative percentage contribution) and used a one-way ANOVA with a post hoc Tukey test to analyze the differences in optimum shifts and the changes in distribution area among the species groups. Only the environmental variables that contributed the most to at least five species distribution models were considered for ANOVA.

To evaluate whether traits can be used as proxies to predict species range shifts and distributional area changes, we regressed shifts in species elevation and changes in species distribution area against species conduit diameter—one of the easy-to-understand traits that best explain tree species positions along Himalayan elevational gradient (for details see Maharjan et al., 2021)—using a linear regression. Conduit diameter (average diameter of the 100 randomly sampled conduits, in mm) relates to hydraulic efficiency. At low elevations with benign environmental conditions, wide conduits facilitate water transport and growth whereas at high elevations with harsh environmental conditions, narrow conduits reduce freezing-induced cavitation and enhance species persistence. For this analysis, we used subset of 28 tree species for which we had both range shift data and conduit diameter data (species in bold in Table S2).

3 | RESULTS

3.1 | Climate change predictions for Nepal for 2050

Under the worst-case RCP 8.5 scenario, by 2050, the mean annual temperature is predicted to increase with 2–3 °C and particularly the northwestern region is predicted to experience substantial warming (Table S1a). Both the annual (Table S1b) and diurnal (Table S1c) ranges of temperature are predicted to decrease for the major parts of the country. However, the isothermality (Table S1d) is predicted to increase indicating that rate of decrease in annual temperature range will be higher than rate of decrease in diurnal temperature range for the major part of the country. Annual precipitation is predicted to increase and particularly in the central and western lowlands and mid-hills, it is predicted to increase by more than 200 mm (Table S1e). Whereas the dry season precipitation is predicted to decrease (Table S1f) consequently leading to the increase in precipitation seasonality (Table S1g). Overall, the country is predicted to become warmer (Table S1a) and wetter (increase in annual precipitation, Table S1e; and decrease in aridity index, Table S1h).

3.2 | Rates of shift among low and high elevation species

To evaluate whether climate warming results in different rates of elevational range shift among low and high elevation species, the estimated species' minimum, optimum, and maximum elevations for 1985 were compared with their predicted values for 2050 using a linear regression. For all three species elevation values, the slopes of regression lines are significantly larger than 1 (Figure 2) indicating that highland species are predicted to shift their minimum, optimum, and maximum elevations faster than the lowland species. In order to maintain their climatic niches, species are (on average) predicted to shift their minimum elevations upslope with 57 m, the optimum elevations with 156 m, and the maximum elevations with 511 m under the RCP 2.6 scenario and their minimum elevations upslope with 125 m, the optimum elevations with 204 m, and the maximum elevations with 512 m under the RCP 8.5 scenario in 65 years (Figure 2 insets), corresponding to rate of respectively 1, 2 and 8 m/year under the RCP 2.6 scenario and, respectively, 2, 3, and 8 m/year under the RCP 8.5 scenario. Some of the mid-elevation species show large (>2000 m) shifts in their optimum and maximum elevation (e.g., species labeled with their name abbreviations in Figure 2). However, the intercepts of regression lines for each of the three species elevation values are not significantly different from zero indicating that some of the species at lower elevations are predicted to maintain their elevations or even shift their minimum (42 species) and optimum (5 species) elevations slightly downslope (Figure 2). As is normally expected, the rates of the upslope shifts were comparatively higher under the worst-case RCP 8.5 scenario than the best-case RCP 2.6 scenario (Figure 2), we focused mainly on results for the worst-case RCP 8.5 scenario in the following sections. The predicted future elevations, range shifts and changes in distribution area unless stated otherwise represent elevations, range shifts, and changes in distribution area under the worst-case RCP 8.5 scenario.

3.3 | Changes in distribution area among low and high elevation species

To evaluate whether climate warming results in differential changes in distribution area among low and high-elevation species, changes in distribution area of species were regressed against the optimum elevation of the species. Twenty-nine percent (i.e., 40 species) of the tree species are predicted to reduce their distribution area whereas the other 71% (97 species) are predicted to gain distribution area (Figure 3). Particularly, lowland and highland species are predicted to gain distribution area, but mid-elevation species are predicted to lose distribution area (Figures 3 and 4). The results are similar when regression analysis was carried out by excluding *Larix griffithii* with the largest predicted gain in distribution area ($R^2 = 0.36$, see Figure S1a) or by log-transforming percentage change in distribution area ($R^2 = 0.44$, see Figure S1b). Some lowland and highland species (e.g., species labeled with their name abbreviations in Figure 3) are predicted to more than double their distribution area by 2050. On average, species are predicted to gain 33% of their distribution areas ranging from −62 to 373% (Figure 3). Additionally, to confirm whether predicted change in distribution area is also influenced by species range shift parameters, a stepwise multiple regression analysis was carried out. This showed that change in distribution area not only depends on optimum elevation but also declines with shift in minimum elevation (*change in distribution area* = 91.54 − 0.113×*species optimum elevation*+0.00003×(*species optimum elevation*)^2 − 0.063×*species shift in minimum elevation*, $R^2 = 0.42$, $N = 137$, all coefficients were significant at $p < .1$).

3.4 | Which environmental variable controls species range shifts?

To evaluate which environmental variable controls the species range shifts, we grouped the species by the environmental variables contributing the most to the species distribution models (variables with the highest relative percentage contribution) and used a one-way ANOVA with a post hoc Tukey test to analyze the differences in optimum shifts and the changes in distribution area among the species groups. Species that showed significant and strongest upslope shifts are species whose distribution models are driven by responses to the aridity index, soil clay content, and mean annual temperature. The 95% confidence intervals of upslope shifts for species whose distribution models are driven by responses to other environmental variables such as available soil water capacity until wilting point, soil organic carbon content, and slope overlap with zero indicating that these environmental variables are not associated with upslope shifts (Figure 5a). Similarly, species that show significant gains in distribution area are species whose distribution models are driven by responses to mean annual temperature whereas species that show significant losses in distribution area are species whose distribution models are driven by responses to aridity index. The 95% confidence intervals of changes in distribution area for species whose distribution models are driven by responses to other environmental variables such as available soil water capacity until wilting point, soil clay content, soil organic carbon content, and slope overlap with zero indicating that these environmental variables are not associated with changes in distribution area (Figure 5b).

3.5 | Can traits predict species range shifts and changes in distribution area?

To evaluate whether traits (in our case conduit diameter) can be used as proxies to predict species range shifts and distributional area changes, we regressed shifts in species elevation and changes in species distribution area against species conduit diameter using a linear regression.

Species that show large predicted upslope shifts in minimum, optimum, and maximum elevation have small trait values and vice versa (Table 1; Figure 6a–c). The association between changes in distribution area and trait values is positive but not significant (Table 1; Figure 6d).

4 | DISCUSSION

We evaluated how climate warming affects the elevational ranges and the distribution areas of low and high elevation tree species, which environmental variable controls species range shifts, and how plant traits are associated with species range shifts. The modeling results indicate that highland species are predicted to show faster elevational shifts than lowland species. Lowland and highland species are predicted to enlarge their distribution area whereas mid-elevation species are predicted to reduce their distribution area. Tree species that show the largest upslope shifts are species for which species distribution models are driven by responses to aridity expressed as the aridity index, soil clay content,

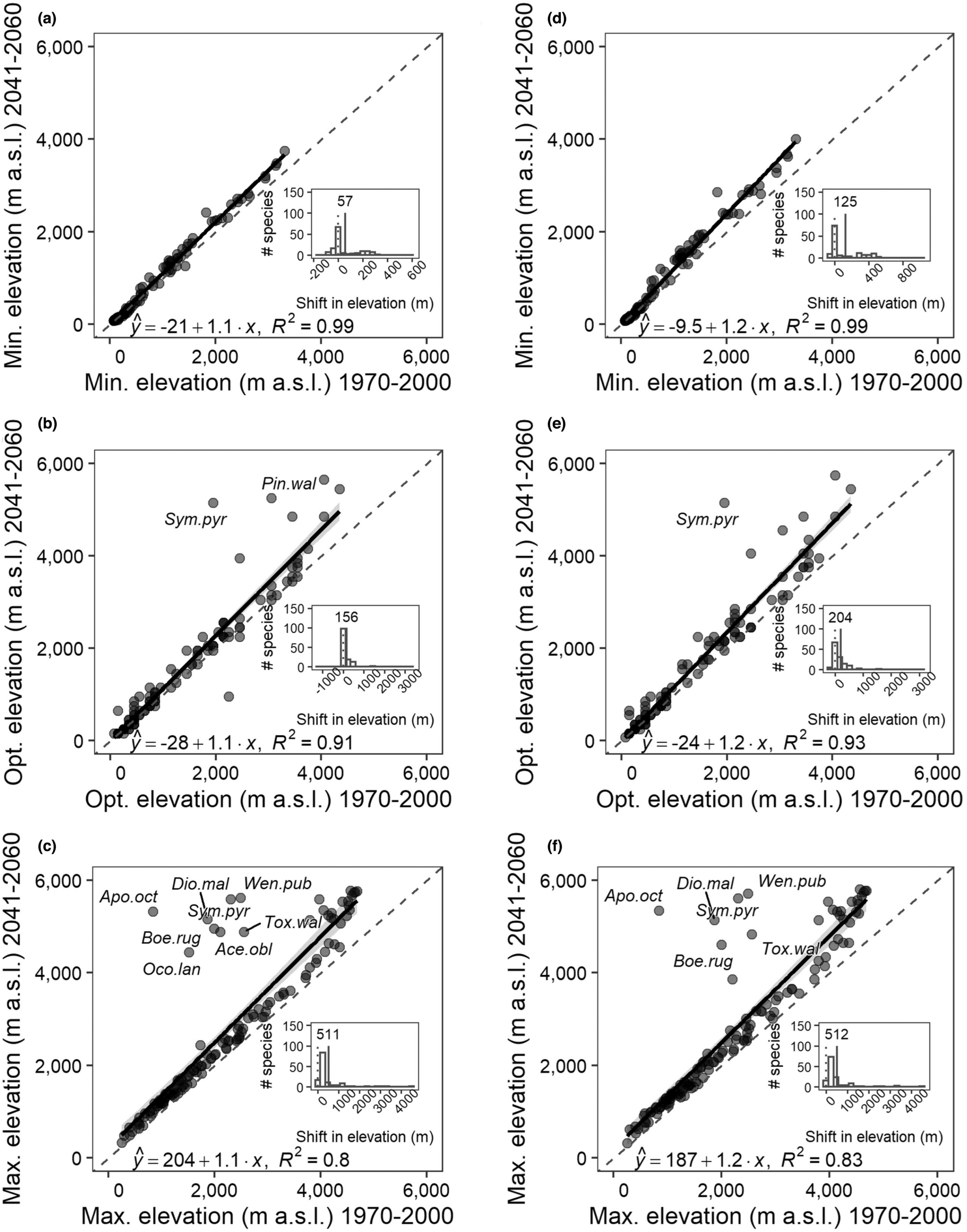

(a)
Min. elevation (m a.s.l.) 2041-2060
Min. elevation (m a.s.l.) 1970-2000
0
2,000
4,000
6,000
species
150
100
50
0
57
-200
0
200
400
600
Shift in elevation (m)
$\hat{y} = -21 + 1.1 \cdot x, \; R^2 = 0.99$
(b)
Opt. elevation (m a.s.l.) 2041-2060
Opt. elevation (m a.s.l.) 1970-2000
Pin.wal
Sym.pyr
156
-1000
0
1000
2000
3000
$\hat{y} = -28 + 1.1 \cdot x, \; R^2 = 0.91$
(c)
Max. elevation (m a.s.l.) 2041-2060
Max. elevation (m a.s.l.) 1970-2000
Apo.oct
Dio.mal
Wen.pub
Sym.pyr
Tox.wal
Boe.rug
Ace.obl
Oco.lan
511
4000
$\hat{y} = 204 + 1.1 \cdot x, \; R^2 = 0.8$
(d)
125
800
$\hat{y} = -9.5 + 1.2 \cdot x, \; R^2 = 0.99$
(e)
204
$\hat{y} = -24 + 1.2 \cdot x, \; R^2 = 0.93$
(f)
512
$\hat{y} = 187 + 1.2 \cdot x, \; R^2 = 0.83$

FIGURE 2 Scatterplots comparing the elevational distributions of 137 Himalayan tree species between periods 1985 and 2050 under representative concentration pathways (RCPs) 2.6 (a-c) and 8.5 (d-f). Each circle represents one species. The dashed line indicates the 1:1 line (no change in distribution). Solid regression lines are significant at $p < .05$. Gray shade around regression line indicates 95% confidence interval. The 95% confidence intervals of slopes of regression lines range between for (a) 1.10–1.13, (b) 1.09–1.21, (c) 1.05–1.24, (d) 1.17–1.22, (e) 1.13–1.24, and (f) 1.07–1.24 indicating that the slopes of regression lines are significantly larger than 1. The 95% confidence intervals of intercepts of regression lines range between for (a) −37.69 to −4.68, (b) −129.02 to 72.81, (c) −34.50 to 442.39, (d) −34.44–15.42, (e) −113.48 to 66.13, and (f) −29.69 to 403.13 and in all cases do not differ from zero. Insets show the frequency distributions of elevational shifts over the 65 years. The vertical dashed line indicates zero or no shift, the vertical solid line indicates the mean elevational shift, and number on the top indicates the magnitude of the mean elevational shift. Species with elevational shifts >2000 m are labeled with their names. Species name abbreviations are based on the first three letters of their genus and species names. For the complete list of study species and their near current and predicted future elevational distributions under RCPs 2.6 and 8.5 see Table S2.

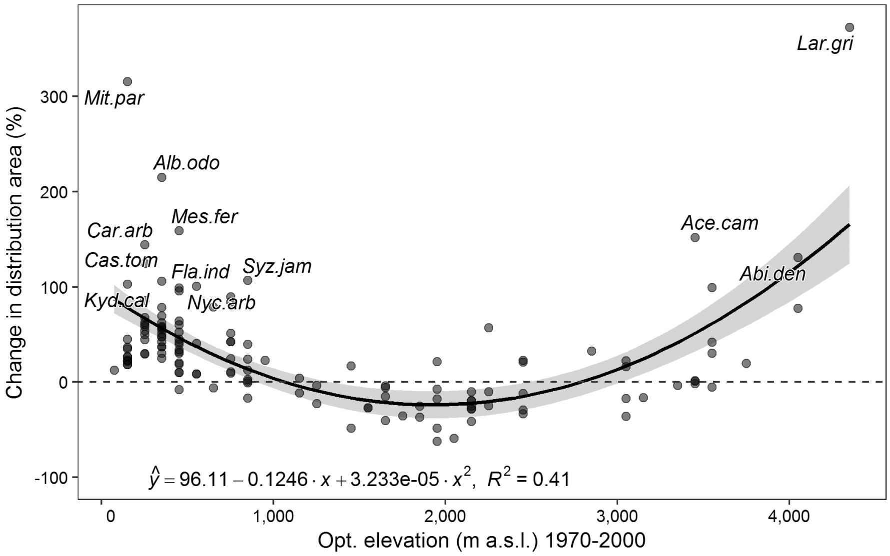


FIGURE 3 Relationship between change in distribution area between periods 1985 and 2050 (RCP 8.5) expressed as percentage change relative to 1985 distribution area and optimum elevation for 137 Himalayan tree species. Each circle represents one species. The horizontal dashed line indicates zero or no change in distribution area. The solid black regression line is significant at $p < .05$. Species with distribution area gain >100% are labeled with their names. Species name abbreviations are based on the first three letters of their genus and species names. For the complete list of study species see Table S2. The evaluated distribution area refers to Nepal.

and mean annual temperature, and have narrow conduits. Below, we discuss the underlying mechanisms.

Before going further into the discussion, however, we would like to acknowledge that future projections of species distribution models have a number of inherent limitations such as (i) there are no future climatic and distribution data to validate how good projected species distribution models are; (ii) the quality of future projections depends on the quality of species occurrence data, current and future environmental data, and the model assumptions; and (iii) the species' ability to adapt to or track changing climatic conditions. All being said, correlative species distribution models (MaxEnt in our case) are useful and frequently used tools to predict potential impacts of climate change on species distributions (Charney et al., 2021). Furthermore, we would like to clarify that we used carefully compiled species occurrence data (for details see Maharjan et al., 2022). We used one of the established methods to generate future climate data based on equally good, if not better, WorldClim climatic data instead of using CHELSA climatic data, which might change results to some extent but not completely. GCMs were selected that best capture monsoonal seasonal patterns. Regarding the modeling assumptions, MaxEnt was restricted to use only linear and quadratic features to comply with the ecological theory that species responses to environmental gradients are often unimodal. We made predictions for both the best-case RCP 2.6 and the worst-case RCP 8.5 scenarios, but we focused mainly on the results for the worst-case scenario because the rates of shifts were comparatively higher for the worst-case scenario than the best-case scenario as it is normally expected.

4.1 | Rates of shift among low and high elevation species

Our climatic niche models show that climate change predictions result in an upslope shift for all three elevational distribution parameters (minimum, optimum, and maximum elevations) for the majority of species (Figure 2). This is in line with the findings of empirical studies from the Himalayas (Bhatta et al., 2018; Gaire et al., 2014; Suwal

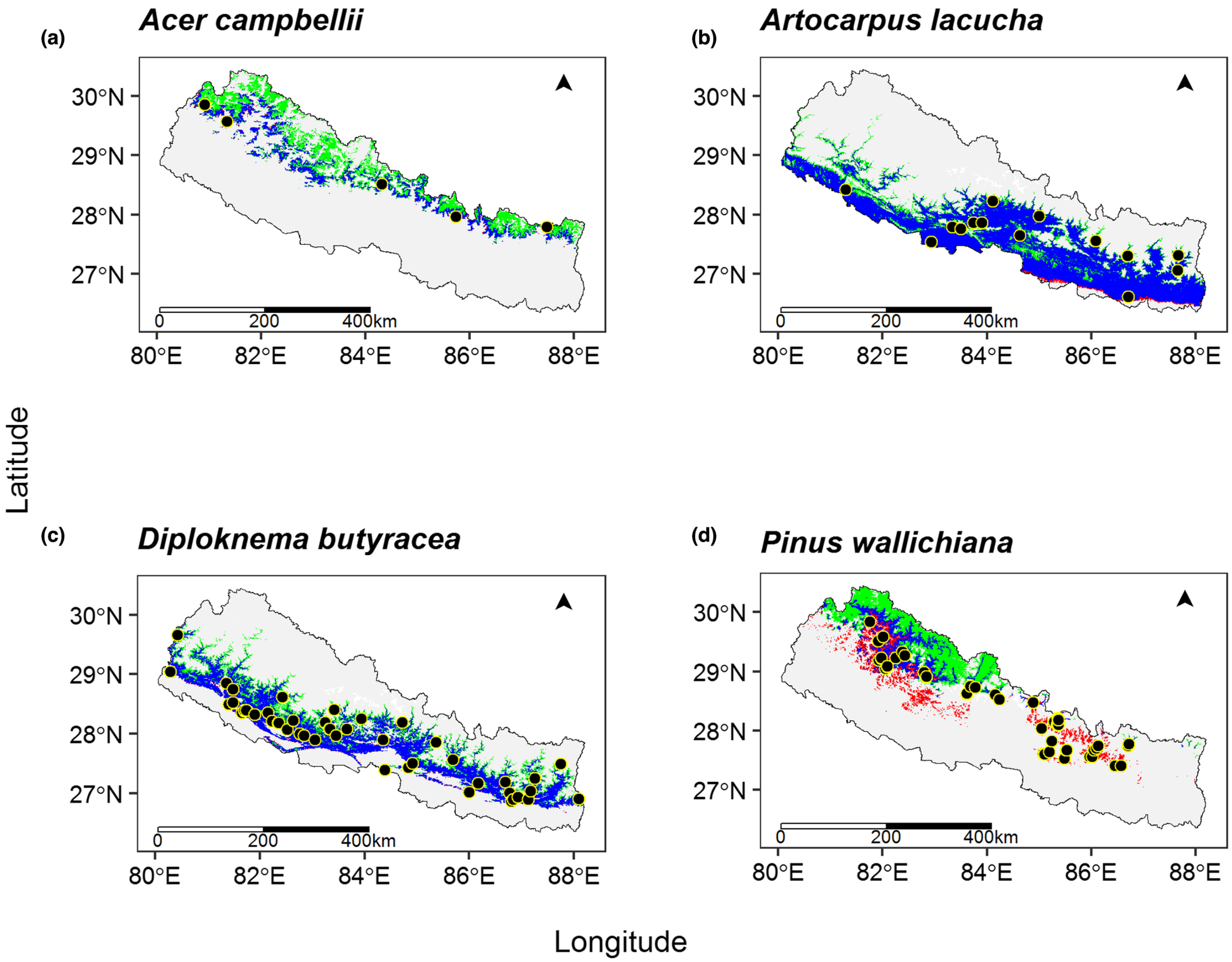
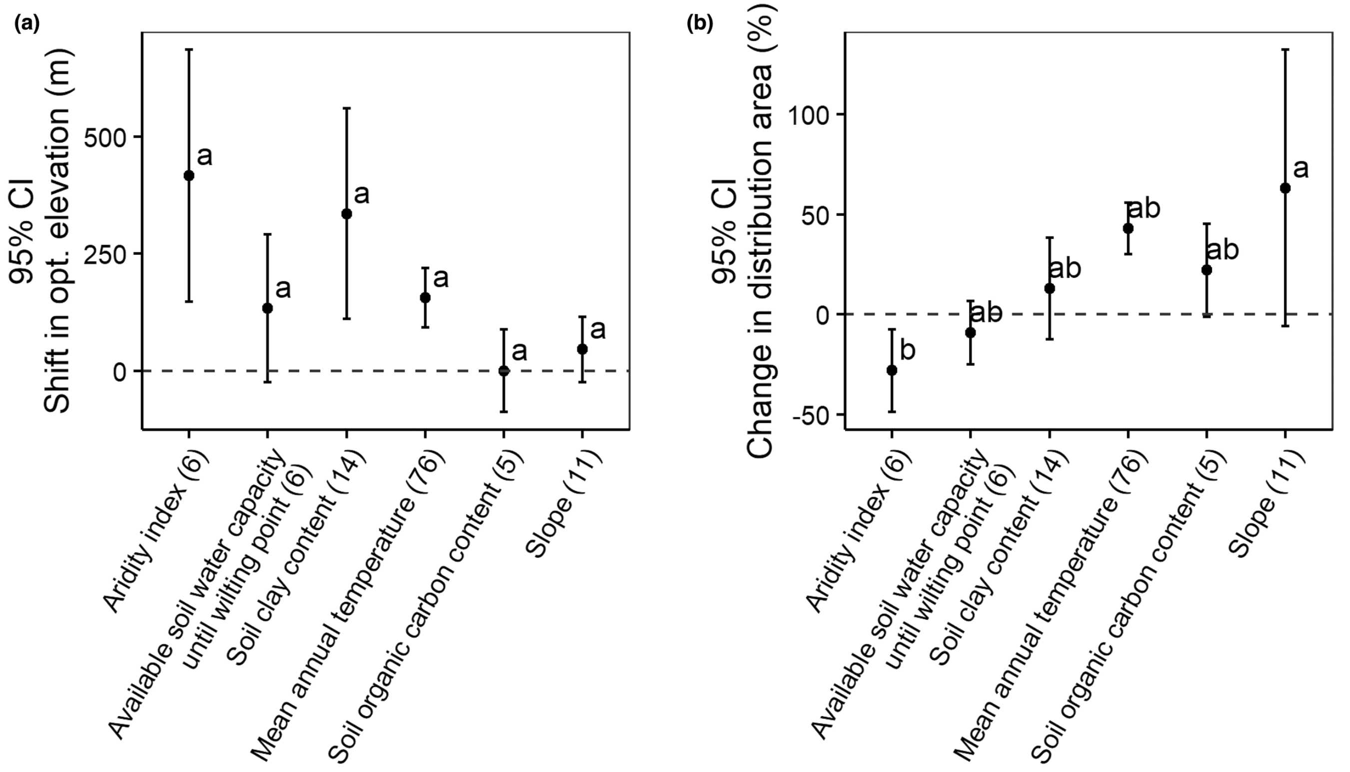


FIGURE 4 Maps showing changes in distribution area between 1985 and 2050 (RCP 8.5) for four tree species: (a) *Acer campbellii*, (b) *Artocarpus lacucha*, (c) *Diploknema butyraceae*, and (d) *Pinus wallichiana*. The black line indicates national boundary of Nepal. The government of Nepal published on May 20, 2020, a new political map including Kalapani, Lipulekh and Limpiyadhura inside the Nepal borders. As our research started in 2016, in our research, we used the previous version of the map without these territories. Colors indicate distribution areas that are predicted to be lost (red), maintained (blue), or gained (green). The areas in white represent areas with missing environmental data. Black circles indicate spatially unique observed species presence records at 30 arc seconds (~1 km) raster resolution from forest inventories, online floral databases and field survey for Nepal used for modeling the species distribution.

et al., 2016; Telwala et al., 2013) and other mountain ranges across the globe: Andes (Feeley et al., 2011), Alps (Geppert et al., 2020), and Pyrenees (Marshall et al., 2020). Because the lowlands are dominated by flat plains and the highlands by steep slopes (Figure 1), we expected that the required velocity for tracking climate change (i.e., rate of species range shift) to be higher for low elevation species than that for high elevation species. However, highland species were predicted to have faster range shifts than the lowland species (Figure 2). Such faster predicted range shifts of highland species suggest that along this extreme elevational gradient upslope range shifts are primarily controlled by the predicted increase in precipitation (i.e., reduced aridity, MoFE, 2019) and the temporal rates of warming that is observed (Luitel et al., 2020) and predicted to be higher for the highland areas (elevation dependent warming, Gao et al., 2018; Pepin et al., 2015).

The average upslope shifts of the maximum elevation of the tree species are predicted to be as high as 8 m/year under both the RCP 2.6 and 8.5 scenarios (Figure 2c,f inset) which is more than 2 times larger than the observed average upward shifts of the upper distribution limit of highland tree species in the Himalayas (3 m/year, Gaire et al., 2014; Telwala et al., 2013) and much larger than global average of 0.6 m/year (Parmesan & Yohe, 2003). Furthermore, some of the mid-elevation species showed large (>2000 m) predicted upslope shifts in their optimum and maximum elevations in 65 years (e.g., species labeled with their name abbreviations in Figure 2). This is again much larger than the observed maximum upslope shift of 998 m between 1850 and 2010 in the Himalayas (Telwala et al., 2013). This suggests that large areas with novel bioclimatic conditions at the upper limits of the species are predicted to become suitable for these species (cf. Greenwood et al., 2014; Morley



Environmental variables contributing the most to the species distribution models

FIGURE 5 Relationships between species range shifts (between 1985 and 2050 (RCP 8.5)): (a) shifts in species optimum elevation and (b) changes in species distribution area and environmental variables. Species are grouped by environmental variables contributing the most to the species distribution models (variables with the highest relative percentage contribution). Differences between the species groups are tested using ANOVA. Error bars with same letters are not significantly different while those with different letters are significantly different (post hoc Tukey test, $p < .05$). Black circles indicate group means and error bars indicate 95% confidence interval. Horizontal dashed line indicates no shift/change. Numbers in parenthesis next to environmental variable names indicate the number of species in the group.

TABLE 1 Bivariate relationships between current optimum elevation, four species range shift parameters, and conduit diameter. Species range shift parameters were calculated as difference between projected future elevation under the worst-case RCP 8.5 scenario and current elevation.

	Shift in min. Elevation (m)	Shift in opt. Elevation (m)	Shift in max. Elevation (m)	Change in distribution area (%)	Conduit diameter (mm)
	N = 137	*N* = 137	*N* = 137	*N* = 137	*N* = 28
Optimum elevation (m a.s.l.)	**0.82**	**0.50**	**0.28**	−0.16	**−0.77**
Shift in min. Elevation (m)		**0.48**	0.13	***−0.24***	**−0.68**
Shift in opt. Elevation (m)			**0.32**	−0.02	***−0.52***
Shift in max. Elevation (m)				0.04	**−0.65**
Change in distribution area (%)					0.29

Note: Pearson's correlation coefficients in bold are significant at $p < .05$, those in bold and italic are significant at $p < .01$, and those in bold and underline are significant at $p < .001$. *N* indicates number of tree species included in the analysis.

et al., 2020; O'Sullivan et al., 2020). The question remains whether these species are capable to migrate to potentially suitable future highland habitats on their own or that dispersal limitations prevent colonization of suitable habitats. Therefore, to enable species to track climate change, it should be considered to establish migration corridors through the fragmented landscapes or even assist species to migrate to potentially suitable future highland habitats through direct seeding or planting (cf. Yan & Tang, 2019).

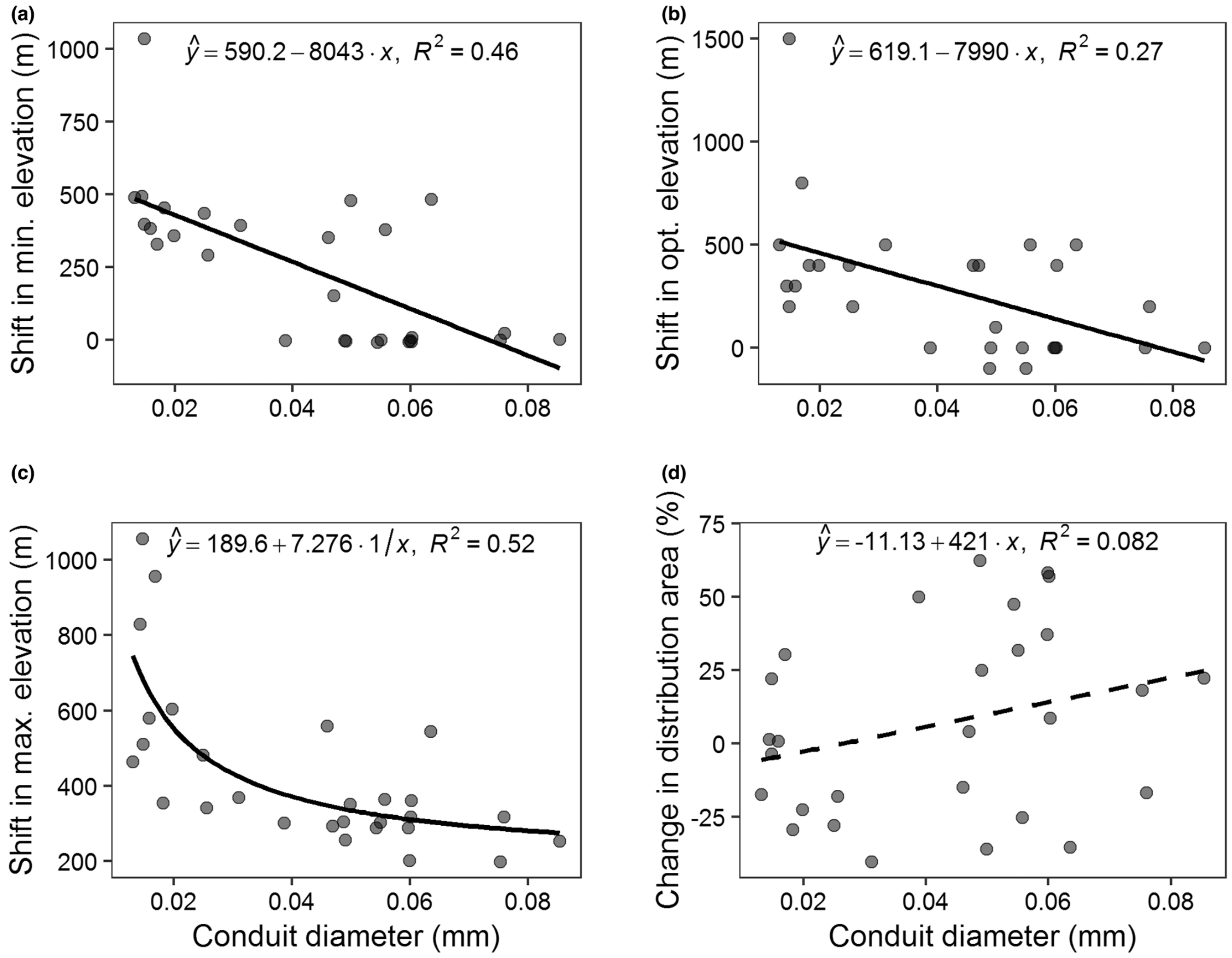


FIGURE 6 Relationship between predicted species elevational shifts (between 1985 and 2050 (RCP 8.5)) and conduit diameter for (a) minimum elevation, (b) optimum elevation, (c) maximum elevation, and (d) relationship between change in species distribution area and conduit diameter. Each circle represents one species ($N = 28$). Solid regression lines are significant at $p < .05$. Regression equations and coefficients of determination (R^2) are shown.

4.2 | Changes in distribution area among low and high elevation species

Because climate warming is expected to force species to shift their distribution ranges to smaller upslope surface areas, we hypothesized that all tree species will reduce their distribution area, and that low elevation species will show the largest reductions in distribution area. In contrast to our hypothesis, the majority (71%) of the tree species are predicted to enlarge their distribution area: these are particularly species from the lowlands or highlands whereas species from mid-elevations may reduce their distribution area (Figures 3 and 4). All else being equal, an upslope shift in minimum elevation should lead to a reduction in distribution area (as there is less surface area at higher elevations, Figure 1; Körner, 2007) and an upslope shift in maximum elevation should lead to an increase in distribution area. However, the actual change depends on the Himalayan topography and the area of each elevational belt (cf. Elsen & Tingley, 2015; Greenwood et al., 2014; Morley et al., 2020; O'Sullivan et al., 2020).

The prediction that lowland species expand their distribution area (Figure 3) is partly explained by the possibility that the Himalayan lowland species extend their upper limits upslope because of their competitiveness and partly by the ability of these species to persist at their lower limits, despite warming because it is likely that they are living at temperature well below their thermal maximums (Figures 2 and 4). This is consistent with observation from the French Alps, where the cosmopolitan and thermophilous nature of the lowland species are reported to contribute to their higher local persistence (Bertrand et al., 2011). However, in long run, further increase in temperature at lowlands may surpass species' thermal maximums and could lead lowland biotic attrition (Colwell et al., 2008; Feeley & Silman, 2010), which should be noted and monitored. The prediction that many mid-elevation species (between 1000 and 2500 m a.s.l.) reduce their distribution area (Figure 3) suggests that the mid-elevation species may face smaller upslope surface areas above 1000 m a.s.l. (see Figure 1a), while their lower limits become unsuitable for them. The prediction that highland species expand their distribution areas (Figure 3) is in line with the findings of other studies in the Himalayas (Anderson et al., 2020; He et al., 2019, 2020; Yan & Tang, 2019) and in alpine ecosystems in general (Rew et al., 2020). This suggests that warming is likely to make a large area of intermountain valleys and highland plateaus situated around 4500 m a.s.l. (Figures 1 and 2c; Elsen & Tingley, 2015) suitable for the upslope shifting highland species. Given their limited dispersal ability, the question remains whether the tree species will be able to get up to those distant plateaus timely. This is especially the case for species with future modeled disjunct distributions, such as *Aporosa octandra*, *Boehmeria rugulosa*, *Diospyros malabrica*, *Symplocos pyrifolia*, *Toxicodendron wallichii*, and *Wendlandia puberula* (Figure S2). These distributions are disjunct because the highland plateaus are intersected by mountain ranges, and because the valleys have different soil conditions, such as clayey deposits (Table S1m) and a higher organic carbon content (Devi & Sherpa, 2019; Table S1o). For these species with predicted disjunct future distributions or for species with continuous distributions for which new remote areas become available, species shifts could be assisted through direct seeding or planting in new potentially suitable highland habitats (cf. Yan & Tang, 2019).

4.3 | Environmental variables controlling species range shifts

Because the Himalayas are already experiencing substantial warming and are predicted to experience even faster rates of warming in the future, particularly at higher elevations (Table S1a), additional to predicted increase in precipitation throughout the Himalayas (Table S1e), we hypothesized that species for which the species distribution models are driven by responses to temperature and precipitation would show upslope shift in their optimum elevation resulting in a reduction of their distribution area. However, the species for which their species distribution model is determined by temperature (i.e., mean annual temperature) showed significant and strongest predicted upslope shifts but significant expansion in their predicted distribution areas (Figure 5). This suggests that for warm-adapted lowland species such increase in temperature may facilitate range expansion in the Himalayas. As predicted climate change leads also to increased precipitation and consequent decrease in aridity, another important environmental factor that controls the magnitude of predicted upslope shifts and changes in distribution area is aridity. Species for which their species distribution model is determined by aridity showed indeed significant and strongest predicted upslope shifts and significant contraction in their predicted distribution area (Figure 5). Several studies from the Himalayas (Gaire et al., 2014; Telwala et al., 2013) and other mountain ranges (Crimmins et al., 2011; Feeley et al., 2011; Lenoir et al., 2008; Pauli et al., 2012; Zhang et al., 2020) have highlighted such important roles of precipitation—in addition to warming—in controlling species range shifts. This suggests that for the species that prefer dry to moist sites such increase in temperature and precipitation may lead to range contraction.

Interestingly, soil clay content (ClayC) appeared as another important environmental variable (Figure 5) suggesting that species responses to climate change are also strongly modified by soil clay content. As species, particularly high-elevation species, shift upslope, they are likely to spill over to large clayey intermountain valleys and highland plateaus situated around 4500 m a.s.l. (Figures 1 and 2c; Table S1m; Elsen & Tingley, 2015) that are presently not suitable as result of present bioclimatic conditions. Hence, fixed soil properties in combination with changing bioclimatic conditions may strongly constrain and modify species responses to climate change along the Himalayan elevational gradient. Other studies—but from Andes—also found that responses of tree species and communities to global warming are highly heterogeneous (cf. Figure 5a; Duque et al., 2015; Fadrique et al., 2018), and depend not only on the magnitude of temperature change at that specific elevation (Fadrique et al., 2018), but also on local soil conditions that can constrain the immigration and establishment of non-specialists (Duque et al., 2015). This suggests that soil effect is not Himalaya specific, but generic.

4.4 | Traits as proxies to predict species range shifts and changes in distribution area

Because acquisitive trait values allow species to acquire resources faster and attain faster growth (Estrada et al., 2016; Maharjan et al., 2021), we hypothesized that species with predicted large range shifts and changes in distribution area have acquisitive trait values. However, the modeling results indicate that species with small predicted upslope shifts have large trait values, that is, acquisitive trait values (Table 1; Figure 6). This suggests that acquisitive trait values are negatively associated with magnitude of species range shifts.

Particularly in the Himalayas, species with acquisitive trait values (wide conduits) dominate lowland areas (Maharjan et al., 2021), probably because wide conduits facilitate water transport and growth, and consequently enhances competitive ability in dense stands in moist and productive lowland environmental conditions (cf. Venturas et al., 2017). The majority of these warm-adapted lowland species with acquisitive trait values are predicted to maintain their current lower distribution limits while they are predicted to shift their upper distribution limits upslope (Figure 2). When they shift their upper distribution limits upslope to higher elevations while maintaining their lower distribution limits, this will lead to increase in their distribution areas. This must have resulted into positive but non-significant association between acquisitive trait values and changes in distribution area. Hence, an easily measurable trait, such as conduit diameter, can be used as a proxy to predict species range shifts and distributional area changes. Although not for conduit diameter, but traits such as fruit type, dispersal modes, and life forms have been shown to be useful in predicting species range shifts among the subtropical mountain plants in the Hengduan Mountains in China (Zu et al., 2021).

Given that the environmental conditions of Nepal are predicted to be warmer and wetter (MoFE, 2019; Table S1a, e), the tree species with wide conduits, that is, species with high hydraulic efficiency (Olson et al., 2018; Pittermann & Sperry, 2006) are the ones going to benefit the most in terms of expansion of their distribution area. Such wide conduits may also make trees species more competitive under the predicted warmer and wetter environmental conditions.

4.5 | Management recommendations

The average upslope shifts of the maximum elevation of the tree species are predicted to be more than 2 times larger (8 m/year, Figure 2c inset) than the observed average upward shifts of the upper distribution limit of highland tree species in the Himalayas (3 m/year, Gaire et al., 2014; Telwala et al., 2013). Therefore, to enable species to track climate change, it should be considered to establish migration corridors through the fragmented landscapes or even assist species to migrate to potentially suitable future highland habitats through direct seeding or planting (cf. Yan & Tang, 2019). Further, the prediction that lowland species expand their distribution area (Figure 3) suggest that lowland species may extend their upper limits upslope and at the same time persist at their lower limits, despite warming. However, in long run, further increase in temperature at lowlands may surpass species' thermal maximums and could lead to lowland biotic attrition (Colwell et al., 2008; Feeley & Silman, 2010). It is thus recommended to monitor lowland species for lowland biotic attrition. Furthermore, the prediction that highland species expand their distribution area (Figure 3) suggest that with climate warming large area of inter-mountain valleys and highland plateaus situated around 4500 m a.s.l. (Figure 1) will become potentially suitable for the upslope shifting highland species. Particularly for the species with disjunct distributions (e.g., *Aporosa octandra*, *Boehmeria rugulosa*, *Diospyros malabrica*, *Symplocos pyrifolia*, *Toxicodendron wallichii*, and *Wendlandia puberula*, Figure S2) or for the species with continuous distributions for which new remote areas become available, upslope shifts should be assisted through direct seeding or planting in new potentially suitable highland habitats (cf. Yan & Tang, 2019). A significant proportion of the species (29%) are predicted to decrease in distribution area. Especially for those species with largest contractions in distributions (e.g., *Betula alnoides*, *Prunus cerasoides*, *Pyrus pashia*, and *Quercus floribunda*, Table S2), it is recommended to monitor whether they are able to maintain a viable population size. Our findings may be used in numerous additional ways such as locating currently undocumented species locations, potential locations where species may occur in the future, or potential locations where the species could be seeded or planted to enable species to track their climatic niches, thus contributing to the species conservation and management.

AUTHOR CONTRIBUTION

S.K.M., F.J.S., and L.P. conceived of the research idea. S.K.M. compiled and processed data. Y.Z., under supervision of L.P. and S.K.M., worked on part of the data for her MSc thesis, which provided preliminary directions for this manuscript; S.K.M., with contributions from N.R., modeled the distributions of plant species;. S.K.M., with contributions from F.J.S. and L.P., performed statistical analyses; S.K.M. wrote the first draft and F.J.S., N.R., and L.P. extensively discussed the results and commented on the manuscript. The authors declare no conflict of interests.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

For the part of the species presence data owned by FR&TC, Nepal, that support the findings of this study, we will deposit only the calculated data, and not the original data. Remaining species presence data that support the findings of this study were downloaded from the following resources available in the public domain: Global Biodiversity Information Facility: http://www.gbif.org, Integrated Digitized Biocollections: http://www.idigbio.org and iNaturalist: http://www.inaturalist.org. Citations for the species presence data thus downloaded are included as an online appendix in Maharjan et al. (2022). Environmental data were derived from the following resources available in the public domain: climate data from WorldClim (http://worldclim.org/version2, Fick & Hijmans, 2017), irradiance data from EarthEnv (http://www.earthenv.org/cloud, Wilson & Jetz, 2016), soil data from ISRIC-SoilGrids (ftp://ftp.soilgrids.org/data/aggregated/1km/, Hengl et al., 2017), topographic data from CGIAR-CSI (https://cgiarcsi.community/data/srtm-90m-digital-elevation-database-v4-1/), river network data from HydroSHEDS (http://www.hydrosheds.org/), and global lakes and wetlands data from WWF (https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database). The calculated species' near current and predicted future elevational distributions (minimum, optimum and maximum elevations and distribution areas) and changes in distribution area data are included in Table S2.

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