

## Research Article

**Cite this article:** Meena RK, Negi N, Bhandari MS, Shankhwar R, Yadav A, Kant R, Pandey S, Sharma R (2023). Species distribution modelling and population genetic analysis of *Yushania anceps*; an endemic temperate woody bamboo of the Uttarakhand Himalayas. *Plant Genetic Resources: Characterization and Utilization* **21**, 357–368. <https://doi.org/10.1017/S1479262123000825>

Received: 4 January 2023

Revised: 19 October 2023

Accepted: 20 October 2023

First published online: 13 November 2023

### Keywords:


genetic diversity; genetic structure; MaxEnt; SDM; temperate bamboo; western Himalayas

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# Species distribution modelling and population genetic analysis of *Yushania anceps*; an endemic temperate woody bamboo of the Uttarakhand Himalayas

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## Abstract

*Yushania anceps* is a temperate woody bamboo taxon of high socio-economic importance occurring in the sub-alpine zone of the western Himalayas. This study was carried out to delineate the potential distribution of *Y. anceps* in the western Himalayas through species distribution modelling (SDM), and genetic characterization using sequence-tagged microsatellite (STMS) markers. The present study revealed an endemic distribution of this species in the Uttarakhand Himalayas, with an estimated area of 211.59 km<sup>2</sup>. The maximum probability of occurrence was recorded in the moderately dense forests between the altitudinal ranges of 2500 and 2700 m. The model output was well supported with high values of different statistical measures, such as the AUC (0.911) and Kappa coefficient ( $K = 0.513$ ). Environmental variables related to precipitation, temperature and topography were identified as the most contributory in current SDM. In addition, diversity measures, namely allelic richness ( $A_r$ ), expected heterozygosity ( $H_e$ ), and fixation index ( $F_{ST}$ ), were calculated in five sampled populations with eight STMS markers, which indicated high genetic diversity ( $A_r = 4.24$ ;  $H_e = 0.689$ ) and little differentiation ( $F_{ST} = 0.062$ ). The diversity maps displayed that the populations located in the Kumaon region captured relatively more genetic diversity than the Garhwal region. Further, genetic clustering and STRUCTURE analysis revealed a substantial level of genetic admixing across the analysed populations, and as a result, no sub-structuring was detected. Due to the rare and endemic distribution of *Y. anceps*, it requires immediate conservation measures, and the knowledge base generated here will be of paramount importance to forest managers, researchers and policymakers.

## Introduction

Bamboos constitute a large group of taxonomically related perennial grasses with significant economic and ecological importance. Worldwide, a total of 1662 species have been recorded under 121 genera (Canavan *et al.*, 2017), and 136 were reported to occur in India (ISFR, 2019). The bamboo genetic resources in India mainly belong to the tribes Bambuseae and Arundinarieae. The former comprises tall and giant bamboo taxa growing at an altitude below 1500 m, whereas taxa under the tribe Arundinarieae are shrubby with thin culms and grow in the subtropical and temperate zones of the western Himalayas between 1500 and 3500 m (Banik, 2016). These hill-bamboos are commonly called 'Ringals' in the western Himalayas and serve as a major source of income for the tribals, nomads, pastoralists and artisans (ICFRE, 2017).

*Yushania* Keng, one of the largest genera of temperate woody bamboos under the tribe Arundinarieae, is distributed in the Himalaya-Hengduan Mountains region (Ye *et al.*, 2019). Along with other allied genera, namely *Himalyacalamus* Keng.f. and *Thamnocalamus* Munro, it forms a shrubby layer in the subalpine or alpine forests of the western Himalayas (Banik, 2016), and plays a profound role in maintaining ecosystem functions and supporting the livelihood of forest dwellers. *Yushania anceps* (Mitford.) Yi (vernacular names: Jhamura or Sarora ringal in India and nigalo in Nepal) is a reed-like bamboo of the Indian Himalayan Regions (IHRs). This species has a non-clumping growth habit with elongated running rhizomes spreading on mountain slopes. The culms are erect and vigorous, 2–4 m tall, 0.5–1.5 cm diameter, 10–30 cm long thin-walled internodes and comprise upright, glossy, light-dark green drooping branches with narrowly lance-shaped leaves. In the natural habitat, it usually grows as patches in well-drained moist-fertile soil and forms undergrowth



inside the broadleaved and coniferous woodland of Kumaon and Garhwal regions of the western Himalayas at an altitudinal range of 2100 to 2700 m (Banik, 2016). Additionally, the species was introduced in Europe (Lin, 1974; Bean, 1981), Ireland and USA (Bahadur and Naithani, 1976) in the late 19<sup>th</sup> century.

Due to its desirable culm characteristics, the species has profound socio-economic importance, particularly in villages at high hills, where it has been used for various household applications (Banik, 2016). In addition, it provides green fodder to wildlife and domestic animals during the lean period of winter. Commercially, the species is used for pulp and paper in England, where an estimate revealed that a well-managed plantation of the smaller clone yielded 2 tons per hectare annually (Bridge, 1973). In San Francisco Bay (USA), a private bamboo nursery sold a clone of *Y. anceps*, 'Pitt White-YUANP', at a price range of \$60 to \$120 (<https://bamboosourcery.com/>). Similarly, in the United Kingdom, the price of potted culms of *Y. anceps* ranges from £29 to £50 (<http://www.uk-bamboos.co.uk/>). These signify the socio-economic potential of the species in the global bamboo market.

Presently, the species is experiencing a serious decline in its natural habitat in the western Himalayas (Rather, 2015). Moreover, earlier estimates also showed a declining trend. For instance, an area of about 130 km<sup>2</sup> was recorded in the Garhwal region (Osmaston, 1922), which was observed to be reduced in the later assessment by Tewari (1992). Notably, endemic species confronting population decline are highly vulnerable to extinction and demand systematic assessment and conservation efforts (Pimm *et al.*, 1995; Lomba *et al.*, 2010).

Species distribution modelling (SDM) provides an estimate for the geographical extent of species and implements computer algorithms for model-based prediction using environmental variables and geospatial data of species occurrence (Phillips *et al.*, 2006; Elith and Leathwick, 2009). Furthermore, SDM-based mapping allows evaluation of the potential impact of global climatic change (Thuiller *et al.*, 2005), demarcation of the potential distribution (Guisan *et al.*, 2006), inferring extinction risk (Benito *et al.*, 2009) and prioritization of conservation areas (Carvalho *et al.*, 2011).

Conversely, the conservation potential of an individual species is conferred by the genetic variability existed in its populations (Ramanatha Rao and Hodgkin, 2002; Porth and El-Kassaby, 2014). Thus, population-level genetic characterization is an indispensable requirement for precise conservation and management. The molecular marker-based assessment generates a reliable dataset for genetic diversity and population structure, and the technique has been widely used in plants, including bamboo (Yang *et al.*, 2012; Ma *et al.*, 2013; Nag *et al.*, 2013; Nilkanta *et al.*, 2017; Oumer *et al.*, 2020). Among various DNA-based markers, simple sequence repeat (SSR) or sequence-tagged microsatellite (STMS) markers are considered a robust technique for genetic analysis in plants due to their genomic abundance, high polymorphic potential, reproducibility and amenability to automation (Varshney *et al.*, 2005; Pfeiffer *et al.*, 2011). Recently, these have also been utilized for population genetic analysis in various bamboo species (Attigala *et al.*, 2017; Bhandawat *et al.*, 2019; Meena *et al.*, 2019; Huang *et al.*, 2021; Pérez-Alquicira *et al.*, 2021).

With the above background, the present study is contemplated to carry out spatial and genetic analysis in *Y. anceps* with the following objectives: (1) estimating the potential distribution of *Y. anceps* in the western Himalayas through MaxEnt modelling; and (2) deciphering the gene diversity and genetic structure in the natural populations.

## Material and methods

### Study area and data acquisition for SDM

The distribution record of *Y. anceps* in the western Himalayas was derived by reviewing secondary information available at various sources, like reports of the Forest Survey of India (ISFR, 2019), working plans of the state forest departments and the National Forest Library Information Center (NFLIC) at the ICFRE-Forest Research Institute, Dehradun. Afterward, the actual sites were surveyed in different forest ranges with the help of forest personnels. Field surveys were conducted in the Himalayan region under the states of Himachal Pradesh (HP) and Uttarakhand (UK) during 2017–2021. However, the targeted bamboo taxon could only be spotted in limited areas of the Garhwal (Chamoli district) and Kumaon (Pithoragarh district) regions in the Uttarakhand Himalayas (online Supplementary Fig. S1).

For the collection of geospatial data, multi-phase random sampling was carried out through an unbiased approach with zig-zag transects of 100 m. The Global Positioning System (GPS; Make Garmin, positional accuracy between 5–8 m) was used for geo-referencing and area demarcation. The geocoordinates and polygons were converted into the point shape file and keyhole markup language (KML) and visualized in Google Earth. Sampling bias was corrected by eliminating closely located 46 geocoordinates that were either fallen into the grid of ~0.64 km<sup>2</sup> spatially or 800 m apart linearly, and the remaining 62 points have been finally considered for MaxEnt modelling as per Rocchini *et al.* (2011). Further, 44 were used for training and 18 for testing the model output.

Additionally, 19 bioclimatic (30 s ~1 km<sup>2</sup> spatial resolution; WorldClim Version 2.1), six climatic, three spatial analysts, direct normal irradiance (DNI) and pedologic variables were also retrieved from different sources. The DNI was downloaded from the Solar Energy Centre, Ministry of New and Renewable Energy (MNRE), Government of India (GoI), New Delhi (<https://maps.nrel.gov>), and the pedologic data were derived from the India Dataset of Soil and Water Assessment Tool (SWAT; <https://swat.tamu.edu/data/india-dataset/>). The Global Digital Elevation Model (GDEM) with a 30-m resolution of the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) was used to generate aspect, elevation and slope (Hijmans *et al.*, 2005). Further, the raster data sets were converted into Digital Number (DN) and cross-correlated variables were delineated using the software Statistical Package for Social Sciences (SPSS; ver. 16.0). Two cross-correlated variables with Pearson Correlation Coefficient (r) values greater than ±0.80 were identified (online Supplementary Table S1), and only one in each such pair was selected based on their percentage contribution and permutational importance in MaxEnt modelling driven by the response curve and Jackknife test.

### Maxent modelling for the potential species distribution

The probabilistic distribution was estimated by running an open-access program, MaxEnt ver. 3.4.4 (Phillips *et al.*, 2006; <https://www.cs.priceton.edu>) in which species occurrence data are mathematically correlated with environmental variables. The model features, such as linear, quadratic, product (0.050), categorical (0.250), threshold (1.000) and hinge (0.500), determine species responses to environmental conditions (Elith *et al.*, 2011). Over-fitting and over-prediction of the model were reduced by setting the regularization multiplier value as 0.1 (Phillips *et al.*,

2004) with 5000 iterations and keeping other parameters as default (Young *et al.*, 2011; Flory *et al.*, 2012; Yang *et al.*, 2013).

The model's performance was assessed through the 'Area Under the 'Receiver Operating Characteristics (ROC)' Curve (AUC)', calculated in MaxEnt which provides a single measure of model performance independent of any particular choice of threshold. Herein, the categorized models with AUC values >0.9 are considered highly accurate (Swets, 1988). In addition, other classification accuracy measures, such as Kappa statistics ( $K$ ), normalized mutual information (NMI) and true skill statistic (TSS), were derived manually from the confusion matrix generated in ArcGIS (Fielding and Bell, 1997; Allouche *et al.*, 2006).

The output maps were first viewed in the World Geodetic System-84 (WGS-84) projection, which was later re-projected into the Universal Transverse Mercator (UTM) system with zone 44. Once the transformation was completed, a raster calculator was used to determine the area under the prediction output, and the final distribution map was overlaid on the satellite data scenes of SENTINEL (online Supplementary Table S2) and the Köppen-Geiger Climate Classification (KGCC) system (1976–2000) (Kottek *et al.*, 2006).

### Population sampling, DNA extraction and marker genotyping

For population genetic analysis, leaf samples were harvested from a natural distribution range in the Uttarakhand Himalayas. A total of 110 individual clumps from five geographical locations were sampled through the line transects method (online Supplementary Table S3), where two sampled individuals were 100 to 300 m apart at each location. To avoid sample deterioration and fungal contamination during long field tours, leaf tissues were desiccated with silica gel. The completely dried samples were stored at  $-80^{\circ}\text{C}$ . The genomic DNA was extracted using the method given by Doyle and Doyle (1987) with minor modifications as per Krizman *et al.* (2006).

As SSR marker information was not available in the *Y. anceps*, the SSRs developed in another Indian temperate woody bamboo taxa, *Drepanostachyum falcatum* (Nees) Keng f., were tested for their cross-transferability (Meena *et al.*, 2021). A total of ten successfully transferred polymorphic markers given in Table 1 were used for genotyping through polymerase chain reaction (PCR) amplification. Nine of these were genomic STMS markers developed in *D. falcatum*, and one was expressed sequence tags (EST)-based SSR identified in *Dendrocalamus latiflorus* (Bhandawat *et al.*, 2015). For PCR amplification, a reaction mixture was prepared by mixing 2  $\mu\text{l}$  genomic DNA (50 ng), 1.8  $\mu\text{l}$  enzyme buffer (10 $\times$ ), 1.8  $\mu\text{l}$   $\text{MgCl}_2$  (25 mM), 1.2  $\mu\text{l}$  dNTPs (2.5 mM), 0.15  $\mu\text{l}$  primers (20  $\mu\text{M}$ ) and 0.2  $\mu\text{l}$  *Taq* DNA Polymerase enzyme (3 U  $\mu\text{l}^{-1}$ ) (Genei, India). Finally, a total reaction volume of 15  $\mu\text{l}$  was constituted with nuclease-free sterile water. The PCR amplification was carried out in the thermal cycler machine (Eppendorf Mastercycler Nexus) with an initial denaturing step (95 $^{\circ}\text{C}$  for 5 min) followed by 35 cycles of 94 $^{\circ}\text{C}$  for 1 min, 48.1–62.3 $^{\circ}\text{C}$  for 1 min and 72 $^{\circ}\text{C}$  for 1 min and then final elongation at 72 $^{\circ}\text{C}$  for 10 min.

The fragment analysis was done through single-plex capillary electrophoresis using Nucleic Acid Analyzer (LabChip GX Touch 24, PerkinElmer, USA). Non-integer values of the allelic sizes generated by the machine were first transformed to integers using the power function and then binned as per the periodicity of repeat motifs of each marker locus using the software

TANDEM ver. 1.07 (Matschiner and Salzburger, 2009). Marker data were further evaluated for the presence of null alleles using the software FreeNA (Chapuis and Estoup, 2007), and SSR loci with a significant proportion of null allele frequency were excluded from analysis.

### Marker data analysis for gene diversity, differentiation and genetic structure

The measures of gene diversity, viz., number of different alleles ( $N_a$ ), effective number of alleles ( $N_e$ ), percentage of polymorphic loci (PPL), gene flow ( $N_m$ ), observed heterozygosity ( $H_o$ ) and expected heterozygosity ( $H_e$ ), were calculated using the software GenAlEx ver. 6.5 (Peakall and Smouse, 2012). The polymorphic information content (PIC) was analysed using PowerMarker ver. 3.25 (Liu and Muse, 2005). Genetic differentiation among the studied populations was measured through the analysis of molecular variance (AMOVA), Wright's fixation index ( $F_{ST}$ ) and inbreeding coefficient ( $F_{IS}$ ) using the software Arlequin ver. 3.1 (Excoffier *et al.*, 2005). Mean allelic richness ( $A_r$ ) and private allelic richness ( $P_Ar$ ) were calculated using the software HP-Rare ver. 1.0 (Kalinowski, 2005), which were further spatially exemplified over the distribution map using the inverse distance weighted (IDW) algorithm employed in the ArcGIS ver. 9.3 (Hengl, 2009; Chiochini *et al.*, 2016).

The genetic relationship among sampled populations was derived by clustering analysis through the unweighted pair group method with arithmetic mean (UPGMA) and the principal coordinate analysis (PCoA) using the software POPTREE2 (Takezaki *et al.*, 2009) and GenAlEx, respectively. Further, the isolation by distance was examined by correlating pairwise genetic and geographical distances between sampled populations through the Mantel test (Mantel, 1967) in the software GenAlEx. Finally, the population genetic structure was deciphered through the Bayesian model-based clustering method using STRUCTURE software ver. 2.2 (Pritchard *et al.*, 2000). Posterior probability [ $\text{Pr}(K)$ ] was calculated for each set K-value from 1 to 5 using an ancestry model with admixture under the assumption of correlated allele frequencies. The model was run 10 times with 300,000 Markov Chain Monte Carlo (MCMC) sampling runs after a burn-in period of 300,000 iterations. The optimal K-value ( $\Delta K$ ) was finally determined using the web-based program Structure Harvester 0.6.92 (Earl and vonHoldt, 2012).

## Results

### Site geographical features and associated species of *Y. anceps*

The ground surveys revealed a rare and restricted distribution of *Y. anceps* in the sub-alpine zone of the western Himalayas of Uttarakhand. A total of 108 geo-coordinates of species presence were collected from five sites in Uttarakhand; two were in district Pithoragarh and three in Chamoli. This study has reported the geographical range of the *Y. anceps* extended from 29 $^{\circ}50'$  to 30 $^{\circ}32'$  in the north and 79 $^{\circ}11'$  to 80 $^{\circ}39'$  in the east, and altitudinally from 2300 m at Ghes (Chamoli) to 3200 m at Munsyari (Pithoragarh). The species inhabits the sites with 25 to 60 $^{\circ}$  slopes and is mostly associated with evergreen forests of *Abies* spp., *Acer* spp., *Picea* spp., *Quercus* spp., *Rhododendron* spp., *Taxus wallichiana*, etc. However, in some areas of Pithoragarh, it has also been observed on the slopes of hilltops, where this is growing under treeline species like *R. companulatum*, *Betula utilis*, *Tsuga dumosa*, *Abies spectabilis*, etc.

**Table 1.** Characteristics of 10 polymorphic SSR markers used for genotyping of *Yushania anceps* populations

Sl. no.	Locus name	Primer sequence (5'-3')	Repeat motif	T <sub>a</sub> (°C)	Expected product size (bp)	Observed product size (bp)	No. of alleles per loci	Polymorphism information content (PIC)	Inbreeding coefficient (F <sub>IS</sub> )	Frequency of null alleles
1.	D/Stm-56*	F: GCCTTACCGCTGTTCT R: TGTGAGGTCATGGTGTGA	(CT)7	61.4	210	189-256	22	0.849	0.633	0.28
2.	D/Stm-945*	F: GGGAGGAGCGATTTCCTCC R: GTTCTCGCTCTGGCAAGA	(AGC)5	62.3	180	146-221	10	0.387	0.705	0.11
3.	D/Stm-405	F: GACTCAGCAGCTCGACGAG R: CACCTCTCGTTAGGGCTG	(AGG)6	48.1	213	195-234	12	0.394	0.201	0.07
4.	D/Stm-1782	F: ACCCTGACCGGAGTTCTTCT R: CTCCCCTTGACTCCGGTGAT	(AGG)5	62.3	186	145-297	20	0.822	0.172	0.08
5.	D/Stm-1651	F: ATCCTTGTGGCCCCCTATG R: GCTTGACTCCTCGGTGACC	(GTG)5	57.2	212	147-284	26	0.819	-0.215	0.00
6.	D/Stm-1542	F: CTACCCCCTCCGACACC R: CTCCTCGTCCGTCCAAAGAC	(CCG)5	54.3	171	123-371	22	0.866	0.046	0.03
7.	D/Stm-1144	F: GAGAACGTGGCCTCGTC R: GGGAGGCAGTAGACGTTG	(CGC)5	49.6	213	198-306	26	0.921	-0.073	0.01
8.	D/Stm-762	F: AGCTCAAGATCCCAAAGCT R: TCCACTCCCATCCATCCCA	(CT)12	62	210	153-276	18	0.857	0.110	0.06
9.	D/Stm-55	F: TCGACCAACGGAAGAACG R: CTGTTGGCCAAAGTGGAGAA	(CTT)5	62	175	202-262	10	0.788	0.184	0.15
10.	DGUMS-25	F: GAGGACTTGATGATTTGGA R: ATGTTATTGGCCTTGCTG	(GAA)8	51	150-1000	144-236	14	0.370	0.063	0.05

Note: SSR loci indicated with asterisk (\*) were excluded from the data analysis due to significant proportion of null allele frequency and high inbreeding

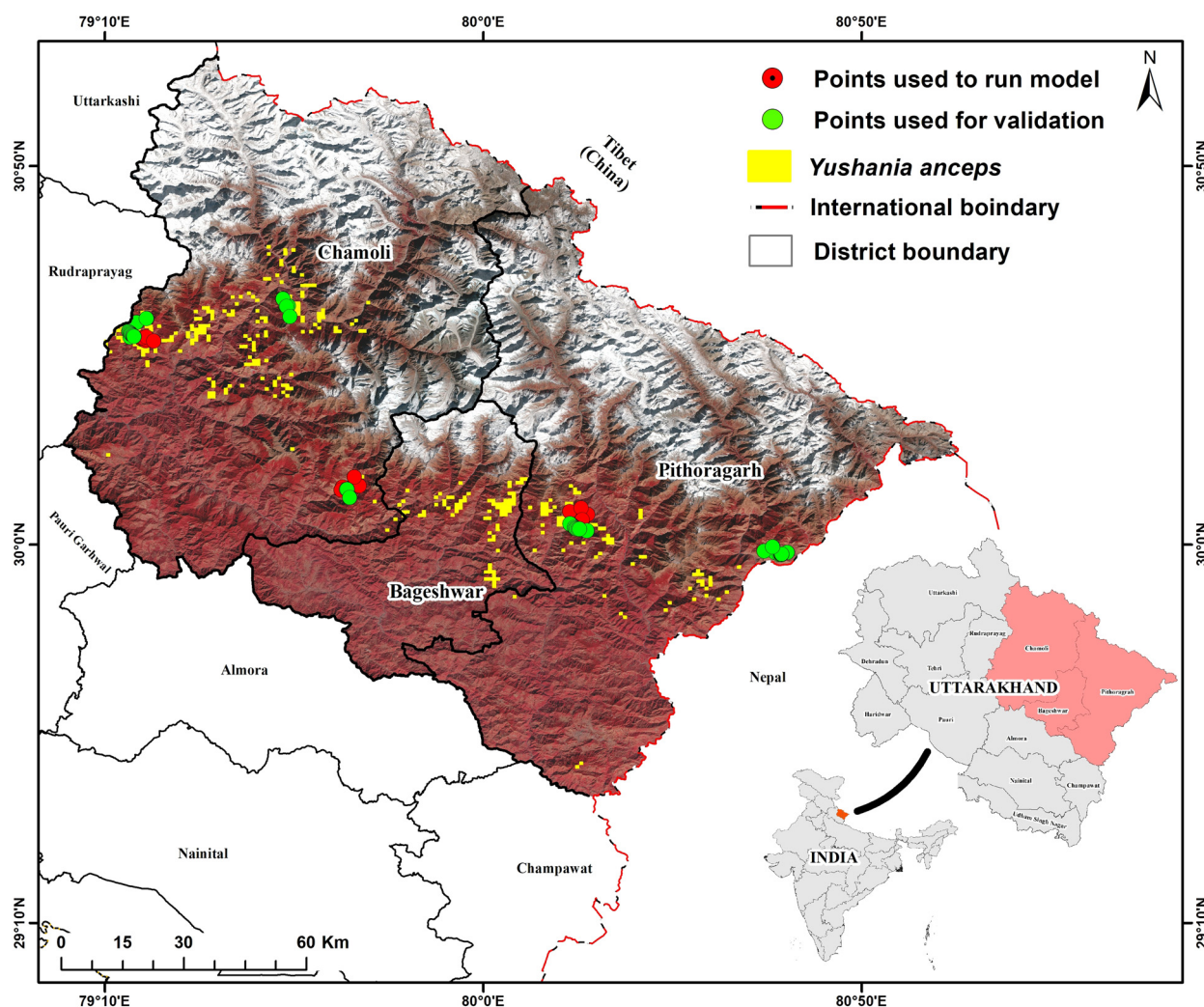
### Model performance and relative contribution of bio-climatic variables in SDM

In the MaxEnt-derived probabilistic distribution, 77.78% of test data (14 out of 18 geo-coordinates) were suitably overlaid with the prediction threshold of 0.7 (Fig. 1). The higher AUC value ( $0.911 \pm 0.13$ ) has revealed optimal model performance with the best-fitting ability of the used bioclimatic variables (Fig. 2a). The model precision was further confirmed by the classification accuracy measures derived through the confusion matrix, such as K (0.513), NMI (0.447) and TSS (0.906) (online Supplementary Table S4).

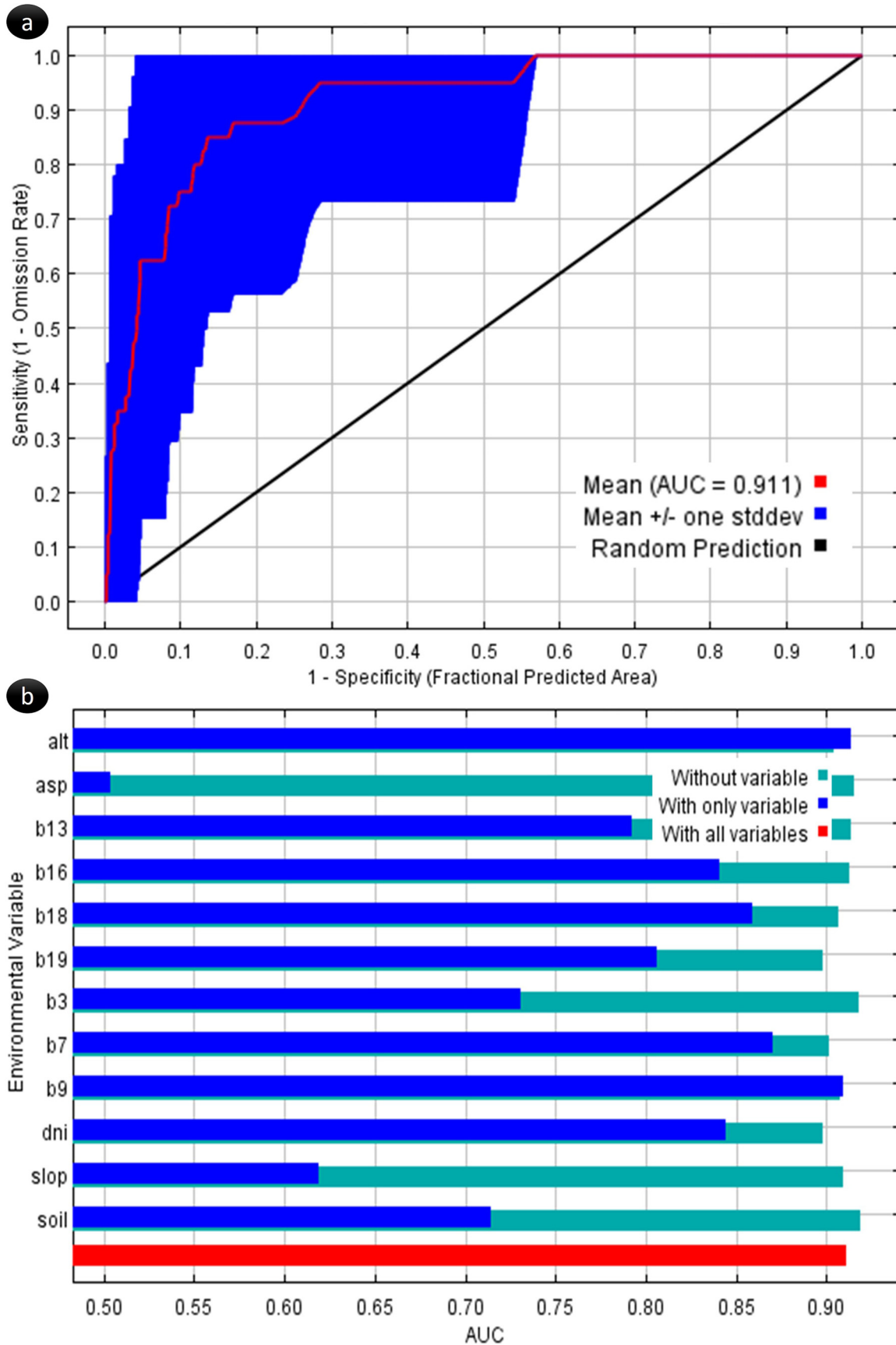
Based on the relative importance and permutations, the percentage contribution was assessed for each environmental variable (Table 2). The variables, namely annual temperature range (Bio 7), precipitation of the wettest quarter (Bio 16), precipitation of the coldest quarter (Bio 19), aspect (Asp), precipitation of the wettest month (Bio 13), precipitation of the warmest quarter (Bio 18), slope (Slop) and direct normal irradiance (DNI), showed the highest cumulative percentage contribution ( $\sim 88\%$ ) and permutation importance ( $\sim 79\%$ ). Besides, some other variables, such as soil and iso-thermality (Bio 3) and altitude (Alt), playing

crucial roles in SDM were also considered. The Jackknife test (Fig. 2b) further elaborated that altitude (Alt) showed the highest gain when used in isolation, while the variable that decreases the gain most when omitted is Bio 7, signifying their imperative role in habitat prediction.

The response curves presented in online Supplementary Fig. S2 showed that the predicted probability of presence varies as the variable changes. Based on these curves, the annual temperature range (Bio 7) varied from 22 to 26°C, with a maximum probability ( $P$ ) of presence between 22.2°C ( $P = 0.99$ ) and 22.8°C ( $P = 0.80$ ). The response curves of factor Bio 7 revealed that *Y. anceps* distribution ranges are affected by extreme temperature conditions, where the major effect has been observed due to the differences between the maximum and minimum temperatures of the warmest and coldest months, respectively. Similarly, precipitation played a critical role in determining habitat suitability, where the maximum probability of presence was found in areas with precipitation ranging from 800 to 1200 mm. Also, the rainfall requirement is higher in the warmest quarter (Bio 18) than in the wettest quarter of the year (Bio 16). Another important factor is aspect (Asp), which revealed most of the distribution inclined towards the north-eastern aspect. Other factors, such as altitude



**Figure 1.** Distribution map of *Yushania anceps* generated for three districts of Uttarakhand through MaxEnt modelling and overlaid over the satellite data scenes of SENTINEL



**Figure 2.** MaxEnt model output and performance indicators: (a) Model performances evaluated by the area under the receiver operating characteristic curve or AUC; (b) Jackknife test revealing relative importance of environmental variables

**Table 2.** Per cent contribution and permutation importance of the environmental variables in MaxEnt modelling

Label	Variables	Scaling factor	Units	Per cent contribution	Permutation importance
Bio 1	Annual mean temperature	10	°C	–	–
Bio 2	Annual mean diurnal range	10	°C	–	–
Bio 3*	Iso-thermality [(Bio 2 / Bio 7) × 100]	100	°C	3.8	0.9
Bio 4	Temperature seasonality (Std. deviation × 100)	100	C of V	–	–
Bio 5	Max. temperature of warmest month	10	°C	–	–
Bio 6	Min. temperature of coldest month	10	°C	–	–
Bio 7*	Annual temperature range (Bio 5 – Bio 6)	10	°C	22.6	3.8
Bio 8	Mean temperature of wettest quarter	10	°C	–	–
Bio 9*	Mean temperature of driest quarter	10	°C	5.1	10.3
Bio 10	Mean temperature of warmest quarter	10	°C	–	–
Bio 11	Mean temperature of coldest quarter	10	°C	–	–
Bio 12	Annual precipitation	1	mm	–	–
Bio 13*	Precipitation of wettest month	1	mm	7.5	12.8
Bio 14	Precipitation of driest month	1	mm	–	–
Bio 15	Precipitation seasonality	100	C of V	–	–
Bio 16*	Precipitation of wettest quarter	1	mm	14.2	2.8
Bio 17	Precipitation of driest quarter	1	mm	–	–
Bio 18*	Precipitation of warmest quarter	1	mm	6.9	11.8
Bio 19*	Precipitation of coldest quarter	1	mm	12.4	27.0
Alt*	Altitude		m	1.4	10.3
Slop*	Slope		°	6.8	0.6
Asp*	Aspect		°	11.3	1.5
Soil*	Soil			1.3	0.0
DNI*	Direct normal irradiance			6.6	18.2
Prec	Precipitation		mm	–	–
$T_{av}$	Average temperature		°C	–	–
$T_{max}$	Maximum temperature		°C	–	–
$T_{min}$	Minimum temperature		°C	–	–
Vap	Vapor		mm	–	–
Wind	Wind		m/s	–	–

Note: The variables marked with asterisk (\*) were selected by multi-collinearity test and used in MaxEnt.

(Alt range: 2000–3000 m, maximum  $P = 0.9$  at 2700 m) and direct normal irradiance (DNI: 17,200  $Wm^{-2}$ ,  $P = 0.85$ ) were also crucial in the SDM of *Y. anceps*.

#### Potential eco-distribution mapping and area estimation

Based on the environmental variables, the model has predicted the habitat suitability in the entire distribution range, but the final eco-distribution map was generated only for the area verified by ground-truthing, i.e., three districts of Uttarakhand. The predicted species distribution in these districts was overlaid on the satellite data scenes of SENTINEL (Fig. 1) and KGCC (online Supplementary Fig. S3). The KGCC map has displayed the distribution of *Y. anceps* into 4 out of 5 climate subtypes. Maximum species occurrence was found in subtropical highland oceanic climate (Cwb; C = warm temperate, w = winter dry and b = warm

summer) and rainfed oceanic climate (Dwc; D = Snow, w = winter dry and c = cool summer) at upper zonation of the middle Himalayas in districts Chamoli, Bageshwar and Pithoragarh.

This study revealed an actual sampling area of  $\sim 53 km^2$  (1 km buffer zone) and an estimated area of  $\sim 212 km^2$  in the Uttarakhand Himalayas. Notably, the total estimated area is 0.40% of the total geographical area and 0.87% of the forest cover of the state (online Supplementary Table S5). Further, the eco-distribution map was superimposed on the Land Use Land Cover (LULC) map to estimate the area under different forest cover and altitudinal classes (online Supplementary Table S6). The area under very dense, moderately dense and the open forest was estimated to be  $\sim 60$ ,  $\sim 116$  and  $\sim 36 km^2$ , respectively (online Supplementary Table S7). Altitudinally, the maximum probability of species occurrence was recorded between 2501 and 2700 m.

### Gene diversity and population genetic structuring

Genotyping of 110 individuals with 10 STMS markers has generated a total of 148 alleles; the highest 26 alleles were generated by markers *DfStm1144* and *DfStm1651*, while a minimum of 10 alleles each was displayed by *DfStm55* and *DfStm945* (Table 1). All the marker loci displayed high polymorphism with a mean PIC value of 0.707. The STMS locus *DfStm-1144* displayed the highest polymorphism (PIC = 0.92), whereas the lowest was exhibited by the EST-SSR marker DGUMS25 (PIC = 0.37). The presence of null and inbreeding is a common problem in SSR marker genotyping, which may lead to misinterpretation of inbreeding or Hardy-Weinberg Equilibrium (HWE). Thus, all 10 analysed SSR loci were first examined for the presence of null alleles as well as inbreeding (Table 1). In brief, no evidence of null alleles was detected in most analysed SSRs except *DfStm-56*, *DfStm-55* and *DfStm-945*. Likewise, positive values of the inbreeding coefficient recorded at some loci showed a sign of inbreeding. In order to minimize the errors, two SSR loci exhibiting higher null allele frequency and inbreeding, namely *DfStm-56* and *DfStm-945*, were excluded from the final data analysis. Population-wise diversity indices calculated with eight SSR loci are depicted in Table 3.

Being the key indicators of gene diversity, the mean values recorded for allelic richness ( $Ar = 4.24$ ), observed heterozygosity ( $Ho = 0.658$ ) and expected heterozygosity ( $He = 0.689$ ) have depicted high genetic diversity in the *Y. anceps* metapopulation. The diversity maps generated by spatial overlaying of allelic richness and private allelic richness have displayed that the populations located in the Kumaon region captured relatively more gene diversity than the Garhwal region (online Supplementary Fig. S4a), and most of the populations of both regions harbour a significant proportion of unique alleles (online Supplementary Fig. S4b).

The AMOVA revealed that most genetic variance (93.77%) was restricted within the populations, and only 6.23% variance was recorded among the populations (online Supplementary Table S8). Inadvertently, gene flow is a key process involved in partitioning the genetic variance, which counteracts the genetic variation between the populations. Owing to high gene flow ( $Nm = 4.09$ ) over a narrow distribution range, very low genetic differentiation ( $F_{ST} = 0.062$ ) was recorded among the experimental populations. Lower genetic differentiation was further supported by the results of genetic clustering and STRUCTURE analysis. In STRUCTURE analysis, the optimum K-value was determined to be three (online Supplementary Fig. S5) but none of the population has qualified to be assigned to any inferred cluster with a proportional membership coefficient of more than 0.70 (online Supplementary Table S9). As a result, a

high level of genetic admixing was observed among the experimental populations [Fig. 3(a) and (b)]. It is conspicuously evident in the bar plot, where none of the three inferred clusters were clearly defined and all the populations displayed a significant proportion of individuals with mixed inferred ancestry.

In addition, the Mantel test revealed that the relationship between genetic and geographical distances was not significant and that the populations do not follow the isolation by distance (online Supplementary Fig. S6). As a result, the clustering pattern was not observed in accordance with their spatial distribution. Invariably, the UPGMA clustering displayed two major groups (Fig. 3c), first constituted by three populations, namely Ghes (YA03), Narayan Ashram (YA04) and Chopta (YA05), whereas the remaining two populations, i.e., Auli (YA01) and Munsyari (YA02) were clustered in another group. A similar clustering pattern was also displayed by the two-dimensional PCoA plot, in which the first coordinate separated most populations, accounting for 58.33% of the genetic variance (online Supplementary Fig. S7).

### Discussion

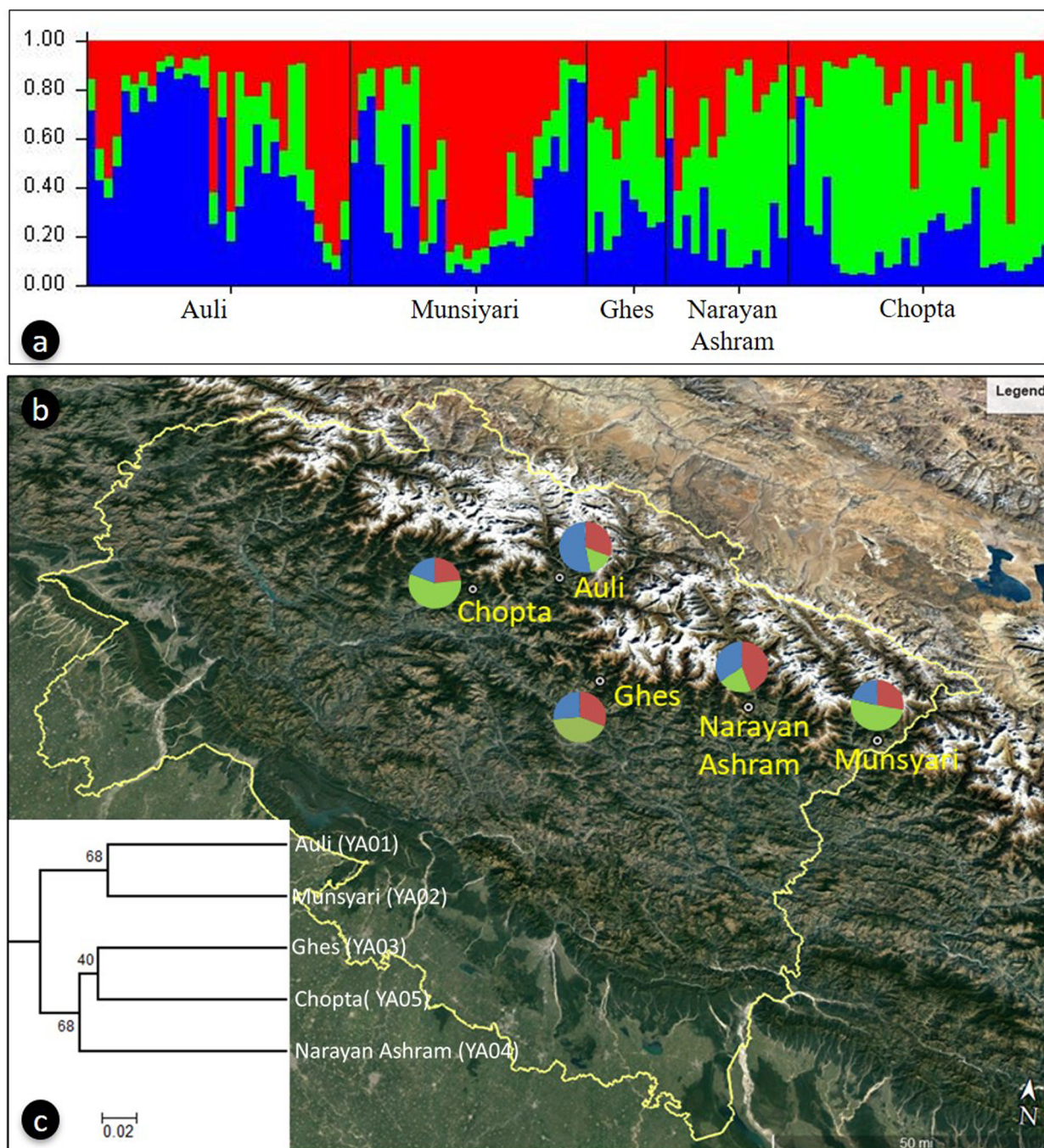
As envisaged in this study, a potential distribution map of *Y. anceps* has been generated through the SDM approach, and bioclimatic variables associated with habitat suitability have been identified. Likewise, SSR-based marker analysis revealed the baseline information on genetic diversity, differentiation and genetic structure of five experimental populations occurring in the Uttarakhand Himalayas. Both ecological and genetic information generated herein is crucial for devising a scientific programme for the conservation and management of the species.

Ground surveys and MaxEnt-based SDM revealed an endemic distribution of *Y. anceps* in the Uttarakhand Himalayas. In agreement with the earlier report by Bahadur and Naithani (1976), species distribution has been verified in the western Himalayas, from the Jaunsar region of Uttarakhand through Chamoli in Garhwal to the source of the Pindar River in Kumaon. Previously, this species has been described with the synonyms *Arundinaria jaunsarensis* Gamble (1896) and *Chimonobambusa jaunsarensis* (Gamble) Bahadur and Naithani (1976), where the species name was derived from the place of occurrence, i.e., the Jaunsar region of Uttarakhand. Surprisingly, the healthy populations of *Y. anceps* could not be spotted in this region during our surveys. Instead, a sparse distribution was observed in the Deoban range of the Jaunsar region. This indicates a sign of population deterioration in the natural habitat. In addition, it has been observed that the populations occurring in both community forests and reserve forests are vulnerable to anthropogenic activities like grazing and manual harvesting; hence, they need conservation efforts.

**Table 3.** The measures of gene diversity for sampled population of *Yushania anceps*

Pop Id	Location detail	N	Na	Ne	Ho	He	Ar	PAr
YA01	Auli_Chamoli	30	11.00	4.92	0.733	0.692	4.25	1.05
YA02	Munsyari_Pitoragarh	26	9.63	5.27	0.717	0.732	4.44	1.16
YA03	Ghes_Chamoli	9	6.25	4.49	0.609	0.642	4.21	0.85
YA04	Narayan Ashram_Pitoragarh	14	6.38	3.92	0.652	0.712	4.08	0.76
YA05	Chopta_Chamoli	30	10.00	5.08	0.583	0.670	4.23	1.08
	Population mean	21.8	8.65	4.74	0.658	0.689	4.24	0.98





**Figure 3.** Genetic structure of *Yushania anceps* metapopulation: (a) Bar plot illustrated the proportional membership coefficient for all the genotypes at  $K=3$  where each population is separated by vertical line and individual samples are represented by coloured bars; (b) Spatial representation of the inferred ancestry in sampled populations where yellow line shows the state boundary of Uttarakhand; (c) UPGMA clustering

MaxEnt-based SDM revealed that the variables related to precipitation (Bio 13, Bio 16, Bio 18 and Bio 19) and temperature (Bio 3, Bio 7 and Bio 9), along with other variables such as Asp, Slop and DNI, have an imperative role in defining the habitat suitability of *Y. anceps* (Table 2). It has also been observed in a recent study on its co-associate, *D. falcatum*, where the precipitation and temperature maximize the probabilistic distribution of hill bamboos in the western Himalayas (Meena *et al.*, 2023). Similarly, variables related to temperature and precipitation were also found important for the occurrence of six lesser-known

temperate bamboo species in Meghalaya, India (Kharlyngdoh *et al.*, 2016) and *Phyllostachys edulis* in China (Shi *et al.*, 2020). In another recent study carried out for SDM in a highland bamboo, *Oldeania alpina* (K. Schum) Stapleton in Ethiopia (Yebeben *et al.*, 2022), variables such as Bio 3, Bio 8, Bio 12, Bio 14, soil pH and soil CEC were identified as the key contributory variables for its habitat suitability.

The present study depicts an estimated area cover of about 212 km<sup>2</sup> in Uttarakhand, with the maximum occurrence in moderately dense forests. In the earlier probable estimates, the species

was predicted to cover about 130 km<sup>2</sup> in the Garhwal region (Osmaston, 1922), which was observed to be reduced in later assessments (Tewari, 1992). The natural habitats of *Y. anceps* are continuously dwindling, probably due to changing climates, anthropogenic activities and grazing pressures. The overlaying of the species distribution on the KGCC map has indicated that habitats with subtropical highland oceanic climate (Cwb) and subarctic climatic (Dwc) conditions are most suitable, where the species prevalence mainly depends on the monsoon. As demonstrated in several studies, SDM is an immensely useful approach for mapping the current and future species distribution, area prioritization and conservation (Carvalho et al., 2011; Franklin, 2023). Hence, the eco-distribution map and the area estimates generated herein are of utmost importance to forest managers for the conservation and management of this valuable resource.

Further, SSR-based population genetic analysis in *Y. anceps* revealed a high genetic diversity, with most genetic variance existing within the populations. Consequently, the populations demonstrated negligible genetic differentiation with a subtle genetic structure, which could be anticipated in a narrowly distributed and open-pollinated plant taxa (Nybom and Bartish, 2000). For instance, the amount of genetic variation scattered between the populations indicates the degree of differentiation, which tends to be high for the annual, self-pollinated and widespread taxa as compared to the long-lived perennial, open-pollinated and endemic taxa, respectively (Nybom and Bartish, 2000). In general, bamboo is an open-pollinated plant with a mixed mating system (Chen et al., 2017; Xie et al., 2019). Hence, the high genetic diversity with negligible differentiation recorded in *Y. anceps* could be attributed to its open-pollinated floral behaviour and endemic distribution in the Uttarakhand Himalayas.

In congruence with this study, a high genetic diversity with little genetic differentiation was also recorded in *D. falcatum*, which is one of its co-associates in the western Himalayas with a wide and abundant distribution (Meena et al., 2023). Besides, low to medium genetic diversity was documented with varied level of genetic differentiation in some other bamboo taxa based on the threat perception imposed by various causes such as habitat degradation, overexploitation, anthropogenic activities, etc. For instance, natural populations of *Dendrocalamus hamiltonii* (a tropical woody bamboo) in northeast India were characterized by moderate genetic diversity, high genetic differentiation and significant genetic structure, which was attributed to their indiscriminate extraction (Bhandawat et al., 2019; Meena et al., 2019). Likewise, moderate to high genetic diversity and differentiation were also recorded in Chinese bamboo taxa, namely *P. edulis* (Jiang et al., 2017) and *D. sinicus* (Yang et al., 2018). Moreover, high genetic admixing observed in STRUCTURE and cluster analysis could be possible due to significant gene flow within a smaller distribution range, either through pollen as well as vegetative propagule, because of the sporadic and massive synchronized flowering recorded in the genus *Yushania* and strong capability of asexual reproduction (Zheng et al., 2020).

### Conservation implications

The present study revealed an endemic distribution of *Y. anceps* in the Uttarakhand Himalayas, where precipitation and temperature play an imperative role in defining habitat suitability. Hence, the taxon needs to be periodically assessed for population structure and threat perception. Moreover, the maps and area estimates generated in this study could serve as valuable resources in the

planning and execution of future conservation programmes. The high level of genetic diversity with insignificant structuring detected in this study revealed substantial adaptive potential in the natural populations. Nevertheless, conservation efforts are still warranted due to the sparse and endemic distribution.

Being a diversity hotspot, populations in the Kumaon region could be prioritized first for immediate conservation, either *in situ* or *ex situ*. Besides, smaller populations need to be enhanced up to the standard effective size for maintaining higher genetic diversity and avoiding the deleterious effects of genetic drift. Considering lesser genetic divergence and insignificant genetic structure, the entire range could be treated as a single management unit. In addition, the forest manager needs to focus on the expansion of the area under *Y. anceps* through manual plantations or farm cultivation.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S1479262123000825>

**Data availability.** The additional data required to understand the manuscript is available in the supporting information of this manuscript.

**Acknowledgements.** The work was financially supported by the Indian Council of Forestry Research and Education (ICFRE) via a project grant (number: OG-49/CR-19). The authors are thankful to the Director, Forest Research Institute, Dehradun, for providing facilities for laboratory and field work. We extend our sincere gratitude to the state forest departments of Uttarakhand and Himachal Pradesh for providing the necessary permissions for surveys and sample collection. Suggestions obtained from anonymous reviewers are highly appreciated.

**Competing interest.** None.

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