



Spatio-temporal distribution of broad-leaved *Quercus semecarpifolia* indicates altitudinal shift in northwestern Himalayas

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Abstract The Himalayan region is not only threatened by rapid anthropogenic activities but also by the effects of global climate change. Given the uncertainties in magnitude and characteristics of climate change, it is of crucial importance to accumulate prior knowledge of existing and the adaptive future change in the distribution pattern of tree species, especially in the Himalayas which are pronounced with highly heterogeneous ecology. *Quercus semecarpifolia*, a high-altitude Oak, ranges up to timberline in the Himalayan region. This species forms the climax community on the southern aspect of the mountainside, and

is considered to be one of the oldest trees belonging to the Himalayan region. Due to climate-influenced phenomena like masting and inherently slow growth rate, this dominant species is under severe decline. Hence, the present study aimed to delineate and predict the potential distribution range of *Q. semecarpifolia* in the Uttarakhand region of northwestern Himalayas in relation to associated species, land use land cover, wind, edaphic and bioclimatic variables. Furthermore, potential spatio-temporal variations within the purview of climate change were also predicted through MaxEnt modelling. In total, 589 geo-coordinates were recorded during field surveys (2016–2021) that cover a wide-range of slope, aspect and elevation. Over the WorldClim dataset, ~70% well-distributed geo-coordinates were used for training the model and the remaining for validation. The model performance

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was supported by statistically significant and high AUC value of 0.943 ± 0.059 ; whereas, the Jackknife test showed that bioclimatic variables, namely annual temperature range (Bio 7), precipitation of the driest month (Bio 14), minimum temperature of the coldest month (Bio 6), and mean temperature of the coldest quarter (Bio 11) contributed significantly in predicting the current distribution of *Q. semecarpifolia*. The species is majorly distributed in a total of 29 sites belonging to nine districts (dominated in Pithoragarh, Chamoli and Uttarkashi) with altitude ranging from 2249 (Ghes) to 3652 m (Karandam Bugyal). The distribution was further overlaid on KGCC map, which showed maximum occurrence in Cwb (C=warm temperate, w=winter dry, and b=warm summer), i.e., subtropical highland oceanic climate of middle and upper Himalayas constituted by the northwestern Bageshwar, southern Chamoli, small stretch of northeastern Pauri, southeastern Rudraprayag, northern Tehri and Uttarkashi. In the study area, *Q. semecarpifolia* has been observed to be associated with 19 tree species, where the highest density ratio was recorded with *Rhododendron arboreum*. The MaxEnt model-based prediction revealed an area of $\sim 832 \text{ km}^2$ with the loss of $\sim 79 \text{ km}^2$ (RCP 8.5_2050) and $\sim 168 \text{ km}^2$ (RCP 8.5_2070), in advancing upslope of the northwestern Himalayas. Geological analysis indicated that tectonic uplift, an important control to the altitudinal shift modelled for the distribution of *Q. semecarpifolia* due to time scale divergence. Bedrock composition variations, however, might control distribution by means of influencing soil acidity. This study predicts an upslope movement of *Q. semecarpifolia* in response to climate change where topography and climatic factors could play a significant role.

Keywords *Quercus semecarpifolia* · Eco-distribution mapping · Altitudinal shift · MaxEnt model · Northwestern Himalayas

Introduction

Plant communities living in extreme environmental conditions and growing at the edges of their distribution range are usually more sensitive to climate change. Consequently, they are more prone to experience altitudinal and latitudinal shifts, whilst maintaining normal or adaptive physiological responses

(Telwala et al. 2013). The effects of climate change are quite severe in the Himalayas as evident by an increase in the global average temperature (Srinivasan 2006). Further, near surface temperature lapse rate ($-5.3 \text{ }^\circ\text{C}$ in western Himalayas $> -6.5 \text{ }^\circ\text{C}$ World's average per km) dipped gradually in the steep mountain slopes and warming remained for a prolonged period in the Himalayas when equated across the globe (Joshi et al. 2018). These anomalies suggest that climate in the Himalayan mountains is warming two to three times faster than the global average rate (Shrestha and Aryal 2011). Despite great uncertainty in climate change-induced impacts, global estimates show marked influences over species extinction rates, distribution patterns, phenology, ecosystem structure and composition (Urban 2015). Several other concurrent stressors, such as spread of invasive species, habitat degradation, over-extraction, grazing, diseases and insect-pests, further aggravate the impacts, which either act independently or in combination (Mantyka-Pringle et al. 2015). Thus, the long-lived plant communities, i.e., *K*-selected trees perhaps grow and migrate slowly (Pearson 2006), and the unprecedented climate change will not allow immediate adaptation to newer climatic conditions (Aitken et al. 2008). However, more comprehensive assessments are required to understand the impact of climatic and non-climatic forces on the ecological niches, distribution patterns and probable shifts of keystone forest tree species (Gairola et al. 2013).

Quercus semecarpifolia (Vern: Khasru Oak), a broad-leaved sub-alpine tree, is an important foundation species of the central Himalayas. The Steppe biome was colonized by *Q. semecarpifolia* and therefore, Oaks became a dominant element of the sub-alpine and alpine forests (Singh and Singh 1992). The Oak forest is found throughout the Indian subcontinent in the Indian Himalayan Region (IHR), where *Q. semecarpifolia* is reported to exist between 2000 and 3700 m. Oak forest types usually predominate in the exposed ridges of mountains, where *Q. semecarpifolia* frequently occurs in association with conifers, such as *Abies* spp., *Picea* spp. and *Taxus wallichiana*. In some localities, it has been found mixed with *Pinus wallichiana* and occasionally associated with broad-leaved species, namely *Acer* sp., *Betula* sp., *Juglans regia*, *Pyrus* sp. and *Prunus* sp. (Troup 1921). In hill slopes and ridges, it forms pure gregarious forests, where heavy snowfall occurs in winter with an

annual rainfall ranging from 70 to 250 cm. Being a later successional species with poor colonizing habit, achieving good regeneration has been a matter of concern for *Q. semecarpifolia*. Recently, a considerable decline in the number of saplings and complete absence of seedlings was observed for this species (Negi and Negi 2021). Main causes are the masting event (long fruiting cycle of 8–10 years), low seed viability, vivipary and sensitivity to shade (Singh and Singh 1986; Negi and Naithani 1995), which may potentially be influenced by climate change in the Himalayas (Chakraborty et al. 2018). Further, tree diversity and the temporal stability of mountain forest are prejudiced by climate change, which affect ecosystem processes directly besides changing community composition indirectly (Jourdan et al. 2021).

Changing climatic regimes are predicted to examine for its influence over vegetation composition and forest structure. These associations will remain intact and move together in response to changing climatic conditions or whether the co-occurring companion species will be changed according to the differential adaptive potential, are the key questions that require a more detailed explanation. It is interesting to find out the ecological behaviour of the *Q. semecarpifolia* in association with the tree species occurring on a biogeographical region in purview of the present and future climate scenarios. However, given the uncertainties in future climate change, prior investigations on the long-term changing distribution patterns of forest species are of crucial importance. Further, owing to the heterogeneity of the mountain ecosystem in the Himalayas, knowledge on the potential impacts over species association is of paramount concern (Sharma 2014; Chakraborty et al. 2018). For instance, waning and replacement of *Q. semecarpifolia* forest is mostly linked with associate species, such as *P. roxburghii*, *P. wallichiana*, *Eupatorium adenophorum*, and *Lantana camara* (Singh et al. 1984; Nautiyal 2015). In addition, human-induced impacts, such as agricultural expansion, grazing, lopping of branches, dry season fodder, manure, charcoal making, high quality fuelwood, durable timber, felling of trees, litter collection, and harvest of important ground vegetation may also link to the reduced natural regeneration in the Oak forests (Subedi 2006).

Based on the above facts, the declining population of *Q. semecarpifolia* has been attributed to the climatic and non-climatic factors. All the gentle-sloped

and accessible meadows in the alpine, sub-alpine and temperate regions have undergone extensive habitat degradation and perhaps altitudinal shift, with a considerable loss of the natural vegetation (Ives and Messerli 1989; Singh 1991). These relevant observations could be implied with the use of species distribution modelling (SDM) tools, where MaxEnt has an additive advantage as it works on the ‘presence only’ data relative to both bioclimatic and non-climatic determinants. The MaxEnt model has been widely used for niche modelling and developing distribution maps in several Himalayan Oaks, namely *Q. floribunda*, *Q. leucotrichophora*, *Q. semecarpifolia* (Chakraborty et al. 2016), *Q. lanata* (Bhandari et al. 2020b), *Q. leucotrichophora* (Dhyani et al. 2020) and *Q. semecarpifolia* (Singh et al. 2021). Globally, the MaxEnt model has been successfully applied to determine the potential consequences of future climate change on the distribution of *Diospyros virginiana*, *Oxydendrum arboreum*, *P. virginiana*, *Q. falcata* var. *falcata* in Ohio, USA (Schwartz et al. 2001), *Larix occidentalis* in North America (Rehfeldt and Jaquish 2010), fourteen threatened forest tree species in the Philippines (Garcia et al. 2013), *T. baccata* in the Bolkar Mountains of southern Turkey (Koç et al. 2018) and *Pterocarya stenoptera* in China (Zhang et al. 2020). Many of these studies indicated that change in the area of species occurrence, such as altitudinal shift, upslope movement, in response to global climate change scenarios as depicted by a Representative Concentration Pathways (RCPs) trajectory adopted by the Intergovernmental Panel on Climate Change (IPCC). Generally, the four RCP pathways (RCP 2.6, 4.5, 6.0 and 8.5 W m⁻²) for each of the projected time scales (2041–2060 and 2061–2080), were used for climate modelling as discussed in the IPCC fifth Assessment Report (AR5) (IPCC 2014).

A habitat suitability can be predicted by ecological niche modelling (Pearson and Dawson 2003), besides explicitly recognizing climatic response functions (Wang et al. 2010; Chakraborty et al. 2018). Whereas other non-climatic factors are also important and crucial for any shift and future projections. In the present study, we hypothesized that the current distribution of *Q. semecarpifolia* may show upward shift movement in purview of climate change scenarios and future community structure will be determined on the basis of edaphic, geological and associated species composition. The foremost goal was to quantify the

potential altitudinal shift of *Q. semecarpifolia* in the Himalayas. With this, our study aimed to: (i) survey the distribution range and compare density of all the tree species associated with *Q. semecarpifolia* in Uttarakhand Himalayas; (ii) build models to predict the current and future spatio-temporal distribution of this species through MaxEnt; and (iii) quantify the predictions regarding altitudinal shifts on *Q. semecarpifolia* and the key role of non-climatic associates in the prediction of species ecological niche. The study provides scientific support for policy making on the impact of species shifting whilst advocating mitigation measures. Overall, the research work contributes towards conservation, protection and habitat restoration of *Q. semecarpifolia* in the Himalayan region.

Material and methods

Recording of field data

The study sites are located in the state of Uttarakhand, which is one of the 12 Himalayan states of India, known for its highly varied physiography and biodiversity. The study area ranged between geo-coordinates E 77° 34′–81° 03′; N 28° 43′–31° 28′ and occupying a total area of 53,483 km². Based on the geological evolutionary history, the state comprises a cross-section of the northwestern Himalayan orogen, which can be further categorized into the following sub-domains: Trans-Himalaya, the Greater Himalaya or Himadri, Lesser Himalaya, Shivalik Ranges, Foothills, Terai and the Plains (<https://sbb.uk.gov.in>). The first two zones represent alpine and temperate climatic conditions; whereas Lesser Himalaya and Shivalik correspond to subtropical and subtemperate regions, and the last three zones imbibe the tropical ecological climate niche (FSI 2019). However, based on the altitude, there are five climatic zones in Uttarakhand, namely warm temperate (900–1800 m), cold temperate (1800–2400 m), cold zones (2400–3000 m), alpine zone (3000–4000 m), glacier zone (4000–4800 m) and perpetually frozen zone (> 4800 m) (Uttarakhand Forest Statistics 2012–2013). Typically, the mean annual temperature ranged from – 4.7 to 40.7 °C, and the mean annual rainfall has been recorded as 1613 mm in the year interval of 2018–2019 (Uttarakhand at a Glance 2018–2019). The study area is one

of the main hot spots for biological diversity of forest genetic resources and habitat of five Oak species.

The comprehensive mapping scheme and procedure used to predict the altitudinal shift is shown in Fig. 1. The maps of Forest Survey of India (FSI 2015) and the working plans of the state forest department (Uttarakhand, India) were reviewed to locate the distribution status of the species. Species occurrence data were also acquired from the herbarium specimens available at Forest Research Institute (FRI), Wildlife Institute of India (WII) and northwestern Botanical Survey of India (BSI), Dehradun; and by reviewing the literature available at the National Forest Library Information Center (NFLIC) of FRI, Dehradun.

During 2016–2021, field surveys were conducted in 11 districts of Uttarakhand. However, *Q. semecarpifolia* was found to occur only in nine districts, namely Bageshwar, Chamoli, Dehradun, Nainital, Pauri, Pithoragarh, Rudraprayag, Tehri and Uttarkashi (Table 1). The sampling was performed throughout the distribution range, thus representing density variation of the focal species. Despite our efforts to include the most representative areas of *Q. semecarpifolia* forests, in some areas, the geographical terrain was difficult to access due to very steep slopes. Therefore, the quadrat and line transect approaches were used for unbiased sampling of forest areas. The latitude, longitude and altitude were recorded with Global Positioning System (GPS; 5–8 m precision accuracy) and quadrats (10×10 m) were laid with a minimum of 300 m distance apart. A total of 29 line transects were laid across the sampling sites as per the standard methodology devised to map *R. arboreum* (Mamgain et al. 2017). For precise distribution mapping, individual trees and patches were also demarcated in polygons through GPS. Furthermore, the quadrats were used for density analysis, whereas line transects were used to acquire more GPS points for eco-distribution mapping and population status analysis. In total, 589 geo-coordinates of *Q. semecarpifolia* were recorded in the nine districts of Uttarakhand.

Based on the tree density, populations surveyed along 29 line transects were classified into the following categories: (i) reduced (10–20 trees per 500 m); (ii) disturbed (20–30 trees per 500 m); (iii) fair (30–40 trees per 500 m); (iv) healthy (40–50 trees per 500 m); and (v) pristine (> 50 trees per 500 m). Further, the population distribution was categorized

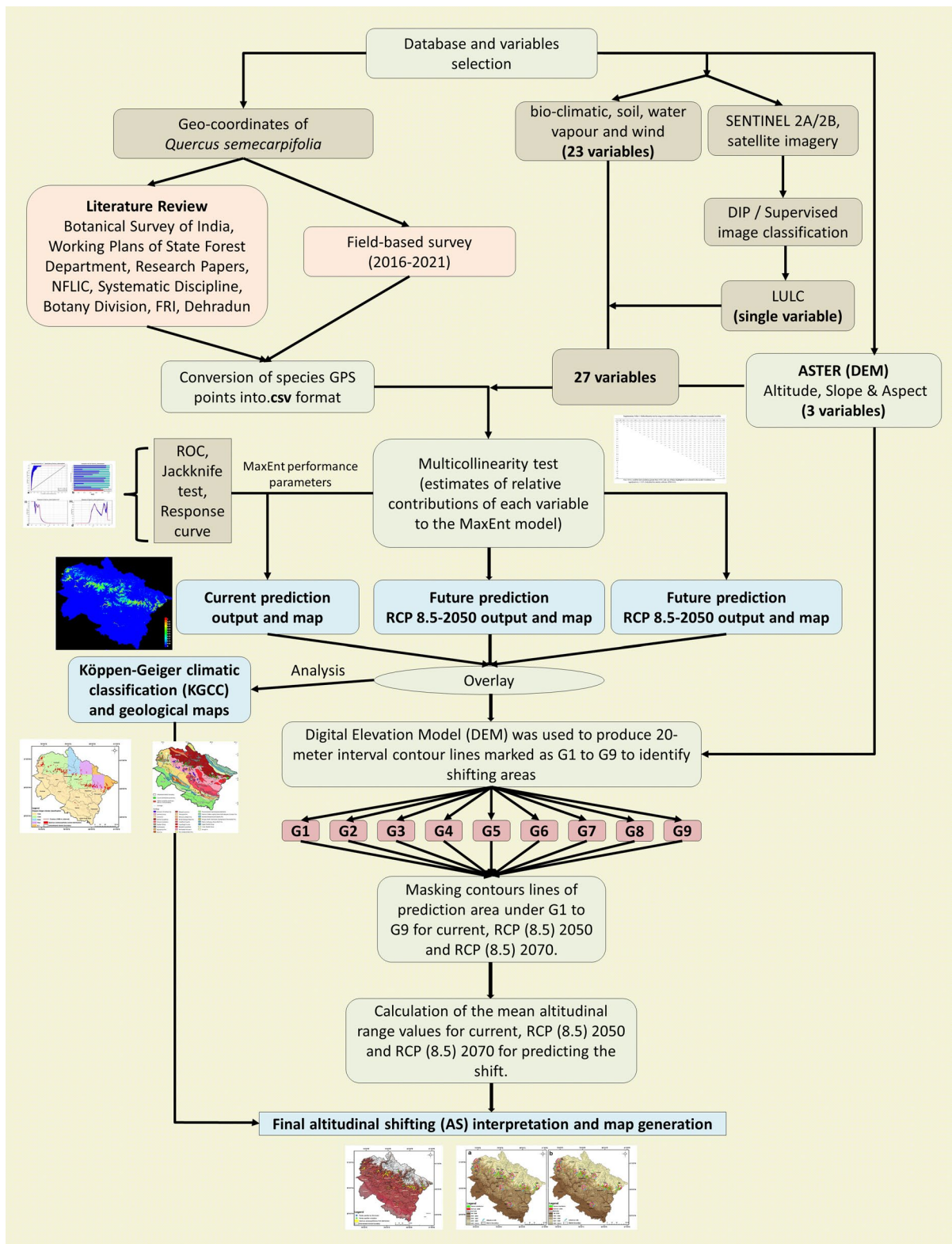


Fig. 1 Flow chart of database and methodology for the preparation of eco-distribution map and climatic shifts prediction

Table 1 Location of sites surveyed to assess the population of *Q. semecarpifolia* in different districts of Uttarakhand Himalayas

Sl. no.	Districts	Study sites	Geographical location [longitude (E), latitude (N) and altitudinal range (AR; m)]	Forest area types	Associated trees/shrubs species	Population status	Population distribution
1	Bageshwar	Jatoli village (On Pindari glacier way)	79° 55' 30.25" 30° 09' 32.75" 2340–2775	Rhododendron-Oak Forest	<i>Rhododendron arboreum</i> , <i>Quercus floribunda</i> , <i>Acer</i> spp.	Fair	Uniform
		Dwali-kafni/Kaphni (On kafni glacier way)	80° 21' 05.10" 30° 05' 21.95" 2400–2800	Rhododendron-Oak Forest	<i>Taxus wallichiana</i> , <i>R. arboreum</i> , <i>Q. floribunda</i> , <i>R. barbatum</i>	Pristine	Uniform
2	Chamoli	Kanchula Kharak, Gopeshwar	79° 14' 29.90" 30° 27' 11.50" 2400–2569	Rhododendron-Oak Forest	<i>R. arboreum</i> , <i>Q. floribunda</i> , <i>T. wallichiana</i> , <i>Acer</i> spp., <i>Fraxinus micrantha</i> , <i>R. barbatum</i> , <i>Carpinus viminea</i>	Healthy	Uniform
		Auli, Joshimath	79° 33' 53.80" 30° 31' 26.30" 2927–3038	Oak-Taxus Forest	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Cedrus deodara</i> , <i>Q. floribunda</i> , <i>F. micrantha</i>	Healthy	Uniform
		Bamni village, Badrinath	79° 29' 27.80" 30° 44' 18.14" 2761–3194	Birch-Oak Plantation	<i>Betula utilis</i> , <i>Pinus wallichiana</i>	Disturbed	Random
		Ghes, Dewal	30° 08' 34.40" 79° 43' 40.80" 2249–2417	Oak-Taxus Forest	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. floribunda</i> , <i>B. utilis</i> , <i>Q. leucotrichophora</i>	Disturbed	Random
		Rudranath, Gopeshwar	79° 18' 31.80" 30° 29' 11.40" 2340–3145	Rhododendron-Oak Forest	<i>R. arboreum</i> , <i>T. wallichiana</i>	Healthy	Uniform

Table 1 (continued)

Sl. no.	Districts	Study sites	Geographical location [longitude (E), latitude (N) and altitudinal range (AR; m)]	Forest area types	Associated trees/shrubs species	Population status	Population distribution
3	Dehradun	Bhujkoti, Chakrata	77° 54' 58.80" 30° 46' 52.40" 2550–2809	Oak-conifer Forest	<i>Acer</i> spp. <i>Cedrus deodara</i> , <i>R. arboreum</i> , <i>Lycium ovalifolia</i>	Healthy	Uniform
		Lokhandi, Chakrata	77° 49' 57.80" 30° 45' 30.40" 2560–2694	Oak-conifer Forest	<i>C. deodara</i> , <i>R. arboreum</i> , <i>Q. floribunda</i> , <i>Acer</i> spp.	Healthy	Uniform
		Mundhol, Tyuni	77° 45' 20.42" 30° 56' 34.25" 2664–2735	Oak- <i>Taxus</i> Forest	<i>R. arboreum</i> , <i>Q. floribunda</i>	Healthy	Uniform
		Balcha, Tyuni	77° 56' 31.22" 31° 04' 20.41" 2500–2817	Oak- <i>Taxus</i> Forest	<i>R. arboreum</i> , <i>L. ovalifolia</i> , <i>T. wallichiana</i>	Healthy	Uniform
		Deoban, Chakrata	77° 51' 58.03" 30° 44' 52.48" 2540–2857	Pine-Oak- <i>Taxus</i> Forest	<i>C. deodara</i> , <i>Picea smithiana</i> , <i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. floribunda</i>	Healthy	Uniform
4	Nainital	Naina peak, Nainital	79° 26' 08.08" 29° 24' 22.68" 2402–2611	<i>Rhododendron</i> -Oak –Pine Forest	<i>R. arboreum</i> , <i>Quercus lanata</i> , <i>Q. floribunda</i> , <i>C. deodara</i> , <i>Cupressus torulosa</i>	Fair	Uniform
		Kunjkhark, Pangot	79° 19' 40.78" 29° 30' 09.92" 2478–2546	<i>Rhododendron</i> -Oak Forest	<i>R. arboreum</i> , <i>C. deodara</i>	Fair	Uniform
5	Pauri	Dudhatoli, Thalिसain	79° 06' 10.11" 30° 03' 06.35" 2356–2500	Broad leaves mixed forest	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>L. ovalifolia</i> , <i>Picea smithiana</i>	Healthy	Uniform
		Chorikhal, Bharsar	78° 59' 35.99" 30° 02' 58.89" 2438–2623	<i>Rhododendron</i> -Oak Forest	<i>L. ovalifolia</i> , <i>R. arboreum</i> , <i>Q. floribunda</i>	Fair	Uniform

Table 1 (continued)

Sl. no.	Districts	Study sites	Geographical location [longitude (E), latitude (N) and altitudinal range (AR; m)]	Forest area types	Associated trees/shrubs species	Population status	Population distribution
6	Pithoragarh	Khaliya top, Munsiyari	80° 12' 45.14" 30° 03' 51.08" 2680–3175	Alpine meadow	<i>R. campanulatum</i> , <i>T. wallichiana</i> , <i>B. utilis</i> , <i>R. barbatum</i> , <i>Abies spectabilis</i> , <i>Abies pindrow</i> , <i>Q. floribunda</i>	Pristine	Uniform
		Narayan Ashram, Dharchula	80° 39' 18.43" 29° 58' 46.13" 2574–2881	<i>Rhododendron</i> -Oak Forest	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. lanata</i> , <i>Tsuga dimosa</i> , <i>P. wallichiana</i>	Healthy	Uniform
		Karndam Bugyal, Himkhola, Dharchula	80° 38' 54.87" 30° 01' 47.73" 2568–3652	Alpine meadow	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>B. utilis</i> , <i>Tsuga dimosa</i> , <i>Abies spectabilis</i>	Pristine	Uniform
7	Rudraprayag	Badhanital forest, Jakholi	78° 56' 47.02" 30° 29' 40.90" 2352–2460	<i>Rhododendron</i> -Oak Forest	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. leucotrichophora</i>	Fair	Uniform
		Chopta, Gopeshwar	79° 12' 07.12" 30° 29' 11.31" 2554–3285	<i>Rhododendron</i> -Oak Forest	<i>B. utilis</i> , <i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. floribunda</i> , <i>R. campanulatum</i> , <i>B. utilis</i>	Pristine	Uniform
		Triyuginarayan, Sonprayag	78° 56' 04.00" 30° 38' 05.00" 2371–3015	<i>Rhododendron</i> -Oak Forest	<i>R. arboreum</i> , <i>T. wallichiana</i>	Healthy	Uniform
8	Tehri	Nagtibba, Nainbagh	78° 08' 29.49" 30° 35' 08.20" 2421–2810	Oak- <i>Taxus</i> Forest	<i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. floribunda</i>	Pristine	Uniform
		Pinswar, Budhakedar	78° 40' 21.60" 30° 40' 53.50" 2328–3138	Oak- <i>Taxus</i> Forest	<i>R. arboreum</i> , <i>T. wallichiana</i>	Healthy	Uniform
		Pawalikantha, Ghuttu	78° 50' 22.00" 30° 40' 27.81" 2600–3100	Alpine meadow	<i>R. arboreum</i> , <i>R. campanulatum</i> , <i>T. wallichiana</i>	Healthy	Uniform

Table 1 (continued)

Sl. no.	Districts	Study sites	Geographical location [longitude (E), latitude (N) and altitudinal range (AR; m)]	Forest area types	Associated trees/shrubs species	Population status	Population distribution
9	Uttarkashi	Raditop, Barkot	78° 12' 38.99" 30° 45' 23.34" 2550–2703	Rhododendron-Oak Forest	<i>P. smithiana</i> , <i>R. arboreum</i> , <i>T. wallichiana</i> , <i>Q. floribunda</i> , <i>B. alnoides</i>	Fair	Random
		Chaurangi Khal, Uttarkashi	78° 30' 17.60" 30° 39' 53.40" 2524–2857	Rhododendron-Oak Forest	<i>Q. floribunda</i> , <i>R. arboreum</i> , <i>T. wallichiana</i>	Healthy	Uniform
		Yamunotri, Jankichatti	78° 27' 36.40" 30° 59' 42.60" 2693–2864	Broad-leaves mixed Forest	<i>R. arboreum</i> , <i>R. campanulatum</i> , <i>T. wallichiana</i> , <i>B. utilis</i>	Healthy	Uniform
		Bhukkitop, Bhatwari	78° 39' 37.20" 30° 50' 28.40" 2350–2937	Oak-Taxus Forest	<i>R. arboreum</i> , <i>T. wallichiana</i>	Healthy	Uniform

as random (where the trees were unevenly distributed in scattered or mixed forest) and uniform (dominant, gregariously present and evenly distributed). In addition, the data on tree associates in or nearby the sampling quadrat were also recorded for the phytocoenological analysis. In total, ten sample plots of 0.1 ha each were randomly laid out in every population. The species name and numbers were recorded in each plot (Mishra 1968). Density (individuals ha⁻¹) was calculated on the basis of data recorded in 29 sites. A heat map was developed for the species with its associates on the basis of density ratio.

Geoinformatics data and MaxEnt modelling

The recorded geospatial parameters were converted into point shape-file (.SHP) and transformed into a Keyhole Markup Language (KML) file, which was later used in Explore Google Earth for visible interpretation at the Forest Informatics Laboratory, FRI, Dehradun. Different bioclimatic variables representing annual trends in rainfall and temperature data, seasonality, and extreme environmental factors represented by wind and water vapour, were derived from WorldClim Ver. 2.1 (<http://www.worldclim.org>). Global Digital Elevation Model (GDEM) was

used to generate aspect, elevation and slope maps (Hijmans et al. 2005). Further, the data on direct normal irradiance (DNI) and pedologic variables were downloaded from the Solar Energy Center, Ministry of New and Renewable Energy (MNRE), Government of India, New Delhi (<https://maps.nrel.gov>) and the India Dataset of Soil and Water Assessment Tool (SWAT; <https://swat.tamu.edu/data/india-dataset/>), respectively. Lastly, the SENTINEL datasets (2A–2B; Supplementary Table 1) were downloaded from the United States Geological Survey (USGS) (<https://www.usgs.gov>). The softwares' ArcGIS Ver. 9.3 and QGIS were used for Digital Image Processing of the SENTINEL satellite data to compose False Colour Composite (FCC) image. To generate Land Use Land Cover map (LULC) of Uttarakhand Himalayas, the image was classified through features, such as forest (very dense, moderate and open), agriculture, barren land, settlements, scrubland and water body. All data were resampled in the same projection parameters as well in the same spatial resolution (30 arc second match with 27 layers representing bioclimatic and non-climatic parameters). Cumulatively, all these variables were subjected to multicollinearity test, where cross-correlation coefficient value greater than ± 0.70 was excluded to delineate common variables. As a

result, only 14 variables were used for the modelling purpose (Supplementary Table 2).

A model based on the maximum entropy (MaxEnt) was used for estimating the distribution and habitat suitability of *Q. semecarpifolia* with a set of 14 (current prediction) and 12 (two variables were removed due to their dynamicity in the future prediction scenarios) variables in MaxEnt Ver. 3.4.4 programme (Table 2; <https://www.cs.priceton.edu>). Using above-mentioned parameters, the model was allowed to run with 100 replicates for prediction mapping (Flory et al. 2012). Over the WorldClim dataset, out of 589 geo-coordinates, 413 were used for training (Blue in colour) and the rest ~30% (Green in colour) for validation (Fig. 2). Maximum number of background points (10,000) along with linear or quadratic or product (0.050), categorical (0.250), threshold (1.000) and hinge (0.500) features were used as input variables in the software (Phillips et al. 2004). Predictions from 100 models were averaged to produce the final map of probability to determine the presence of *Q. semecarpifolia*. Based on the bioclimatic data, the MaxEnt predicts high values for grid cells that are suitable for species occurrence. Afterwards, accuracy of the probability distribution was enhanced by masking the non-forest and the over-predicted area using FCM.

The model performance was evaluated by Area Under ‘Receiver Operating Characteristic (ROC)’ Curve (AUC) with values ranging between 0 and 1. The categorized models with values > 0.9 are considered as highly accurate in prediction modelling (Swets 1988). In addition, model accuracy and precision were also evaluated by calculating other measures, such as kappa coefficient (K), true skill statistic (TSS), sensitivity (Sn), specificity (Sp), prevalence (P). (Fielding and Bell 1997; Allouche et al. 2006). Further, the MaxEnt-derived response curves and Jackknife test were used to determine the relative contribution and permutation importance of each variable used in prediction modelling (Phillips et al. 2006).

As MaxEnt gives the probabilistic distribution of a species occurrence with probability ranging from 0 to 1, we chose a more conservative value of 0.7 to delineate species distribution. The remaining area with probability between 0.7 and 1.0 was retained to represent the probable sites of a species across its distribution range. A buffer of 1 km around the sampling point was used to calculate the actual sampled

distribution of *Q. semecarpifolia*. Additionally, the distribution map was overlaid on Köppen-Geiger climatic classification (KGCC; 1976–2000; Kottek et al. 2006) and the geological map (Geological Survey of India; <http://bhukosh.gsi.gov.in>). The KGCC describes the types of vegetation in a given geographical region, where the agroecological climatic conditions could be analyzed. Notably, the geological map reveals the edaphic factors and rock types influence on the distribution pattern of *Q. semecarpifolia*.

Determination of altitudinal shift

To assess the potential distribution shifts within a real landscape, we selected a geographical setting that met several criteria. First, we sought a site located in the eco-distribution map predicting future distribution shifts. The region must be characterized by: (a) available satellite coverage of forest habitat availability; (b) known tree distribution and density through sampled plots; (c) a minimum distance of 300 m span to cover the maximum landscape; and (d) variability in the relative amount of forest availability. Within Uttarakhand Himalayas, we selected a few sites for measuring the shifts in association with neighbouring tree species. The associated species varied in terms of the required abiotic and biotic constituents of the geographical sites, which might be affected by the life history attributes across the fragmented landscapes.

All landscape analysis and map production were conducted using the Geographical Information System (GIS)-based softwares. The altitudinal shift, i.e., projected area under *Q. semecarpifolia* was demarcated. This was measured using MaxEnt modelling prediction output by subtracting the projected area of the species under the two time-periods, i.e., RCPs 8.5 for 2050 and 2070 from the current occurrence. For future climate scenarios, the RCP 8.5 pathway arises from little effort to reduce emissions and represents a failure to curb warming by 2100 mentioned in the IPCC AR5 (<http://www.ipcc.ch/>), was selected. The RCP 8.5 is developed by the Model for Energy Supply Strategy Alternatives and their General Environmental Impact (MESSAGE) modelling team and the Integrated Assessment Framework at the International Institute for Applied Systems Analysis (IIASA), Austria (Rao and Riahi 2006; Riahi et al. 2007). Importantly, the RCP 8.5 is characterized by increasing greenhouse gas emissions over time and

Table 2 The AUC, permutation importance and the percentage contribution of different variables

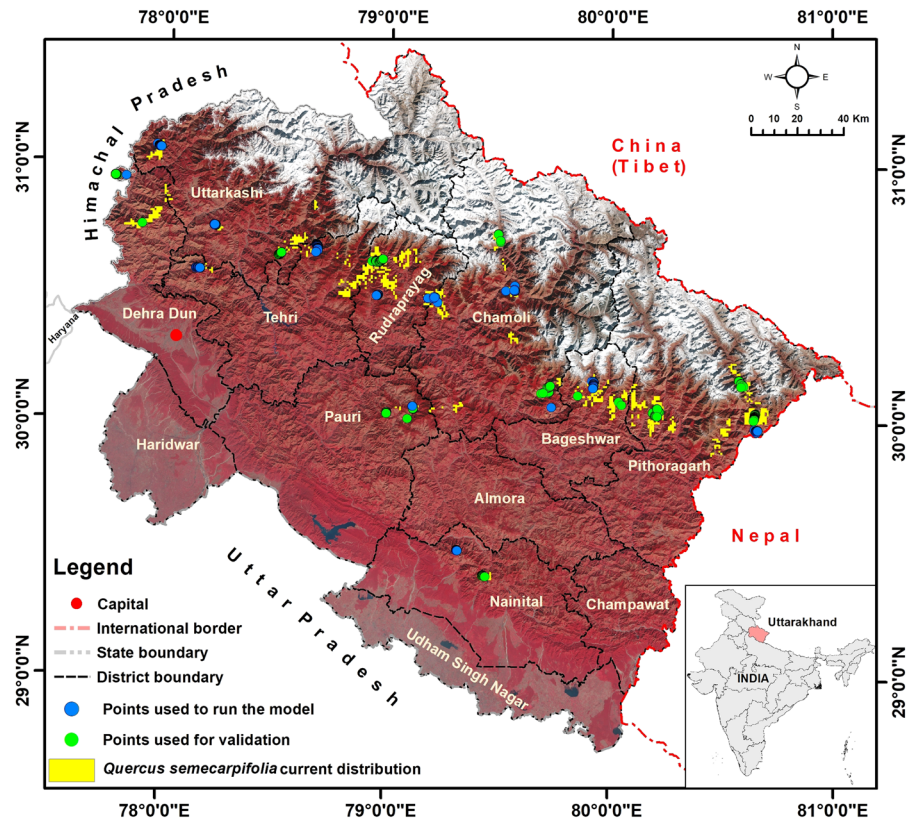
Label	Variables	Scaling factor	Units	Current		RCP 2050		RCP 2070	
				Percent contribution	Permutation importance	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Bio 1	Annual mean temperature	10	°C	–	–	–	–	–	–
Bio 2	Annual mean diurnal range	10	°C	3.8	3.8	2.3	2.0	2.4	4.7
Bio 3	Iso-thermality	100	°C	3.6	1.5	1.3	1.6	2.3	3.2
Bio 4	Temperature seasonality	100	C of V	–	–	–	–	–	–
Bio 5	Max. temperature of the warmest month	10	°C	–	–	–	–	–	–
Bio 6	Min. temperature of coldest month	10	°C	8.0	20.3	11.8	23.5	11.6	14.8
Bio 7	Annual temperature range	10	°C	30.3	12	26.5	3.4	29.1	2.9
Bio 8	Mean temperature of the wettest quarter	10	°C	–	–	–	–	–	–
Bio 9	Mean temperature of the driest quarter	10	°C	–	–	–	–	–	–
Bio10	Mean temperature of the warmest quarter	10	°C	–	–	–	–	–	–
Bio11	Mean temperature of the coldest quarter	10	°C	6.8	21.1	1.0	26.5	0.5	13.9
Bio12	Annual precipitation	1	Mm	–	–	–	–	–	–
Bio13	Precipitation of the wettest month	1	mm	2.5	1.8	12.5	10.7	1.6	14.7
Bio14	Precipitation of the driest month	1	mm	30.3	12.7	2.8	2.7	1.3	9.0
Bio15	Precipitation seasonality	100	C of V	–	–	–	–	–	–
Bio16	Precipitation of the wettest quarter	1	mm	–	–	–	–	–	–
Bio17	Precipitation of the driest quarter	1	mm	3.5	7.3	2.0	12.6	12.1	15.2
Bio18	Precipitation of the warmest quarter	1	mm	–	–	–	–	–	–
Bio19	Precipitation of the coldest quarter	1	mm	–	–	–	–	–	–
Alt	Altitude		m	1.9	14.1	19.8	10.1	18.6	18.1
Slop	Slope		°	3.1	1.3	2.0	1.4	2.2	0.7
Asp	Aspect		°	–	–	–	–	–	–
Dni	Direct NormalIrradiance		W m ⁻²	–	–	–	–	–	–
Soil	Soil			3.8	0.7	17.9	5.4	18.4	2.9
LULC	Land Use Land Cover			1.9	0.3	–	–	–	–

Table 2 (continued)

Label	Variables	Scaling factor	Units	Current		RCP 2050		RCP 2070	
				Percent contribution	Permutation importance	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Wind	Wind		(m s⁻¹)	0.5	3.1	–	–	–	–

The boldly written variables, selected through multicollinearity test, were used in modelling

Fig. 2 MaxEnt model generated distribution of *Q. semecarpifolia* on SENTINEL in northwestern Himalayas



represents scenarios in the literature leading to high greenhouse gas concentration levels.

In each district, geographical areas (regions) on the map (qualitative data) were identified. After that, the GDEM was used to produce 20 m interval contour lines marked as G1 to G9, covering the entire nine areas where the shift was presumed to have occurred. Further, the area between two time periods, i.e., RCP 8.5 2050 and 2070, was masked through contour lines. For the nine regions, a circular plot of diameter 3.14 km was laid on the final output map for calculating the average elevation covered in the presumed area of shift. In the next step, masked contour lines

representing elevation were calculated to find the average value of current prediction. Similarly, the same method to determine the average elevation was applied for RCP 8.5 2050 and 2070. Afterwards, the contemporary habitat suitability and average altitudinal range of *Q. semecarpifolia* were compared with that of the projected RCPs. Herein, the altitudinal shift for the entire distributional range was calculated in a probabilistic manner by subtracting the differences in the average value of the altitude between RCP 8.5 (2050) and the current prediction; as well as RCP 8.5 (2070) and current prediction. The maximum and minimum value of the altitudinal shift were

marked in the probability range of 0–1. The same methodology of shift calculation was applied for *R. arboreum* in the western Himalayas (Veera et al. 2019).

Results

Field surveys, distribution status and associated species of *Q. semecarpifolia*

A total of 29 sites distributed in nine districts of Uttarakhand, India was surveyed from 2016 to 2021. Only one site near *Badrinath* shrine in district Chamoli was planted whilst the rest 28 sites were naturally inhabited. Field surveys revealed that the species altitude ranged from 2249 (Ghes, Chamoli) to 3652 m (Karandam Bugyal, Pithoragarh). Out of 29 sites explored for population distribution, 12 new sites were explored, i.e., not described in the findings of earlier research work. Further, 26 sites showed uniform and three had a random distribution. The majority of the surveyed populations were under fair and healthy status (Table 1), but inadequate seedling recruitment was observed during the expedition.

The populations of *Q. semecarpifolia* were distributed across a wide altitudinal gradient in Uttarakhand Himalayas, where it has been associated with 19 tree species (Table 3). Due to wide-ranging distribution and broad species associations, it forms a key component of distinct forest types and landscapes, like tree lines, dominating zones in temperate forest, mixed forests and climatic-climax vegetation. The data acquired in the lower altitude range (2000–2500 m) indicated fragmented and disturbed population status. However, the middle (2500–3000 m) and higher (3000–3500 m) range showed uniform distribution with healthy population status. The species in the lower elevation zone assembled with mixed forestry species, such as *Cedrus deodara*, *Lyonia ovalifolia*, *Q. floribunda*, *Q. leucotrichophora* and *Rhododendron barbatum*. Composition of association in temperate regions were shown by *Acer caesium*, *Fraxinus micrantha*, *Q. floribunda*, *R. arboreum* and *Taxus wallichiana* as a middle-storey trees; whilst *Abies pindrow*, *Picea smithiana*, *Pinus wallichiana* and *Q. lanata* can be classified as upper-storey vegetation. Finally, in higher reaches of the subalpine zone, the species commonly occurs with *Betula utilis* as a

middle-storey tree; and *A. spectabilis* as an upper-storey tree, whereas *R. campanulatum* shrub was present as a ground-based lower-vegetation.

The density per hectare of *Q. semecarpifolia* associates were calculated in a total of 29 geographical sites and a heat map was also generated (Fig. 3). Overall, a tree density of 673 individuals ha⁻¹ was recorded in the populations of *Q. semecarpifolia*. Field surveys and density data indicate that the species is mainly associated with *R. arboreum* (abundance in 27 sites; 60 trees ha⁻¹), *T. wallichiana* (abundance in 21 sites; 48 trees ha⁻¹) and *Q. floribunda* (abundance in 15 sites; 25 trees ha⁻¹). However, minimum density of association was recorded with *P. wallichiana* (2 sites; 5 trees ha⁻¹). Further, the heat map validated the density ratio of the associated species with respect to *Q. semecarpifolia*, where the highest density ratio (0.1000) was observed with *R. arboreum* followed by *T. wallichiana* (0.0700), *Q. floribunda* (0.0367), *L. ovalifolia* (0.0299) and *B. utilis* (0.0293). The lowest density ratio (0.0075) was associated with *P. wallichiana* followed by *C. torulosa* (0.0135), *R. barbatum* (0.0136), *Q. leucotrichophora* (0.0138) and *A. pindrow* (0.0145).

Validation and prediction of the MaxEnt model

A total of 589 geo-coordinates were recorded in nine districts of Uttarakhand based on species occurrence. Of these, 413 (~70%) geo-coordinates were used for training and the remaining 176 were used for validation of the MaxEnt model. In the modelling exercise, when the 176 geo-coordinates of the test data set overlaid on the predicted species distributions, a total of 150 (~85%) of the test data points fell within the predicted area. This reveals a high level of accuracy in prediction and estimation of distribution (Supplementary Fig. 1a; Supplementary Table 3). Notably, the prediction output revealed an actual area of validation for the model, where maximum percentage of geo-coordinates falls in the districts Chamoli and Pithoragarh (88.89%) and minimum in Nainital (60.00%).

Out of 27 environmental variables, 14 were selected through the multicollinearity test to run the MaxEnt programme for current prediction, whereas 12 of them were used for future prediction (Table 2). Herein, the assessment of literature survey and ground-based assessment of the forest types

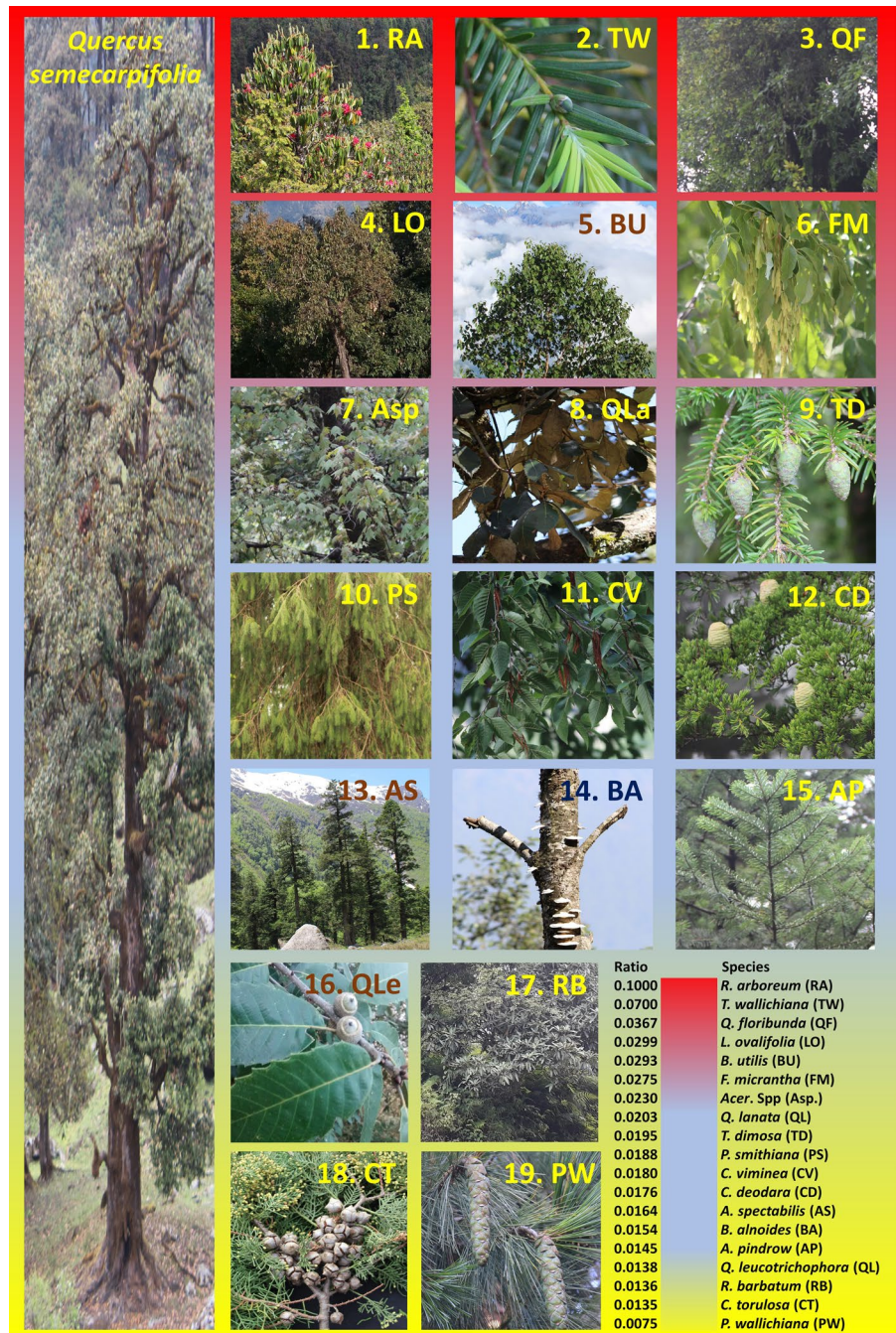
Table 3 Density of the associated tree species and *Q. semecarpifolia* with corresponding ratio

Sl. no.	Associate species	Vernacular name	Altitudinal range (Troup 1921; Luna 1995)	Altitudinal range of associates in our surveys	Overall trees density of associated species (individual ha ⁻¹) (A)	Overall density of <i>Q. semecarpifolia</i> (individual ha ⁻¹) (B)	Density ratio (A B ⁻¹)
1	<i>A. pindrow</i> (AP)	Fir	2250–3350	2700–3300	10	689	1:69
2	<i>Acer. spp.</i> (Asp.)	Maple	1800–2500	2300–2700	16	696	1:44
3	<i>A. spectabilis</i> (AS)	East Himalayan fir	2600–3800	2700–3200	11	670	1:61
4	<i>B. alnoides</i> (BA)	Indian birch	900–3000	2300–2600	10	650	1:65
5	<i>B. utilis</i> (BU)	Bhojpatra	3500–4200	3150–3610	19	648	1:34
6	<i>C. deodara</i> (CD)	Deodara	1800–2600	2255–2500	12	681	1:57
7	<i>C. torulosa</i> (CT)	Himalayan cypress	1800–2750	2300–2700	09	665	1:74
8	<i>C. viminea</i> (CV)	Himalayan Hornbeam	1800–2700	2300–2400	12	667	1:56
9	<i>F. micrantha</i> (FM)	Aangu	2100–3000	2270–2500	19	690	1:36
10	<i>L. ovalifolia</i> (LO)	Ayar	1500–3000	2280–2700	20	669	1:33
11	<i>P. smithiana</i> (PS)	Spruce	2150–3350	2500–2850	13	690	1:53
12	<i>P. wallichiana</i> (PW)	Kail	2000–3000	2600–2900	05	666	1:13
13	<i>Q. floribunda</i> (QF)	Moru	2000–2500	2249–2450	25	681	1:27
14	<i>Q. lanata</i> (QL)	Rianj	2200–2600	2300–2500	14	688	1:49
15	<i>Q. leucotrichophora</i> (QLe)	Banj	800–2300	2260–2300	09	654	1:73
16	<i>R. arboreum</i> (RA)	Burans	1500–3300	2289–2800	60	600	1:10
17	<i>R. barbatum</i> (RB)	Chimal	2700–3700	2550–2800	09	663	1:74
18	<i>T. wallichiana</i> (TW)	Thuner	2500–3200	2550–3100	48	686	1:14
19	<i>T. dimosa</i> (TD)	Tansen	1500–2700	2500–2800	13	666	1:51

(Champion and Seth 1968), assist in choosing the best possible 12 variables in the prediction modelling of *Q. semecarpifolia*. In the current prediction, the average test AUC value for the replicate runs was 0.943 ± 0.059 , which indicates high performance of the model for test data, and best fit with the variables chosen in the study (Fig. 4a). Additionally, the values of classification accuracy measures were 0.504 and 0.723 for *K* and TSS, respectively. However, other precision measures were also analyzed and shown in Supplementary Table 4. On the basis

of response curves and Jackknife test, environmental variables, such as annual temperature range (Bio 7), precipitation of the driest month (Bio 14), minimum temperature of the coldest month (Bio 6), and mean temperature of the coldest quarter (Bio 11), were statistically significant predictors of the current species distribution with an overall percentage contribution of 68.20% [Fig. 4b, c(i) and (ii)]. Further, for future (2050 and 2070) predictions, variables, namely annual temperature range (Bio 7), altitude (Alt) and soil, revealed significant information with

Fig. 3 Heat map showing ratio of density of tree associates with respect to *Q. semecarpifolia* in the north-western Himalayas. Highest and lowest ratio of density of associates shown above and below, respectively



the percentage contributions of 64.20% and 66.10%, respectively.

Conspicuously, the species occurrence areas were mapped on the SENTINEL image using ArcGIS, QGIS and Explore Google Earth Pro imagery tools (Fig. 2). The results showed that *Q. semecarpifolia* occupies an actual area of ~212 km²,

derived on the basis of a 1 km buffer zone created with sampled geo-coordinates. However, a total area of ~832 km² was predicted through the MaxEnt model, which was 1.56% of the total geographical area and 3.43% of the forest cover of the state Uttarakhand (Table 4). Overall, for the species, the predicted area (~250 km² during 2050) was maximum

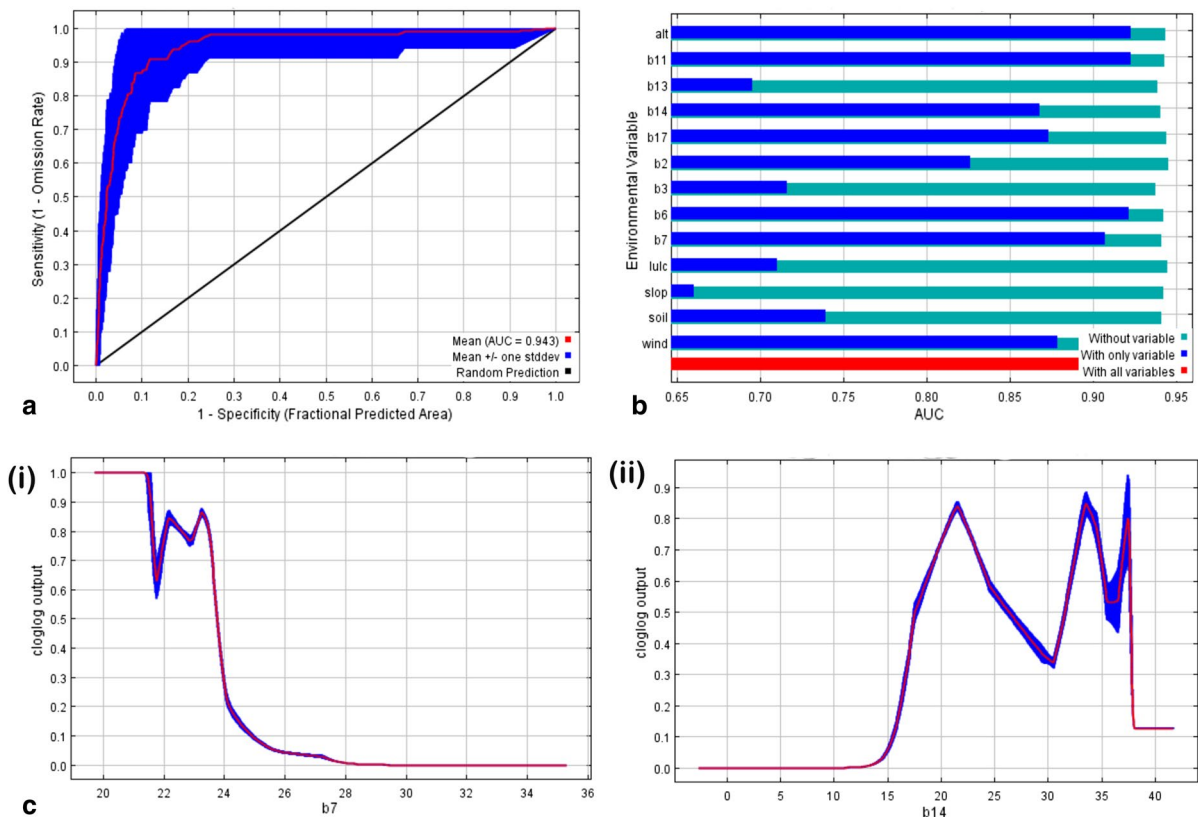


Fig. 4 MaxEnt model output derived using different bioclimatic variables: **a** AUC; **b** Jackknife test; and **c** Response curve (i) Bio 14 and (ii) Bio 7

in Pithoragarh and minimum ($\sim 17 \text{ km}^2$ current prediction) in Nainital.

Furthermore, the aerial distribution was categorized into very dense ($\sim 188 \text{ km}^2$), moderately dense ($\sim 523 \text{ km}^2$) and open forest ($\sim 120 \text{ km}^2$). In another exercise, the area was classified in accordance with different elevation zones. The highest estimate of $\sim 368 \text{ km}^2$ was recorded in the range of 2500–3000 m, where the species grew in mixed forest with *R. arboreum*, *T. wallichiana*, *A. pindrow*, *P. smithiana* and *P. wallichiana*. Secondly, an area of $\sim 270 \text{ km}^2$ was noted for *Q. semecarpifolia* in the lower range between 2000 and 2500 m, overlapping mainly with *Q. floribunda*, *Q. leucotrichophora*, *Q. lanata*, *Acer* sp. and *R. arboreum* forest. Lastly, at higher altitudinal gradient (3000–3500 m), a lowest prediction of $\sim 193 \text{ km}^2$ was recorded, where tree line communities, such as *A. spectabilis*, *B. utilis*, *Juniper* spp. and *R. campanulatum*, were the major associates.

Globally, the climatic regimes of the study area resemble the continental regions in South America, North America, Europe, South Africa, and Asia, where various species of Oaks are presently distributed. The current distribution of *Q. semecarpifolia* was then overlaid on KGCC map to reveal the association between species distribution and climatic conditions. The area is classified into five subtypes (Fig. 5), where *Q. semecarpifolia* occurs throughout the region except in the tropical plains. However, maximum occurrence was found in subtropical highland oceanic climate (Cwb; C = warm temperate, w = winter dry, and b = warm summer) of middle and upper Himalayas constituted by northwestern Bageshwar, southern Chamoli, small stretch of northeastern Pauri, southeastern Rudraprayag, northern Tehri and Uttarkashi. The second prominent distribution occurs in sub-arctic climate (Dwc; D = Snow, w = winter dry, and c = cool summer) conditions of eastern Bageshwar, northern Chamoli, and northern Pithoragarh. Notably,

Table 4 Estimated area of *Q. semecarpifolia* under current prediction and climate change scenarios in different districts of Uttarakhand through MaxEnt Modelling

Sl. no.	Districts	Geographical area (FSI 2019)	Forest cover (km ²) (FSI 2019)	Maxent predicted present area		RCP 8.5 (2050) predicted area		RCP 8.5 (2070) predicted area	
				In (km ²)	% w.r.t GA	In (km ²)	% w.r.t GA	In (km ²)	% w.r.t GA
1	Almora	3144	1719.14	—	—	—	—	—	—
2	Bageshwar	2241	1262.69	69.78	3.11	58.7	2.62	45.62	2.04
3	Chamoli	8030	2709.43	198.96	2.48	76.29	0.95	58.79	0.73
4	Champawat	1766	1225.55	—	—	—	—	—	—
5	Dehradun	3088	1608.69	75.18	2.43	65.79	2.13	60.61	1.96
6	Haridwar	2360	585.25	—	—	—	—	—	—
7	Nainital	4251	3041.56	17.58	0.41	28.03	0.66	24.38	0.57
8	Pauri	5329	3394.99	50.96	0.96	25.34	0.48	19.51	0.37
9	Pithoragarh	7090	2079.80	139.48	1.97	250.11	3.53	235.05	3.32
10	Rudraprayag	1984	1142.17	83.08	4.19	119.54	6.03	110.12	5.55
11	Tehri	3642	2065.98	81.19	2.23	38.82	1.07	32.20	0.88
12	Udham Singh Nagar	2542	431.79	—	—	—	—	—	—
13	Uttarkashi	8016	3036.00	116.19	1.45	90.67	1.13	77.86	0.97
Total		53,483	24,303.04	832.40	1.56	753.29	1.41	664.14	1.24

Fig. 5 Plot of current MaxEnt prediction over the Köppen-Geiger Climatic map. Where: *Cwa* Warm temperate winter dry hot summer, *Cwb* Warm temperate winter dry warm summer, *Dfc* Snow fully humid cool summer, *Dwb* Snow winter dry warm summer, *Dwc* Snow winter dry cool summer, *ET* Polar tundra



a lesser distribution occurs in the humid subtropical climate (*Cwa*; C=warm temperate, w=winter dry, and a=hot summer) of the upper reaches of Dehradun and Nainital.

Altitudinal shifts in the habitable zone of *Q. semecarpifolia*

In the MaxEnt model output of the future climatic RCP 8.5 scenario of 2050 and 2070 (Supplementary Fig. 1b, c), an altitudinal shift was predicted in the habitable zone of *Q. semecarpifolia* (Fig. 6a, b). The range of suitable habitat showed a trend of northwards and an upward shifting (10–115 m) in Uttarakhand. For instance, in district Dehradun, a shift in the altitude of 30 m ($Av.=2675$ m; 2050) and 40 m ($Av.=2685$ m; 2070) has been observed when compared to the current predicted altitude of 2645 m (Supplementary Fig. 2). However, the proportion of suitable habitat for species varied under the RCP (8.5) of the two projected climate scenarios (2050 and 2070) revealed a steady decline in the suitable climatic habitat (area) of *Q. semecarpifolia* (Table 5). Also, the model predicted a change towards the north

and higher elevational zones for suitable habitat, with a climatic shift range from 10–115 m to 15–105 m for 2050 and 2070, respectively. Overall, a probability shift of 0.09–1.00 (2050) and 0.13–0.91 (2070) was observed for the climate change scenarios, with maximum altitudinal shift of 115 m noted in district Bageshwar and Pithoragarh; whereas, lowest shift (10 m) was observed in Rudrapur. In both RCPs, the climatic niche showed a reduction of ~ 79 km² (2050) and ~ 168 km² (2070) as compared to the baseline scenario (currently predicted).

Correlation of rock type occurrence to the distribution of *Q. semecarpifolia*

The current distribution and future predictions of *Q. semecarpifolia* were compared to the rock types occurring in the geological map of Uttarakhand (Fig. 7). Different rock types form soils with varying chemical and physical properties, which in turn may be favourable or unfavourable for species growth and expansion. The geological analysis indicated an interesting correlation between the edaphic factors and the occurrence of rock types influencing the distribution

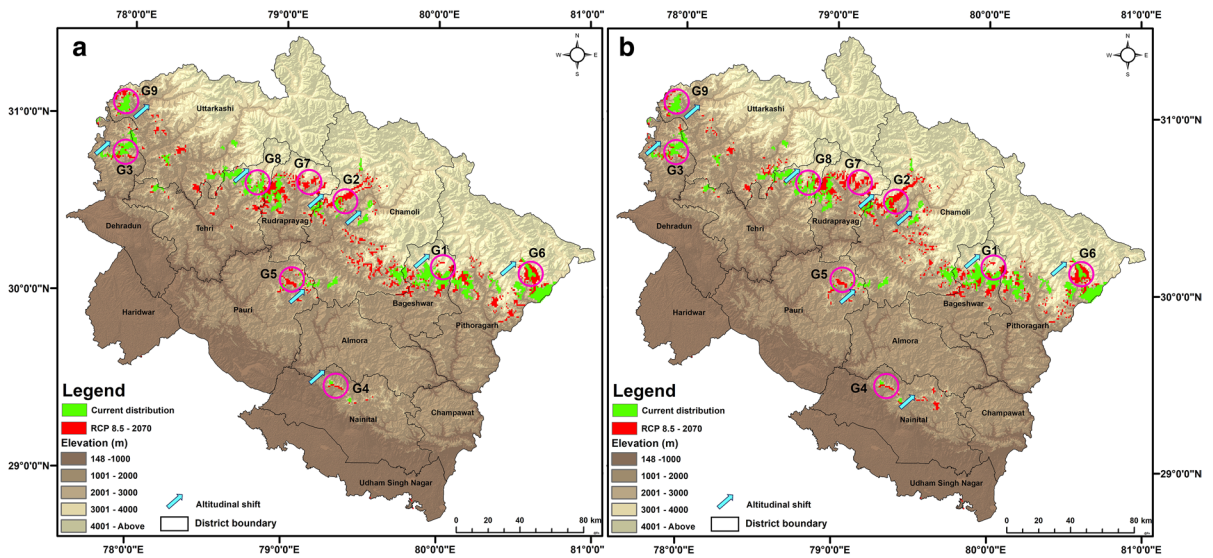


Fig. 6 Representation of future climatic habitat shifts of *Q. semecarpifolia* in the northwestern Himalayas: **a** RCP 8.5_2050; and **b** RCP 8.5_2070

pattern of *Q. semecarpifolia* via soil composition. With respect to the ecology and habitat suitability of *Q. semecarpifolia* in the Himalayas, it was observed that the soils where the species grow tend to have slightly acidic pH. Less acidic soils are formed by the weathering of acidic parent rocks, such as granite and rhyolite. Alternatively, the weathering of basic rocks, such as limestone, marble or chalk will result in alkaline soils. Accordingly, in the geological map (Fig. 7), the occurrence of *Q. semecarpifolia* corresponds to the occurrence of crystalline rocks, such as the Central Crystallines and Garhwal Group (volcanics) at sites 1, 2, 3 and 5, as well as to the Almora Crystallines and Bawali volcanics at site 4. Exceptions occur at the sites 6 and 7, where the mainly occurring Jaunsar Group and associated formations contain limestone and marble that will form alkaline soils. It is important to notice, however, that in spots 6 and 7, the local drainage flows from the crystalline and volcanic rocks located northward. Hence, sediment transport and water acidity may influence the acidity of soils along river margins and flooding areas. The species does not occur or is very scarce over rock groups where limestone is highly abundant, such as in the northeast, southwest and south of the state. When lithology is compared to our results of habitat suitability prediction modelling for 2070, the general trend towards higher altitudes was observed in sites

1, 2, 3, 4 and 5, where acid rocks prevail, and was not observed in sites 6 and 7, where alkaline rocks start to occur.

Discussion

The broad-leaved evergreen *Q. semecarpifolia* usually form abrupt treelines at several locations in the western Himalayas (Körner 2012). Climate change-induced alterations and regeneration problems for this species in the last few decades have been further exaggerated by the ever-increasing human-population impacts (Shrestha 2003; Negi and Negi 2021). The present work represents a first ever attempt to model the impacts of future climate change, species association and topographical factors, on the spatial distribution of this important flagship tree species of the Himalayan region.

Associated species and eco-distribution mapping of *Q. semecarpifolia*

Oaks are an important member of broad-leaved forests of western Himalayas; where they grow gregariously either in pure or mixed-forest (Singh and Singh 1986). Based on the ground surveys, we recorded an altitudinal range of 2249–3652 m for *Q. semecarpifolia*,

Table 5 Current and projected climatic altitudinal range and shift prediction of *Q. semecarpifolia*

Sl. no.	Geographical locations	Sampled altitudinal range ^s (X) (m)	Average of X (A) (m)	Future climatic altitudinal range and shift (m)							
				RCP 8.5 (2050) (Y)	Average of Y (B)	Shift (A–B) (0–1)	Probable shift (0–1)	RCP 8.5 (2070) (Z)	Average of Z (C)	Shift (A–C)	Probable shift (0–1)
1	(G1) Bageshwar	2370–3040	2705	2420–3220	2820	115	1.00	2400–3220	2810	105	0.91
2	(G2) Chamoli	2860–3680	3270	3000–3710	3355	85	0.74	2840–3730	3285	15	0.13
3	(G3) Dehradun	2300–2990	2645	2360–2990	2675	30	0.26	2370–3000	2685	40	0.35
4	(G4) Nainital	2300–2580	2440	2390–2580	2485	45	0.39	2390–2550	2470	30	0.26
5	(G5) Pauri	2320–2680	2500	2350–2670	2510	10	0.09	2380–2650	2515	15	0.13
6	(G6) Pithoragarh	2640–3640	3140	2800–3710	3255	115	1.00	2580–3800	3190	50	0.43
7	(G7) Rudrapurayag	2370–3520	2945	2360–3620	2990	45	0.39	2390–3680	3035	90	0.78
8	(G8) Tehri	2380–3140	2760	2440–3210	2825	65	0.57	2400–3260	2830	70	0.61
9	(G9) Uttarakashi	2400–3220	2810	2430–3340	2885	75	0.65	2380–3370	2825	15	0.13
Overall range		2300–3680	2440–3270	2350–3710	2485–3355	10–115	0.09–1.00	2370–3800	2470–3285	15–105	0.13–0.91

^sDetermined on the basis of qualitative data, where a grid circle of 3.14 km was laid out over the SENTINEL satellite-based map (Fig. 6a, b)

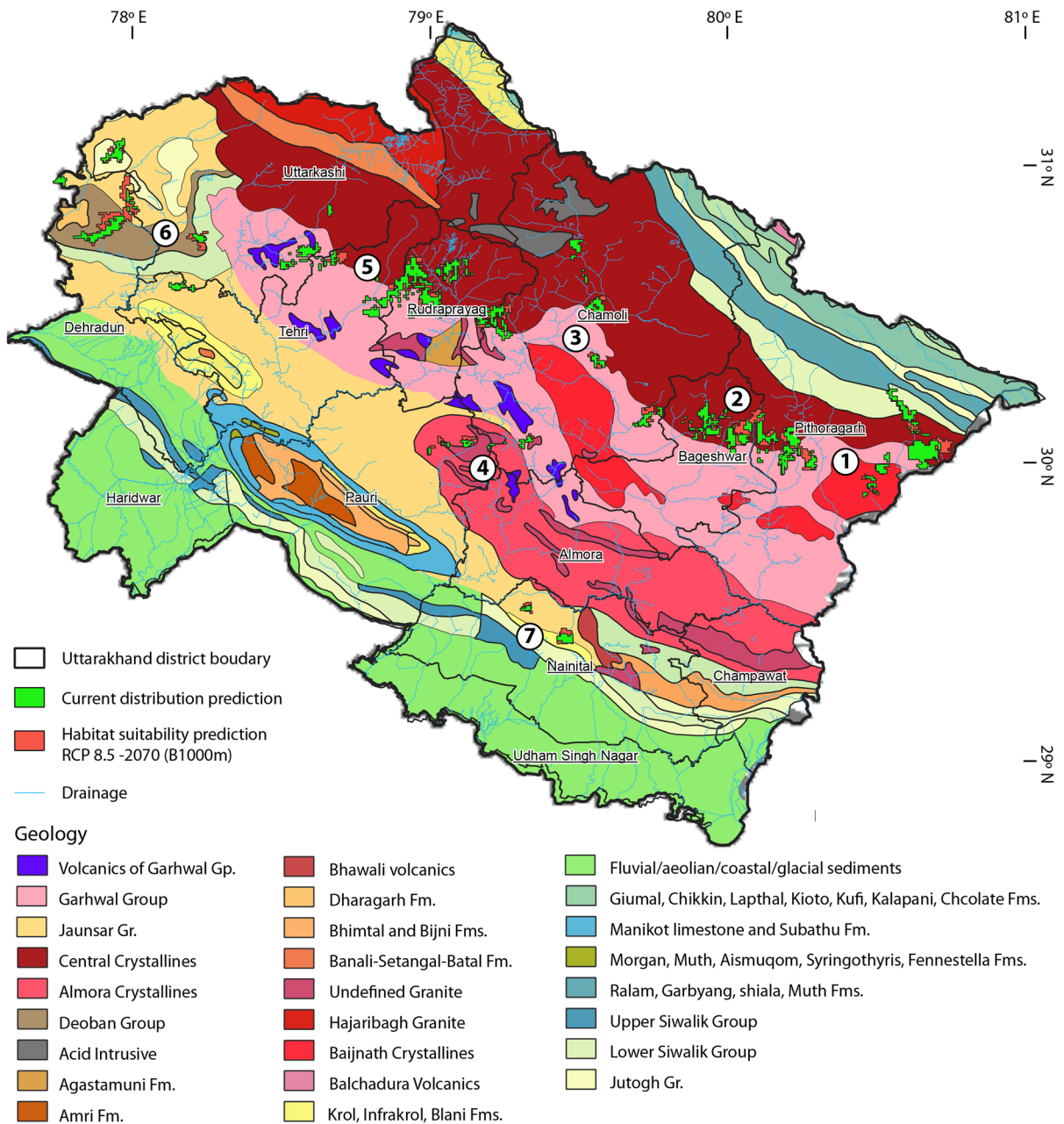


Fig. 7 Geological map of Uttarakhand, India, with overlaid current distribution and future predictions (2070) of *Q. semecarpifolia*

which is in accordance to the other studies conducted in IHR (Negi and Naithani 1995; Orwa et al. 2009). In our surveyed sites, *Q. semecarpifolia* was found to be associated with 19 tree species, where *T. dimosa* was observed for the first time in Narayana Ashram (Pithoragarh). The majority of *Q. semecarpifolia* populations were gregarious with a total density of 673

individuals ha⁻¹, which is in accordance with other studies conducted on vegetation analysis for Oaks in the region (Singh and Singh 1986; Tiwari et al. 2018). Maximum numbers of stands were associated with *R. arboreum* and *T. wallichiana*, as moisture conditions favour both the species. Importantly, the alliance of *R. arboreum* with *Q. semecarpifolia* may be attributed to

the wide altitudinal range (Bhandari et al. 2020a). In the forest areas, we have physically observed the presence of dense populations consisting of old and middle-aged trees, which suggested that frequent monitoring will help to understand the dynamics of the *Q. semecarpifolia* populations in context of anthropogenic factors, ecological attributes and climate change alterations. Notably, the regeneration status of Oaks is determined by monitoring and evaluating the newly emerging seedlings or saplings in the forests (Joshi and Samant 2004; Caignard et al. 2017). In spite of intensive surveying of various populations with different status (undisturbed to little disturbed), new recruits of *Q. semecarpifolia* were inadequately observed (Singh and Singh 1992; Negi and Negi 2021). For instance, literature revealed that *Q. semecarpifolia* shows masting in 8–10 years, which probably compounded the problem due to vivipary and die-back (Troup 1921; Singh et al. 2011). All these considerations highlight the importance to predict and map the species in current and future prospects.

This study provides a detailed eco-distribution map revealed through MaxEnt modelling approach, which estimated an area of ~832 km² under *Q. semecarpifolia*. In total, 589 geo-coordinates were used in prediction modelling, a very high number in comparison to the data points used in earlier studies in the Garhwal Himalayas (Shekhar et al. 2017). The performance of the model output was supported by a significantly high value of AUC (0.943 ± 0.059). Importantly, values around 0.5 indicate optimum performance as compared to random models, whilst values closer to 1.0 indicate quality model performance. Likewise, the MaxEnt with higher output of AUC was used to map the ecologically and economically dominant forest tree species, such as *B. utilis*, *Cedrus deodara*, *Q. incana*, *Q. dilatata*, *R. arboreum*, *P. smithiana* and *P. roxburghii* (Sharma 2014), and *Q. semecarpifolia* (0.899 ± 0.02) (Singh et al. 2021) in Himachal Pradesh; *Q. leucotrichophora* (0.80 ± 0.020), *Q. floribunda* (0.98 ± 0.006), *Q. semecarpifolia* (0.97 ± 0.008) in Kumaun Himalayas (Chakraborty et al. 2016); *M. esculenta* (0.95 ± 0.020) (Shankhwar et al. 2019); *R. arboreum* (0.88 ± 0.023) and *Q. lanata* (0.982 ± 0.021) (Bhandari et al. 2020a, b), and *Q. leucotrichophora* (0.876 ± 0.002) (Dhyani et al. 2020) in Uttarakhand Himalayas. High AUC indicates the significant contribution and overall suitability of the variables chosen for modelling the Himalayan tree species, in

accordance with the AUC prediction values in conservation presence/absence models (Fielding and Bell 1997). In any model, the AUC values are generally high if the species under study is restricted to a specific region or environmental niche. Whereas, species with wide and broad distribution ranges typically exhibit low AUC values (Elith et al. 2011; Phillips et al. 2006). Notably, the classification accuracy measures revealed a value of 0.504 for *K*, which is in fair agreement with Landis and Koch (1977), and 0.723 for TSS, which indicates perfect agreement and high performance of the model (Allouche et al. 2006). The model clearly supported a more defined and restricted ecological niche for *Q. semecarpifolia* in the study area of the northwest Himalayan mountains.

In our approach, a multicollinearity test was performed on 27 bioclimatic and non-climatic variables. These were later reduced to 14 by eliminating the overly dependent variables, thus, enhancing the accuracy in prediction assessment. The precipitation (Bio 14) and temperature (Bio 7, Bio 6 and Bio 11) variables contributed (68.20%) significantly for current distribution. Incongruity to our results, variables, such as Alt, Bio 7 and Bio 19 in Kumaun Himalayas (Uttarakhand) (Chakraborty et al. 2016); Bio 19, Asp, Bio 4 and Bio 12 in Great Himalayan National Park (Himachal Pradesh) (Singh et al. 2021), were used in prediction mapping of *Q. semecarpifolia*, which signifies that annual temperature fluctuation, i.e., minimum and maximum temperature extremes have profound effect on depicting the ecological niche of a species. Similarly, *Q. aegilops* distribution is maximally depicted by Bio 12 (45.4%), Asp (19.9%), Bio 1 (13.5%), and Slo (15.1%) in Iraq (Khwarahm 2020), justifies that Oaks distribution is majorly govern by precipitation and topographical factors. Overall, the modelling-based on Bio 14, Bio 7, Bio 6, Bio 11 and Bio 12 as the most influential variables used in the prediction modelling studies of Oaks. Further, when the current species distribution was overlaid on the KGCC map, the Cwb and Dwc emerged as the most preferable climatic type, which revealed that dry winter conditions prevail in most of the habitat. Similarly, the distribution pattern of *Q. ilex* in France Mediterranean region and Pakistan shows these climatic regimes (Delzon et al. 2013; Gilani et al. 2020). Here, the KGCC map helps to understand the relationship between the species occurrence and favouring climatic conditions, which is based on the threshold

values derived from seasonality of monthly air temperature and precipitation (Beck et al. 2018).

Altitudinal shifts and its effect in the habitable zone of *Q. semecarpifolia*

The MaxEnt model was used to predict the distribution and the future climatic shift, i.e., RCP 8.5 (2050 and 2070) of *Q. semecarpifolia* with 12 variables, where most influential ones were Bio 7, Alt and soil. Both periods have shown a reduction of ~79 km² and ~168 km² as compared to the baseline scenario of ~832 km², revealing suitable habitat with an upslope probability shift range of 0.09–1.00 (2050) and 0.13–0.91 (2070) towards the northwestern direction. The probable shift has been calculated through the methodology applied in *R. arboreum* (Veera et al. 2019), *Q. leucotrichophora* (Dhyani et al. 2020) and *Q. semecarpifolia* (Singh et al. 2021). However, the predicted future ranges of 2360–3710 m (RCP 8.5_2050) and 2370–3800 m (RCP 8.5_2070) implies that the lower habitats of Shivalik and middle Himalayas may have undergone shrinkage or decline due to unfavourable climatic and anthropogenic-driven factors. On the other hand, in higher elevation zones, the range may expand up to timberline. Interestingly, by correlating altitudinal shift prediction with the KGCC map of *Q. semecarpifolia*, most of the populations showed migration from climate type Cwb to Dwc, further validating the results. Previously, KGCC was used to investigate the potential changes in the future vegetation patterns over southern Africa in response to anthropogenic-induced climate change (Engelbrecht and Engelbrecht 2016). A very high resolution KGCC maps and their relationship with altitudinal belts were also presented for the European Alps, where Oaks occurred as a predominant species under the Dfb climates (boreal, no dry season, warm summer) (Rubel et al. 2016). Recently, the KGCC were used to project contractions of the alpine tundra domain and upward elevational shifts of the natural climatic treeline under RCP 4.5 and RCP 8.5 scenarios in Europe, which projected an upward shift of vegetation across the mountain regions (Barredo et al. 2020).

In case of succession events, *Q. ilex* has colonized substantial new areas over the last century in France and Mediterranean regions. Noteworthy, the maximum rate of colonization by this species (22 to 57 m year⁻¹) was much slower than predicted by the

ecological niche models (Delzon et al. 2013). The habitats of *Q. aegilops* under the RCP 2.6 and 8.5 (2070s) showed a reduction of ~1850 km² (3.6%) and ~1627 km² (3.16%) and range expansion of ~777 km² (1.5%) and ~848 km² (1.7%) (Khwarahm 2020). These findings suggest that climate change impacts have been visualized on a globally distributed genus *Quercus*.

The habitat suitability changes require time to time monitoring and the notion on phenology was developed for an altitudinal shift, where the phenological cycle could be bound to be influenced by the non-climatic factors. It is important to note that the ecological population structure of a species is influenced by the reproductive potential, which itself depends on the 13 months period between the pollination and the ripening of the acorn (Shrestha 2003), and the precipitation and temperature variation probably shift the event. For instance, in the Himalayan region, if there is an increase in temperature during the coldest quarter (November–January) with a decrease in precipitation throughout the driest quarter (May–June), an early onset of spring is induced, which leads to the appearance of new shoots during February–March. Furthermore, flowers blooming take place in the month of late-March to April, with acorn formation taking place between late-April and mid-May. This hypothetical situation causes early flowering and fruiting events in *Q. semecarpifolia*, consequently leading to low viability of acorn due to the pre-monsoonal drought conditions. The phenological differences are reported from Nepal, where old leaves begin to fall in May–June, but do not fall entirely until the development of new leaves. At the lower elevations, the new shoots appear in May; whereas on the higher elevations, the new shoots do not commence to appear until June (Orwa et al. 2009). Irrefutably, altitudinal gradient may cause phenological shifts in the populations, which then act as a barrier for pollination amongst individuals of distantly located populations.

Noteworthy, the studied species shows signs of vivipary and masting phenology, with lesser formation of acorn in 6–7-consecutive years (Singh et al. 2011). Since monsoonal rain in the high-altitude zone of Himalayas arrives in late June to July, but the high temperature in May and early fortnight of June after acorn formation could aggravate the problem by causing a negative effect on the regeneration potential of *Q. semecarpifolia*. This could further lead to greater shifts in the distribution of Oaks in the Himalayas.

Qualitative data indicates that the species tends to move upwards to cooler climatic zones (Fig. 6; Supplementary Fig. 2), where decline in the areas of timberline communities were observed. In response to the climate change, the species showed the tendency to shift towards southern aspects at treeline in the Uttarakhand Himalayas. Whereas, on monsoonal sites, *Q. semecarpifolia* is associated with *B. utilis* and conifers but occasionally form treeline (Singh 2018). During surveys, it was observed that at Karandam Bugyal (Pithoragarh), the species is present as a treeline and timberline communities in northern aspect and absent in southern aspect, where the dominant vegetation were *B. utilis* and *R. campanulatum*. In Tungnath and Rudranath (Chamoli) and Yamunotri (Uttarkashi), treeline was formed by *Abies* spp., *R. campanulatum* and *B. utilis*, and *Q. semecarpifolia* was mainly observed in timberline. At Khaliya top (Pithoragarh), treelines were formed by *B. utilis* and *R. campanulatum* in all aspects, and *Q. semecarpifolia* was observed only in the eastern aspect, forming timberline with *Abies* spp. (Supplementary Fig. 3). Thus, it is difficult to interpret and understand the shift towards treeline and across the aspects, but upward movements could be hypothesized as an adaptive response against global warming as revealed by the MaxEnt model. Also, the occupancy of different aspects at diverse locations could be the ecological adaptation for shade, light and moisture (Singh 2018). Invariably, the future prediction scenario and estimated density ratio suggested the habitat of *Q. semecarpifolia* at lower elevation may be encroached by other associates, viz. *A. pindrow*, *Q. floribunda*, *Q. lanata*, *R. arboreum*, etc.

Influence of geological factors in the distribution of *Q. semecarpifolia*

In a preliminary qualitative analysis, the occurrence of different rock types seems to indirectly influence the distribution and habitat suitability prediction of *Q. semecarpifolia* by the acidification of soils. Despite being easily observable in Fig. 7, these early assumptions are qualitative, and demand further quantitative investigation in future studies. It is widely acknowledged that the Himalayas represent a geologically dynamic environment in terms of altitude change through geological time scale (GTS). Thermochronological modelling ages suggest important uplift events in the region of this study at 0.9 and 2.3

million years (Ma) ago (Patel and Carter 2009). Older events are also recorded in the region, indicating important uplift in the middle Miocene (~16–12 Ma), and as well as climate-driven erosional exhumation in the late Miocene–Pliocene (~3–2 Ma) (Wang et al. 2010). Modelled uplift rates were calculated via apatite fission track ages that varied from 0.25 to 0.69 mm year⁻¹ and have been occurring since the Middle to Late Miocene (Adlakha et al. 2019). These events of altitude variation in the Himalayas might have influenced the adaptation of a species through GTS, selecting those able to thrive in different altitudes to adapt to the changes. However, in our models, we cannot consider uplift as an effective variable, since the timescales accounted for these processes are entirely different, millions of years are necessary for significant tectonic changes, whilst a few decades are enough for contrasting climatic changes.

Conclusions

Due to the high economic, ethnobotanical, and ecological significance of Oaks, the evolution of treeline has been the subject of global concern. The present study highlighted several starting points to the current situation of *Q. semecarpifolia* forest that are rapidly changing under the influence of climatic and non-climatic variables, besides being affected by the local anthropogenic activities. The study allows us to draw important conclusions.

1. Field surveys and density analysis revealed the healthy and wide distribution of *Q. semecarpifolia* with an estimated area of ~832 km² but there is a lack of inadequate seedling recruitment in the native habitat.
2. Major tree associates at lower elevation (2200–2700 m) are *R. arboreum*, *Q. floribunda*, *T. wallichiana*, etc.; whereas, *B. utilis* and *A. pindrow* are associated at higher elevation (3000–3500 m).
3. This species tends to shift towards higher elevations in the Himalayas with respect to climate change scenarios of 2050 and 2070, with a sharp decline in potential abundance.
4. The modelled scenarios indicate high risk of extinction of *Q. semecarpifolia* at lower elevations.

5. Geological analysis indicates that tectonic uplift cannot be accounted as an important control to the altitudinal shift modelled in this study for the distribution of *Q. semecarpifolia*. Bedrock variations, however, might redeem distribution by means of influencing soil acidity.

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Data availability All data files have been uploaded and clearly written in the manuscript.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest to disclose.

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