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ORIGINAL PAPER

Habitat characterizations and suitability analysis for conservation implications of *Gymnosphaera gigantea* (Wall. ex Hook.) S.Y.Dong: a threatened tree fern

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Abstract

Elucidating the relative importance of landscape composition including habitat structure, landscape features, and environmental factors can help prioritize management action for developing effective conservation measures. The present study aims to investigate the habitat characteristics, relative influence of key habitat environmental factors on the abundance of *Gymnosphaera gigantea* and to propose suitable habitats for conservation implications in the study area. Statistical modelling, habitat suitability analyses, and micro-level land use planning were done through the generalized linear models (GLMs), geostatistic interpolation based on Entropy Weighted Habitat Index (EWHI) and synthetic indicator (SI), and Strength-Weakness-Opportunity-Threat (SWOT) analysis, respectively, using significant habitat environmental factors derived from principal component analysis (PCA). A total of 57 (28 juvenile and 29 adults) individuals of *G. gigantea* was recorded from 19 populations with altitude varying from 59–747 m asl. GLMs analysis revealed that the vegetation and water occurrence as well as their combination significantly affects the abundance of *G. gigantea*. Suitability analysis and micro-level land use planning resulted in two priority areas (priority area I and II) in Tripura having greater potential for future conservation planning and reintroduction of this threatened fern. Overall, considering the fragmented populations and smaller patch size, the conservation of study species will require an integrated landscape as well as local-scale geospatial habitat management strategies to protect the natural populations and enhance the distributional range.

Keywords Abundance · Entropy Weighted Habitat Index · Habitat suitability · Priority areas · Strength-Weakness-Opportunity-Threat

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Abbreviations

AIC	Akaike's Information Criterion
ΔAICc	Delta Akaike's Information Criterion corrected
ASI	Alternative synthetic indicator
BD	Bulk density
DEM	Digital elevation model
EWHI	Entropy Weighted Habitat Index
GSI	Generalized synthetic indicator
GIS	Geographic information system
GLMs	Generalized linear models
IDW	Inverse distance weighted
IUCN	International Union for Conservation of Nature
IVI	Importance Value Index
LULC	Land use and land cover
NDVI	Normalized Difference Vegetation Index
NDWI	Normalized Difference Water Index
SI	Synthetic indicator
SOC%	Soil organic carbon %
SWOT Analysis	Strengths, Weaknesses, Opportunities, and Threats Analysis
TWI	Topographic Wetness Index

Introduction

Plant community types are influenced by climatic and topographic factors, as well as soil's physical and chemical properties. Physical environmental factors are closely correlated with vegetation distribution and forest tree growth, the ecological niche of species (Chapin et al. 2002; Abella and Covington 2006; Poulos et al. 2007; Solon et al. 2007; Eshaghi and Shafiei 2010; Birhanu et al. 2021). On the other hand, the abundant-center hypothesis proposes that a species' abundance peaks in the center of its distributional range and declines at the edges, where conditions are unfavorable (Ntuli et al. 2020). The high abundance in the center is due to ideal conditions, such as the presence of suitable habitats, whereas the drop in richness at the range boundaries is due to environmental inefficiency (Lira-Noriega and Manthey 2014). As a result, the hypothesis declares that species abundance is exactly proportionate to habitat appropriateness in a geographical sense (Weber et al. 2016). According to Deák et al. (2018), landscape and habitat filters are major drivers of biodiversity of small habitat islands by influencing dispersal and extinction events in plant metapopulations. However, the relationship between the distribution of plant communities and environmental factors is one of the most important research problems in plant ecology (Burke 2001; Yavitt et al. 2009). Therefore, habitat environmental variables are important not only in identifying plant community structure and species distributional variations at a spatial scale but also in providing insight into the environmental requirements of the plant species needed for successful ecological restoration and biodiversity protection (Khurana and Singh 2001; Toledo et al. 2012; Birhanu et al. 2021).

In the context of growth, environments for the members of the family Cyatheaceae are influenced by temperature, light timing, and moisture and damp environments are beneficial for spore germination and growth (Mehltreter 2006; Nagano and Suzuki 2007; Volkova et al. 2011). Habitat quality also affects the persistence of species in fragmented landscapes, which influences population vital rates (Hanski 2015). As per Wan et al. (2019), habitat loss and fragmentation are the most pressing threats to biodiversity, yet assessing their impacts across broad landscapes is challenging. Ferns being the most primitive Tracheophytes, face evolutionary stress due to gradual changes in the environment (Niklas et al. 1983). The majority of the Cyatheaceae are extinct due to changes in ecology and Earth's evolution. Few species that were found to be flourishing in certain limited locations with suitable biological settings managed to avoid extinction (Ho et al. 2016).

Cyatheaceae is an ancient plant family distributed widely in tropical and sub-tropical regions of the world (Hassler and Swale 2001; Labiak and Matos 2009; Ho et al. 2016). There are around 12,000 species of ferns distributed worldwide, of which Cyatheaceae includes ca. 600 species (Smith et al 2006; Korall et al. 2006). Plants of this family are very distinct from other tree ferns for the presence of pluricellular hairs and various types of scale in their inducements (Kramer and Green 1990). Fern diversity in the Indian subcontinent is very high, with approx. 900–1000 reported species (Chandra et al. 2008), and about half of them are reported from Northeast India (Gupta 2003).

Gymnosphaera is one of the most important fern genera in the tropics, constituting the main arborescent fern flora in humid forests (Labiak and Matos 2009). The species has various economic values (e.g., medicine) and, therefore, is facing threats due to over-exploitation in many places (Janssen 2006; Paul et al. 2015). However, population characterization, distribution mapping, reproductive biology, micropropagation protocol standardization, and reintroduction were undertaken for *C. spinulosa* (Barik et al. 2018). Obviously, *G. gigantea* was included in the threatened plants of India by Barik et al. (2018), but to date, no assessment has been conducted by the present approaches.

Many species of ecological and economic significance, including *G. gigantea*, face tremendous pressure and are at risk in this biological diversity-rich region of the Indo-Burma hotspot. Mostly, due to climate change, Northeast India is experiencing a series of environmental problems, viz. habitat loss, habitat modification, land-use, and land-cover change, pollution, over-exploitation of biological resources, and alien species invasion (Roy et al. 2015; Barik et al. 2018). Various anthropogenic activities *viz*., agricultural practices especially slash and burn (Jhum), deforestation, illegal logging of timber, and conversion of the forested area into rubber monoculture plantation resulted in tremendous pressure on the natural habitat of several plant communities in the state of Tripura, India (Majumdar et al. 2012, 2019). Populations of *G. gigantea* are very low in nature which may hinder poor regeneration. *G. gigantea* has been placed in CITES' Appendix II to safeguard it from over-exploitation, and its export has been limited (Sanjappa and Lakshminarasimhan 2011) to prevent anthropogenic interference and the export of valuable plant species around the world (Thomas et al. 2006). IUCN has also included many species of Cyatheaceae in the Red List of Threatened Species category (IUCN 2014). Thus, understanding the distribution, physiological characteristics, and habitat preferences of a particular species is pivotal while selecting conservation areas to maintain its diversity (Burgess et al. 2005; Gachet et al. 2005; Pfab et al. 2011; Roy et al. 2012; Koo et al. 2019).

Geographic information system (GIS) provides the spatial analysis module for applying overlay analysis on the individual species locational map, slope, aspect, sea-level altitude, and various habitat environmental data (Wu and Smeins 2000; Culmsee et al. 2014). One of the most popular geostatistical and mathematical interpolation approaches, the inverse distance weighted (IDW) method, has been used to estimate the target parameters in several scientific fields (Chiang and Chang 2009; Aminu et al. 2015; Rostami et al. 2019). Geostatistical interpolation is a statistical technique used to estimate values at unsampled locations based on the surrounding sampled locations. It utilizes mathematical models to analyze spatial data patterns and relationships, such as the spatial correlation between sampled locations. Entropy Weighted Habitat Index (EWHI) is a weighting scheme used to evaluate and prioritize the conservation value of habitats. It considers multiple factors such as species richness, rarity, and threats to biodiversity, and assigns weights based on the degree of importance of each factor (Guiasu and Guiasu 2010). Therefore, geostatistical interpolation based on EWHI involves using the EWHI weighting scheme as a parameter in the geostatistical model to improve the accuracy of spatial estimation for conservation-related purposes. This approach considers the spatial patterns of the conservation value of habitats, making it particularly useful in biodiversity studies and resource management decision-making.

In this study, the IDW method was used to interpolate the spatial distribution of suitable habitats for the conservation implication of *G. gigantea*. For a threatened species, the habitat environmental data of species integration can be used to select suitable habitats as conservation areas for forest management, prohibiting human disturbances that may result in species death and promoting the growth and health of the species (Burgess et al. 2005; Nagendra et al. 2013). Environmental management and assessment as well as the creation of conservation strategies have both benefited from the widespread use of SWOT (Strengths, Weaknesses, Opportunities, and Threats) analysis over the past 10 years, keeping in mind the primary conservation problem and priority setting (Nikolaou and Evangelinos 2010; Martins et al. 2013; Scolozzi et al. 2014; Dulić et al. 2020). Rauch (2007) claims that this analysis is a practical tool for strategic planning since it identifies internal strengths and weaknesses as well as possibilities and challenges in the current environment. The use of SWOT analysis would be very effective when establishing conservation priority sites and future reintroduction programs for threatened species, particularly for the tree fern community. In most of the conservation studies were confined to Angiospermic plants and pteridophytes have been given poor attention. Many pteridophytic species might be facing threats of extinction and need immediate attention for studying their population dynamics as well as different phenoplastic events.

We assumed that habitat characteristics and habitat environmental factors should exhibit close association with the total abundance of *G. gigantea* in the remnant forest patches, whether intact or disturbed. We first investigated habitat requirements in terms of habitat-based factors closely associated with the growth and survival of *G. gigantea* populations; secondly, investigated the effects of different habitat environmental factors on the *G. gigantea* abundance; thirdly, we built a suitability map of *G. gigantea* for conservation implications and future reintroduction in their natural habitats.

Materials and methods

Study area

The state of Tripura is in a tropical climate and receives plenty of rain during the monsoon season. Flora and fauna of the area are closely related to those of the Indo-Malayan and Indo-Chinese sub-regions. The state is in the 9B-North-East hills bio-geographic zone (Champion and Seth 1968) and has a rich biodiversity. The state lies between 22° 56′ to 24° 32′ N latitudes and 90° 09′ to 92° 20′ E longitudes. The state is characterized by three distinct climates: tropical savanna, tropical monsoon, and humid subtropical. Summer temperatures in the state range from 21 to 38 °C, while winter temperatures range from 13 to 27 °C. The annual rainfall varies between 1922 and 2855 mm (Majumdar et al. 2012). According to the Forest Survey of India (ISFR 2021), the state's total forest and tree cover is 7722 km^2, or equal to

73% of the overall geographical area. The forest cover of the state has been classified into six types: (I) East Himalayan lower Bhabar sal forest (3C/C1b (ii)), (II) Cachar tropical semi-evergreen forest (2B/2S2/C2), (III) East Himalayan moist mixed deciduous forest (3C/C3b (iii)), (IV) low alluvial savanna woodland (3B/E3), (V) dry deciduous forests (5B/C2/5/E1), and (VI) moist bamboo brakes (2B/E3) (Champion and Seth 1968; Majumdar and Datta 2018).

Study species

Gymnosphaera gigantea (Wall. ex Hook.) S.Y.Dong (Synonyms: *Alsophila gigantea* Wall. ex Hook.: *Cyathea gigantea* (Wall. ex Hook.) Holttum; *Dichorexia gigantea* (Wall. ex Hook.) C.Presl is a scaly tree fern distributed in the moist open areas of North-eastern to Southern India, Thailand, Sri Lanka, Nepal, Western Java, Vietnam, Laos, China, Burma, and Bangladesh (Large and Braggins 2004; Kurup 2007; POWO 2022). In India, it is mainly distributed in all eight north-eastern states, namely Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland, Tripura, and Sikkim (Paul et al. 2015); and in West Bengal, Western Ghats, Madhya Pradesh, and Andaman and Nicobar Islands (Khare et al 2005).

G. gigantea prefers 56–60% shade with highly humid soil, average annual rainfall of 2973 mm with maximum occurring during May and August, and an average temperature ranging between 17.7 to 29.5 °C and 46 to 98% relative humidity (Ranil et al. 2017).) The species grows preferably in sandy to sandy loam soil with 11.98% to 41.31% moisture content and a pH value ranging between 4.58 and 7.28 (Paul et al. 2015). *G. gigantea* is a highly medicinal plant with its aerial parts being used as an anti-inflammatory substance (Asolkar et al. 1992). It is also grown as an ornamental plant (Mishra and Behera 2020). Tribes use the fronds to cure body aches and for decorations (Kumar et al. 2003; Kala 2005); the stem is used for epiphytic orchid cultivation in Northeast India as well as for making pots, flower vases, ashtrays, etc. (Khan et al. 2002). Different cultural groups use the rhizome to treat white discharge, chronic jaundice, fever, and body ache (Rout et al. 2009; Kala 2005; Kiran et al. 2012). Some also use it as a source of starch (Paul et al. 2015). The plant also treats cuts and wounds (Nath et al. 2019). It has various pharmacological activities, including synergistic activity (Nath et al. 2019), antioxidant (Das et al. 2013), and larvicidal properties (Narayanan and Antonysamy 2017).

Field sampling

A grid-based approach was used in Tripura, India, to study the habitat of *G. gigantea* (Fig. 1). The size of each grid is ~ 6.3 × 6. 3 km and the area will be about ~ 40 km^2. Two belt transects of 10 m × 500 m were laid in each of the 6.3 × 6.3 km grid with a sampling intensity of 0.01%, which is a standard requirement for such enumerations (Shivaraj et al. 2000). Population-level unique locations and specific observations were also included as part of the metadata. A transect (500 × 10 m) consisted of five (5) 100 m long continuous sub-plots, each of which covered 1000 m^2. Nineteen unique belts transect were assessed as 19 populations and tagged as the habitat of *G. gigantea* out of the entire sampled area (Table 1; Fig. 2). The overall methodological approach used in the present study is presented in Fig. S1. The habitats of *G. gigantea* were sampled at two stages of growth: adult tree (all individuals with ≥ 30 cm girth at breast height (GBH) over bark measured at 1.3 m) and sapling or juvenile (≥ 10 cm to < 30 cm GBH) following Shankar (2001). The abundance in each occurrence locality was expressed as a total count of the adults and saplings or juveniles. However, due to time constraints and habitat complexity, we did not extend our sampling efforts up to the seedling level.

Clinometers were used to measure the height of all the trees in the plot. The equation was derived from the simple formula for the area of a circle (area = πr^2) to compute the basal area (in m^2). The number of trees per unit area and expressed per hectare basis was used to estimate the density of tree species across the habitats of *G. gigantea*.

Specimen verification and database

All tree species, including *G. gigantea*, were recorded, and unidentified specimens were collected from the field for taxonomical examination and turned into standard mounted herbarium sheets, according to Jain and Rao (1977). The taxonomic identification was based on information from regional flora such as Flora of British India by Hooker (1872–1897), Flora of Assam by Kanjilal et al. (1934–1940), and Flora of Tripura by Deb (1981–1983). Champion and Seth (1968) determined the vegetation type in the research locations, and the major tree species were identified by examining the regional flora.

Soil sampling and analysis

Soil samples were taken from 0–15 cm depths from all the habitats of *G. gigantea* using 15-cm-scaled soil cores with a 5.6 cm inner diameter. Three samples were selected from each population, totaling 57 samples. Soil samples were collected and air-dried in the laboratory. Before analyzing physical and chemical properties, samples were passed through a 2-mm sieve to remove stones, roots, and major organic residues. The Walkley and Black (1934) technique was used to calculate the SOC% (soil organic carbon %). Blake and Hedge's (1986) method was followed to determine the moisture content percentage. The soil-core method was used to

Fig. 1 Study population of *Gymnosphaera gigantea*: **A**–**C** habitats, **D** a mature plant

calculate the bulk density (BD) (Blake and Hedge 1986). The pH of the soil was calculated using a 1:2 (soil: water) ratio. The SOC stocks (Mg ha^{-1}) were calculated using Blanco-Canqui and Lal (2008).

Population structure and species diversity

Analytical features of the plant community were quantitatively analyzed for abundance, density, and frequency following Curtis and McIntosh (1950). Relative frequency, relative density, relative basal area, and Importance Value Index (IVI) were calculated following Mueller-Dombois and Ellenberg (1974). Shannon and Wiener (1963), Simpson (1949), and Pielou (1966) indices were calculated using statistical software PAST version 3 (Hammer et al. 2001) to calculate tree species diversity, dominance, and evenness of *G. gigantea* habitats. Using Chao1, species richness and expected species richness for every 19 populations of *G. gigantea* were calculated. The simplest nonparametric estimator, Chao1, calculates the total number of species by adding a term that depends only on the observed number of singletons, i.e., species each represented by a single individual and doubletons (i.e., species each represented by exactly two individuals) to the number of species observed (Chao et al. 2006). The number of species on the *y*-axis was compared to the number of individuals on the *x*-axis to compare species richness across the transects (Simberloff 1972) and species ranking was calculated by plotting the Importance Value Index (IVI) against species rank from the lowest to highest, to obtain the dominance-diversity curve across the habitats of *G. gigantea* (Whittaker 1970).

Table 1 Population structure, disturbance score, and patch characteristics of different study populations of *G. gigantea*

Population Id	Transect Id	Forest and patch type	Patch size (ha)	*Disturbance score	Abundance (no. of individuals)	Tree species richness
P1	TR012T1	Moist mixed deciduous forest; continuous forest	48.00	16.00	2	53
P2	TR038T2	Moist mixed deciduous forest; continuous forest	13.44	20.00	2	19
P3	TR042T1	Moist mixed deciduous forest; fragmented and mostly degraded	1.59	41.00	2	50
P4	TR054T1	Moist mixed deciduous forest; fragmented	6.55	33.00	4	36
P5	TR065T2	Moist mixed deciduous forest; fragmented	5.03	35.00	3	32
P6	TR066T2P1	Moist mixed deciduous forest; continuous forest; Gomati River running along is the key attributes for viable population of *G. gigantea*	35.89	18.00	8	45
P7	TR066T2P2	Moist mixed deciduous forest; continuous forest; Gomati River running along is the key attributes for viable population of *G. gigantea*	43.97	24.00	1	27
P8	TR070T2	Moist mixed deciduous forest; fragmented	1.98	42.00	2	22
P9	TR072T1	Moist mixed deciduous forest; fragmented and degraded	6.45	36.00	3	22
P10	TR109T2	Moist mixed deciduous forest; fragmented	6.27	56.00	2	29
P11	TR115T1	Moist mixed deciduous forest; fragmented	11.00	33.00	4	39
P12	TR116T2	Moist mixed deciduous forest; fragmented and partially degraded	5.05	22.00	3	38
P13	TR117T1	Semi-evergreen forest patches surrounded by moist mixed deciduous forest; continuous forest; viable populations are in severe threat	45.05	15.00	4	30
P14	TR130T1	Semi-evergreen forest patches surrounded by moist mixed deciduous forest; continuous forest and fragmented	14.40	25.00	4	32
P15	TR131T1	Semi-evergreen forest; continuous forest	29.41	15.00	3	20
P16	TR133T1	Moist mixed deciduous forest; fragmented and partially degraded	26.69	19.00	1	61
P17	TR185T1	Moist mixed deciduous forest; fragmented and degraded	2.59	38.00	4	28
P18	TR185T2	Moist mixed deciduous forest; fragmented and degraded	2.44	37.00	2	55
P19	TR222T1	Part of continuous tropical semi-evergreen forest belts; now partially converted to moist mixed deciduous forest; potential habitat of *G. gigantea* at the lower part of hilly tracts	11.59	28.00	3	33

*Disturbance score based on the number of cut trees, number of dead trees, fire, grazing, fuel wood collection, thatch collection, soil removal, and NTFP (non-timber forest product) collection

Extraction of GIS layer

Geospatial techniques have been used for mapping geographical attributes by using ArcMap v.10.8. An administrative map of Tripura was extracted from Diva GIS (Hijmans et al. 2012). Handheld global positioning system (GPS) has been used for demarcates the spatial location of the habitats of *G. gigantea* in the state of Tripura. Relative relief and slope data have been extracted for the radiometric terrain corrected ALOS PALSAR Digital Elevation Model (DEM). DEM data was collected from the earth database of NASA through Alaska Satellite Facility (ASF). Fishnet techniques have been used for relief and zonal slope distribution (Westin 2009). A hydrological model has been used to extract the stream, and stream order has been calculated using the Strahler method (Hughes et al. 2011; Pradhan et al. 2012) (Fig. 3). We used annual average surface temperature of 2021 using GISS Surface Temperature Analysis (v4) and for humidity, we used NCEP/NCAR reanalysis data of 2021.

Statistical analysis

Complete summaries of all the 21 predictor variables including field-based habitat factors, extracted variables through GIS, and soil variables acquired for *G. gigantea* are presented in Table 2. These variables were explicitly used for principal component analysis (PCA) followed by generalized linear modelling and Entropy Weighted Habitat Index to propose a suitable factor affecting *G. gigantea* habitats and to prepare a suitability map in the study area for conservation

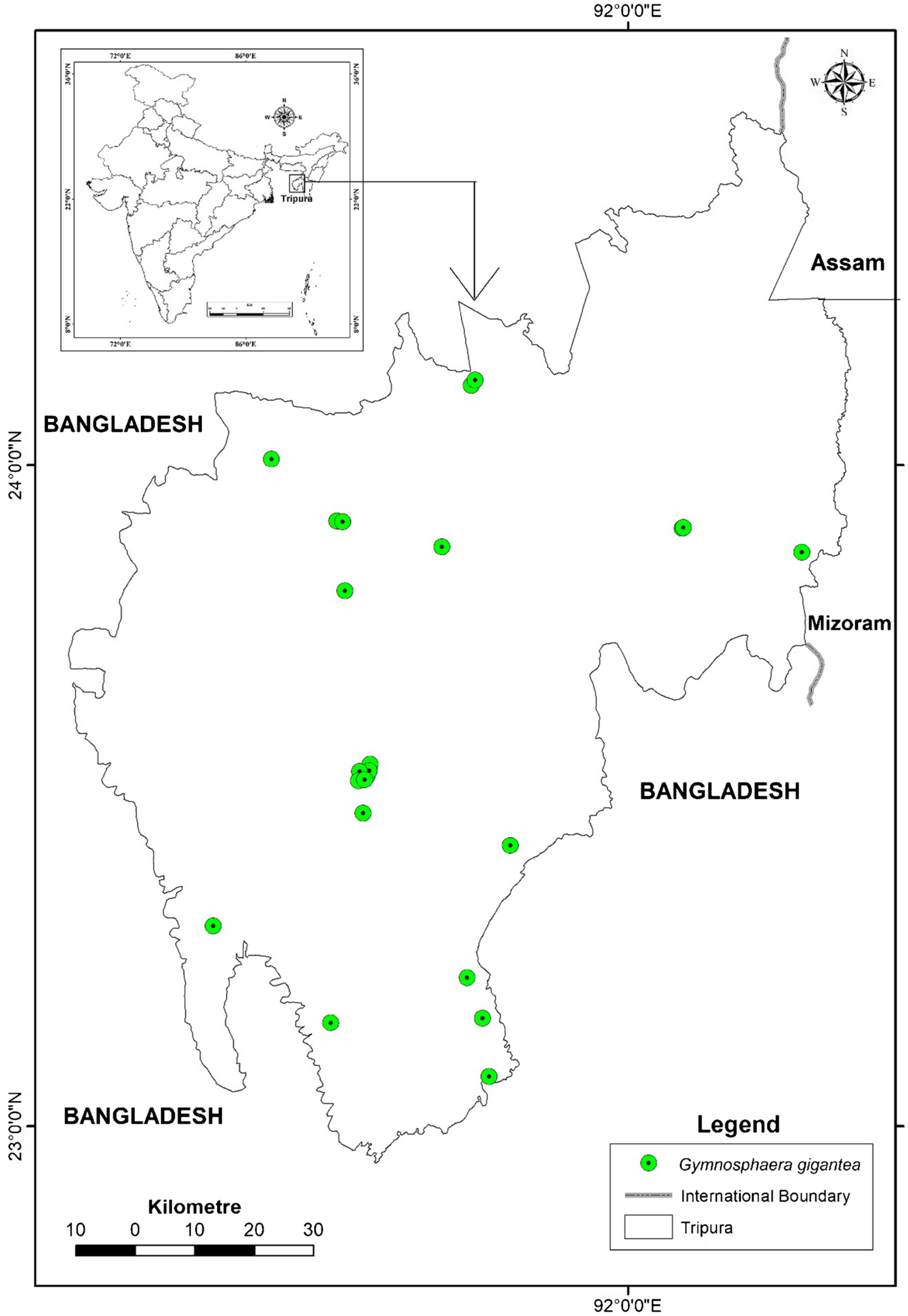


Fig. 2 Location map representing study populations of *G. gigantea* (Source: Prepared by the authors, 2022 using ArcMap v.10.8)

implications. We conducted tests for normality and homogeneity of variances before using parametric testing. We log(x + 1)-transformed the habitat environmental variables before analysis to ensure normality and homoscedasticity because they were not normally distributed (Shapiro–Wilk test) (Piñeiro et al. 2015).

To avoid multicollinearity (Graham 2003), we performed a principal component analysis (PCA) based on correlation matrices to reduce the number of habitat environmental variables. PCA has been used to nullify the correlation of the explanatory variables and the inter-relationship among them (Jolliffe 2002; Cruz-Cárdenas et al. 2014). The PCA reduces the number of orthogonal variables among 21 original habitat environmental predictors. All the predictor variables were subjected to PCA to screen for the factors with significant contributions using the *prcomp* function of R version 4.2.0 (R Development Core Team 2022). The primary variables associated with various habitat characteristics were grouped using PCA after the data for each habitat were extracted. We screened the variables based on their factor score in

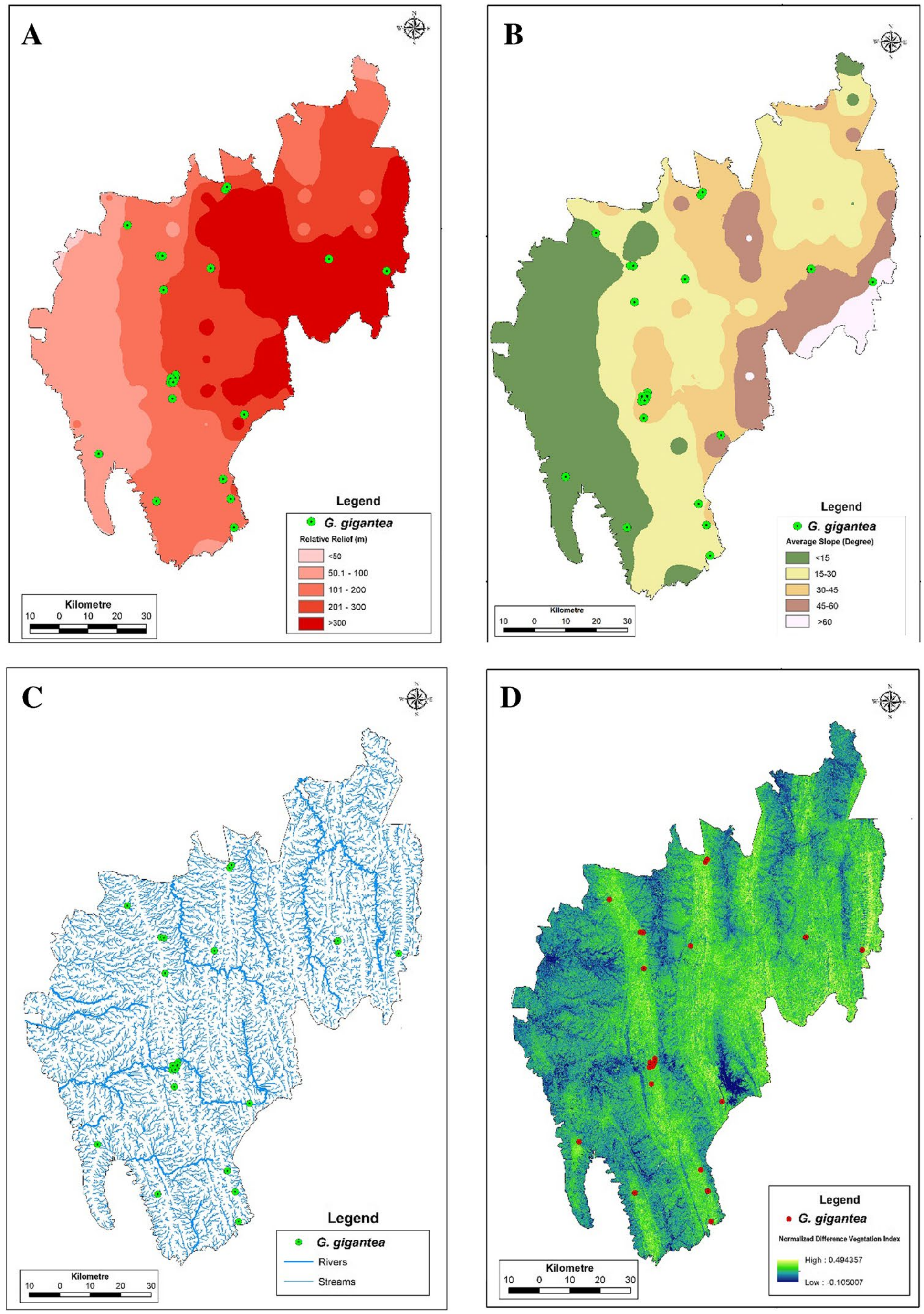


Fig. 3 Thematic layers used in the study: **A** relative relief, **B** average slope, **C** drainage network, and **D** Normalized Difference Vegetation Index (NDVI)

addition to presenting the PCs with eigenvalues greater than 1. We selected 11 habitat environmental variables (factor score > |0.7|) from the first three PCs, representing around 58% of data variances used for developing GLMs. The 11 variables included in the GLMs were (i) elevation, (ii) average surface temperature, (iii) NDVI (Normalized Difference Vegetation Index), (iv) NDWI (Normalized Difference Water Index), (v) patch size, (vi) disturbance score, (vii) disturbance intensity (%), (viii) soil pH, (ix) moisture content (%), (x) SOC (%), and (xi) SOC stock.

In the model, the species abundance was considered as the response (dependent) variable, and 11 habitat environmental variables (PCA factors) were taken as the explanatory (predictor) variable. Akaike's Information Criterion (AIC), ΔAIC, AIC weight, and log-likelihood of each model have been used to evaluate multiple regression models and select the model that explains the best relationship between species abundance and predictor variables (Deák et al. 2018). To evaluate the effect of the predictor variables on the *G. gigantea* abundance, we fitted a

Table 2 Summaries of habitat environmental factors across the populations of *G. gigantea*

Habitat environmental factors	Minimum	Maximum	Average	SD	CV
Elevation (m)	60.000	747.000	134.211	151.409	112.814
Slope (degree)	1.314	31.594	13.454	9.108	67.701
Aspect (degree)	2.911	350.538	206.912	119.000	57.512
Soil moisture (mm)	4.546	22.870	13.763	6.485	47.120
Average surface humidity (g kg^{-1})	27.315	30.833	29.224	1.603	5.484
Average surface temperature (degree)	28.891	29.211	29.098	0.077	0.266
NDVI (Normalized Difference Vegetation Index)	0.179	0.353	0.278	0.043	15.609
NDWI (Normalized Difference Water Index)	−0.331	−0.156	−0.254	0.043	−16.996
Patch size (ha)	1.590	48.000	16.705	16.103	96.397
Disturbance score	15.000	56.000	29.105	11.200	38.480
Disturbance intensity (%)	2.301	8.589	4.464	1.718	38.480
Stand Density ha^{-1}	134.000	514.000	261.579	99.064	37.871
G. gigantea basal area ha^{-1}	0.013	0.460	0.089	0.133	148.485
Stand basal area ha^{-1}	2.759	38.307	8.646	8.556	98.954
Tree species richness	19.000	61.000	36.263	12.409	34.219
Soil pH	4.467	5.473	4.976	0.364	7.317
Moisture content (%)	13.097	21.827	16.744	2.875	17.170
Soil temperature (° C)	17.530	24.893	18.848	1.714	9.094
Bulk density (g cm^{-3})	1.193	1.423	1.309	0.071	5.438
SOC (%)	0.847	1.393	1.048	0.170	16.250
SOC stock (Mg ha^{-1})	16.630	29.196	20.364	3.480	17.088

SD standard deviation, *CV* coefficient of variation

null model with Poisson distribution and log link function and then added significant explanatory variables using the forward addition procedure. We performed model diagnostics and validated that our Poisson models were not overdispersed. All the models were examined with the DHARMa package in R, which uses a simulation-based approach to create readily interpretable scaled residuals from GLMs (Hartig 2018; Harrison et al. 2018).

We built models of single explanatory variables, followed by more complex models with combinations of explanatory variables, and ranked these using AIC values. After fitting GLMs in the full model, we examined the relative importance of the explanatory variables using the model-comparison framework implemented in the AICcmodavg package (Mazerolle 2020) of R. Thereafter calculated the values of Akaike's Information Criterion corrected (AICc) for each model. AICc estimates information lost when a certain model is used, which facilitates the selection of the most relevant models and explanatory variables. We selected the best models (ΔAIC = 0) and models with substantial support (ΔAIC > 2) as suggested by Burnham and Anderson (2002). The statistical analyses were performed using R version 4.2.0 (R Development Core Team 2022).

Entropy Weighted Habitat Index and mapping suitability zone

We extracted pixel values from input rasters using 57 observation points. A multivariate PCA was employed to filter out non-linear noise variables. EWHI was calculated point-by-point, and these 57 EWHI points were interpolated using the IDW technique (Natesan et al. 2021) in ArcGIS v.10.8. software. IDW estimates cell values by averaging the values of sample data points in the neighborhood of each processing cell specifying a lower power that will give more influence to the points that are farther away, resulting in a smoother surface (Roy et al. 2021). Entropy Weighted Habitat Index (EWHI) has been proposed using the following formula:

$$P_{ij} = \frac{x_{ij}}{\sum_{i=1}^{m} x_{ij}} \quad (1)$$

where m represents the number of sampling areas and P_{ij} is the proportional occurrence of the value (x_{ij}) corresponding to jth evaluated parameter (index) in ith sample (ward), calculated by using the following equation

$$E_j = -k \sum_{i=1}^{m} p_{ij} \ \ln \ p_{ij} \tag{2}$$

where K is the proportionality constant and measured as

$$k = {}^{1}\!/_{\ln(m)}$$

The corresponding weight of the jth parameter (index), denoted by W_j, for $j = 1,2,\ldots,s$, is evaluated as

$$W_j = \frac{1 - E_j}{\sum_{j=1}^{n}(1 - E_j)} \tag{3}$$

Finally, EWHI for each sample station "j" ($EWHI_j$) has been calculated by using the following formula

$$EWHI_j = \sum_{i=1}^{m} \frac{W_j \times x_{ij}}{\overline{x_{ij}}} \tag{4}$$

We used synthetic indictor (SI) to classify the suitability zone derived from the approach used by Roy et al. (2022) which uses both synthetic indicator (SI) and alternative synthetic indicators (ASI) to propose generalized synthetic indicator (GSI). SI is appropriate for the normality assumptions of the observational data sets, and the ASI is appropriate for asymmetric or skewed data sets. Since we have tested our datasets for normality and homogeneity of variances before analysis to ensure normal distribution of datasets, we have employed synthetic indicator (SI) in the present study and the equation we used for this indicator is as follows:

$$z_i = \frac{x_i - mean(x)}{\sigma(x)} \tag{5}$$

where x_i is the observed value of selected habitat environmental factors, mean (x) is the average of selected habitat environmental factors, and σ (x) is the standard deviation of selected habitat environmental factors.

LULC analysis for conservation implications

A land use and land cover (LULC) map has been prepared at the micro-level specified at a scale of 1:40 for the conservation planning procedure. Three radiometrically and geometrically corrected Sentinel-2 Surface Reflectance imageries with zero cloudiness were used in this study. The imageries also reprojected to Universal Transverse Mercator/UTM Zone 46N with WGS 1984 datum. Only single imagery was selected to the classification process. We used (L1C_T46QDM_A026285_20220319T042930; Table S1) natural bands and Band 2 (Blue, 490 nm), Band 3 (Green, 560 nm), Band 4 (Red, 665 nm), and Band 8 (Near-Infrared or NIR, 842 nm) spectral indices to identify various features including water bodies, bare land, scrub area, hilly areas, agricultural areas, thick forests, and thin forests. We employed the maximum likelihood (ML) classification method, supervised by 100 training polygons for every class. The final LULC map was selected based on a F1 score of 0.85 and a Kappa coefficient of 0.80, with a minimum polygon size of 0.35 ha (3500 m^2). The classification process was performed using GIS and RS software, i.e., ArcGIS v.10.8 and Map Info v.17.

SWOT analysis

Synthesized SWOT results were used to determine the key drivers and difficulties to future conservation and reintroduction of *G. gigantea* in its natural habitats. The SWOT analysis included data obtained through field surveys through observations and measurements consisting on-site data collection and consultations with community stakeholders, forest officials, and concerned experts which further allows for better decision-making to adopt management and conservation planning. We followed the methodological approach of Braun and Amorim (2014) combined with local perspectives to synthesize qualitative information as a basis for setting up priority areas for conservation. The strengths and weaknesses represent positive and negative features of factors at the habitat level as well as while implementing conservation measures. On the other hand, the positive and negative factors are characterized as opportunities and threats, which indicate the ecological and economic potential of the species investigated and the potential endangerment of the populations examined.

Results

Population structure and abundance of *G. gigantea*

This study analyzed the habitat association of threatened tree fern *G. gigantea* encountered in 17 sampled grids through 19 permanent belt transects (~ 95,000 sq. m or 9.5 ha). In the habit of *G. gigantea*, tree species richness ranged from 19 to 61, with an average of approximately 35 trees in all the sampled patches. Furthermore, the rarefaction curves confirmed that the habitat association of *G. gigantea* is much steeper, suggesting high species richness (Fig. 4A). Using the Chao1 richness estimator, a possible highest total woody species richness of ~ 204 was estimated for the habitat of *G. gigantea* (Table S2). However, the habitats' overall tree species richness was recorded as 183 species. The diversity-dominance curve displayed a natural log series distribution where high species ranked (1–183), from most to least abundant and most of the species had lower abundance and population in the habitat of *G. gigantea*, while few species showed higher values

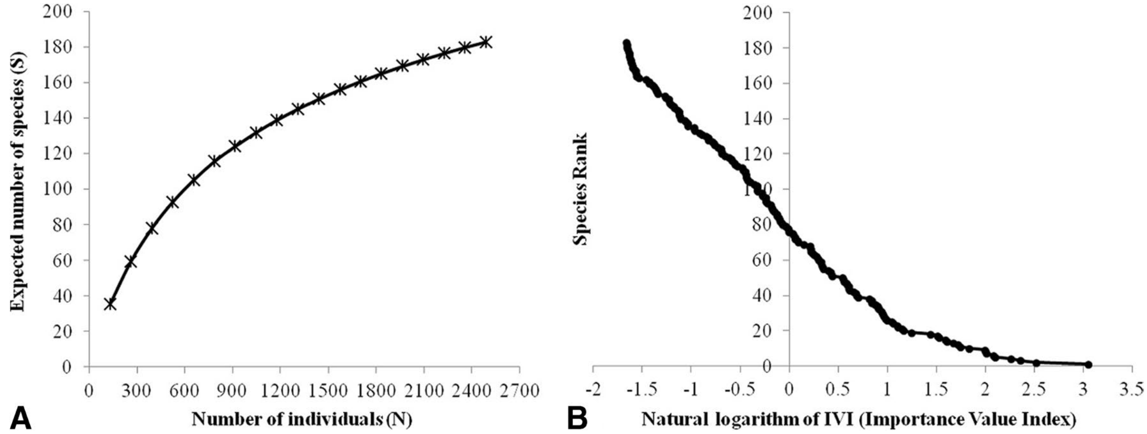


Fig. 4 Rarefaction, species rank, and dominance-diversity curve for habitats of *G. gigantea*. **A** Rarefaction curves for comparing the species richness in the habitat. **B** Species rank and dominance-diversity curve based on the IVI (importance value index) of tree species

(Fig. 4B). A complete list of tree species identified, their relative measures, and overall ecological status (IVI) in the studied population of *G. gigantea* is presented in Table S3. *Tectona grandis* appeared to be the most abundant and had a maximum IVI of 21.12 followed by *Bombax ceiba* (IVI = 12.38), *Callicarpa arborea* (IVI = 10.57), *Artocarpus chama* (IVI = 9.59), *Albizia procera* (IVI = 8.20), *Macaranga denticulata* (IVI = 8.05), *Ficus auriculata* (IVI = 7.49), *Artocarpus lacucha* (IVI = 7.40), *Anogeissus acuminata* (IVI = 7.38), and *Ficus hispida* (IVI = 6.25) as top ten codominant species. *G. gigantea* represents an IVI value of 5.74, although some species may occur predominantly in one site while absent in other sites. Also, some species may occur predominantly in one site while absent in other sites. Therefore site-wise, their local dominance is not exhibited in the overall information. Forest types in the habitats were found to be moist mixed deciduous forest (fifteen locations), semi-evergreen forest (one location), semi-evergreen forest patches surrounded by moist mixed deciduous forest (two locations), and part of continuous tropical semi-evergreen forest belts now partially converted to moist mixed deciduous forest types (one location) (Table 1). The degree of fragmentation of most of the sites was found to be physically dissected along with partially degraded. The understory community was dominated by seedlings and saplings of numerous light-demanding tree species, such as *Macaranga denticulata*, *Glochidion assamicum*, *Holarrhena pubescens*, along with species of grasses, herbs, and lianas. The understorey vegetation also had saplings of shade-loving trees, viz., *Holigarna caustica*, *Saraca asoca*, *Knema* sp., *Palaquium polyanthum*, and other moisture-loving species such as *Tacca integrifolia*, *Polygonum strigosum*, *Elatostema platyphyllum*, *Boehmeria platyphylla*, *Pilea glaberrima*, *Begonia surculigera*, *Pleomele spicata*, *Pleomele angustifolia*, *Brassaiopsis glomerulata*, and members of fern and fern allies viz., *Pteris ensiformis*, *Pityrogramma calomelanos*, *Microlepia speluncae*, and *Equisetum* sp.

A total of 57 individuals *G. gigantea* was recorded from the 19 populations studied at the altitude varying from 59 to 747 m asl of which 28 individuals were juvenile and 29 were adults. The average density of *G. gigantea* (juvenile and adults) was six individuals ha^{-1}, which varied greatly among different populations and/or patches and ranged between 2 and 16 individuals ha^{-1} (Fig. 5A). The highest density was recorded in patches 11–16. The population structure of *G. gigantea* showed that ~ 89% of individuals belonged to ≥ 2–8 m height class and the lowest (~ 10%) to 8–14 m height class (Fig. 5B). The average height for juvenile and adults were 6.2 m (ranges between 2.2 and 13.0 m). Shannon diversity index across all the habitats of *G. gigantea* ranged between 2.069 and 3.762 with an average of 3.141, the Simpson dominance index ranged between 0.029 and 0.238 with an average of 0.065, the Evenness index in which species were more evenly distributed in the habitat of *G. gigantea* ranged between 0.417 and 0.840 to with an average of 0.702 (Table S2).

Effects of habitat environmental factors on *G. gigantea* abundance

Principle component analysis (PCA) revealed the relationship between predictor variables (climatic, soil, vegetation, and topographic factors) and *G. gigantea* abundance. The first and second axis explained 27.83% and 15.72% (cumulative %) of the total variation in the PCA, respectively (Fig. 6). The first PC axis is positively associated with patch size, soil moisture content, SOC, and SOC stock and negatively associated with the disturbance score, disturbance intensity, and soil pH. The second PC axis exhibited a strong

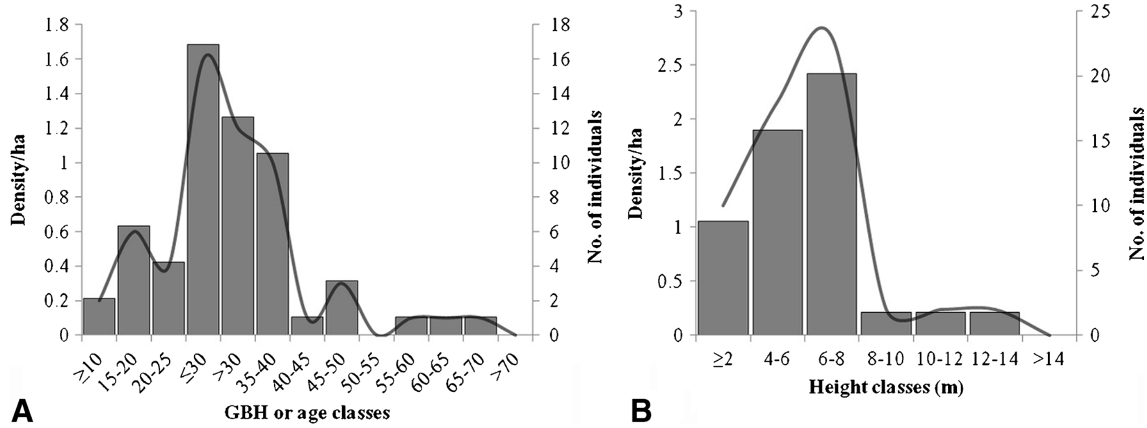
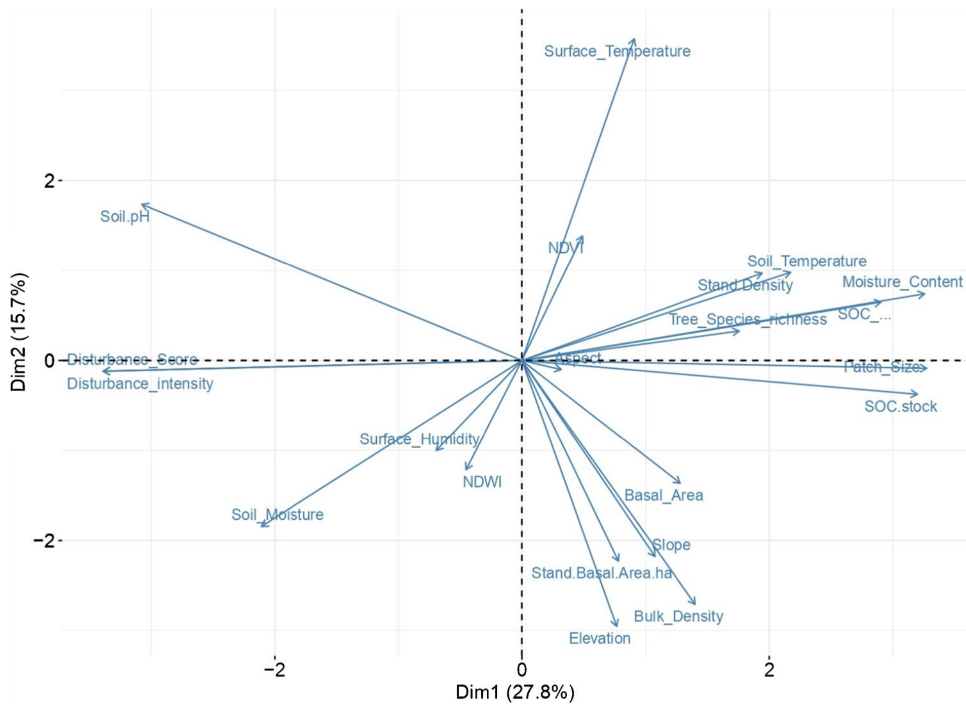


Fig. 5 GBH (girth) or age classes and height classes of *G. gigantea* recorded in different study populations. **A** Population structure and density distribution in different GBH or age classes. **B** Density distribution in different height classes among the studied population

Fig. 6 Principal Component Analysis (PCA) illustrating the relationship between 21 habitat environmental factors and *G. gigantea* abundance



positive association with average surface temperature and a negative association with elevation. The third PC axis accounted for 13.89% of the total variation and exhibited a positive association with NDWI and a negative association with NDVI (Table 3).

We evaluated the effects of 11 selected predictor variables singly and/or in combination on the abundance of *G. gigantea*. Out of 15 models, there were only four competing models (Table 4) that included NDWI, NDVI, Null model, NDVI, and NDWI combined (ΔAICc ≤ 2), which carries > 54% model weight. Due to less model weight coverage, we considered a total of fifteen models which carries ≥ 95% of the model weight. These first two models indicated that the abundance of *G. gigantea* is closely associated with the increase and decrease in NDWI and NDVI. Further combination of these two variables (AIC ~ 2) also has a significant effect on *G. gigantea* abundance. The next model was separated from the best model by AIC value ~ 3, indicating little influence on the species abundance, i.e., with the increase in disturbance intensity and disturbance score, the species abundance is likely to be decreased. The combined effect of NDWI and average surface temperature exhibited a significant effect on the abundance. The combined effect of NDVI and average surface temperature, soil pH, soil moisture, patch size, SOC stock, SOC%, average surface temperature, and

Table 3 Factor loadings of all 21 variables of the first 3 components (PCs) and cumulative variance percent for the principal component analysis (PCA)

Habitat environmental factors	PC1	PC2	PC3
Elevation (m)	0.189	**− 0.728**	− 0.074
Slope (degree)	0.265	− 0.537	0.549
Aspect (degree)	0.078	− 0.025	0.325
Soil moisture (mm)	− 0.520	− 0.455	− 0.513
Average surface humidity (g kg^{-1})	− 0.171	− 0.246	− 0.323
Average surface temperature (degree)	0.224	**0.881**	0.117
NDVI (Normalized Difference Vegetation Index)	0.121	0.341	**− 0.741**
NDWI (Normalized Difference Water Index)	− 0.112	− 0.299	**0.747**
Patch size (ha)	**0.807**	− 0.021	0.083
Disturbance score	**− 0.835**	− 0.029	0.227
Disturbance intensity (%)	**− 0.835**	− 0.029	0.227
Stand density ha^{-1}	0.479	0.239	0.324
G. gigantea basal area ha^{-1}	0.316	− 0.336	0.099
Stand basal area ha^{-1}	0.192	− 0.549	− 0.242
Tree species richness	0.433	0.081	0.675
Soil pH	**− 0.758**	0.427	− 0.019
Moisture content (%)	**0.803**	0.182	− 0.187
Soil temperature (° C)	0.535	0.241	0.268
Bulk density (g cm^{-3})	0.345	− 0.667	− 0.122
SOC (%)	**0.716**	0.160	− 0.246
SOC stock (Mg ha^{-1})	**0.788**	− 0.092	− 0.307
Eigenvalue	5.844	3.301	2.917
Variance explained (%)	27.829	15.718	13.892

*Variable PC scores that are in bold used for model building (GLM)

Table 4 Model ranking for detection of most significant habitat environmental variables that contributes to *G. gigantea* abundance

Model variables	K	AICc	ΔAICc	AICcWt	Cum.Wt	Log-likelihood
NDWI	2	69.210	0	0.190	0.190	−32.230
NDVI	2	69.470	0.260	0.170	0.350	−32.360
Null	1	70.220	1.010	0.110	0.470	−33.990
NDWI + NDVI	3	71.170	1.950	0.070	0.540	−31.780
NDWI + average surface temperature (degree)	3	72.060	2.850	0.050	0.590	−32.23
Disturbance intensity (%)	2	72.120	2.900	0.040	0.630	−33.680
Disturbance score	2	72.120	2.900	0.040	0.670	−33.680
NDVI + average surface temperature (degree)	3	72.310	3.100	0.040	0.710	−32.360
Soil pH	2	72.520	3.310	0.040	0.750	−33.890
Moisture content (%)	2	72.590	3.370	0.030	0.790	−33.920
Patch size (ha)	2	72.600	3.380	0.030	0.820	−33.920
SOC stock (Mg ha^{-1})	2	72.690	3.480	0.030	0.850	−33.970
SOC (%)	2	72.700	3.490	0.030	0.890	−33.980
Average surface temperature (degree)	2	72.720	3.510	0.030	0.920	−33.990
Elevation (m)	2	72.720	3.510	0.030	0.950	−33.990

elevation also has a significant effect on the abundance of *G. gigantea* (AIC ~ 4). This highlights the importance of nature's variability and relationships between habitat environmental factors and plausible limitations of the data sets observed during the current study.

Mapping of habitat suitability and conservation implications

It has been found that the 143.79 km^2 (1.38%) area of Tripura found with the most potential habitat for *G. gigantea*

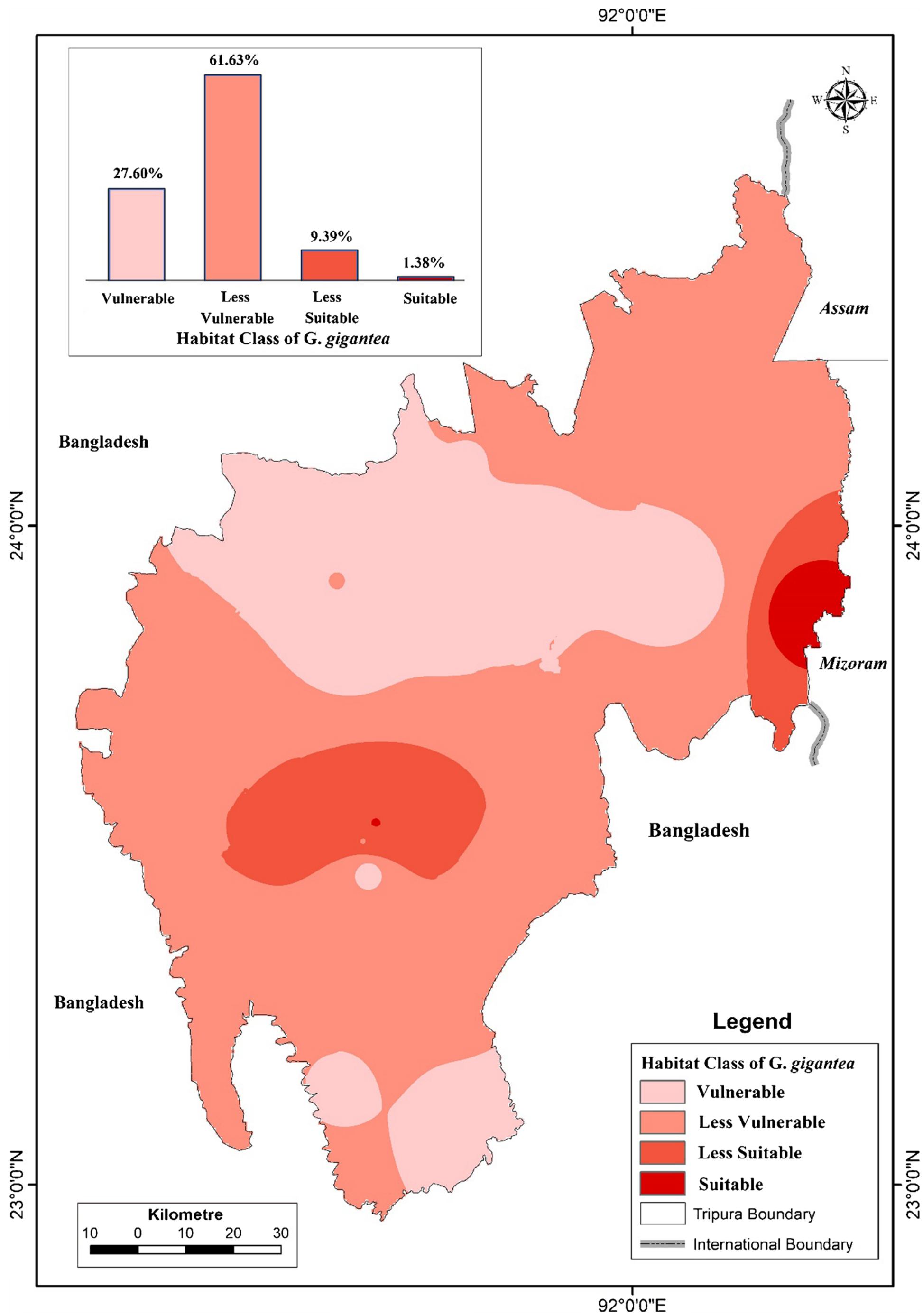


Fig. 7 Suitable habitats and conservation priority areas of *G. gigantea*, inferred from Shannon entropy using the inverse distance weighted interpolation technique

and is considered a priority area I. The area is in the Jampui Hill range of the North Tripura district, the eastern part of the state (Fig. 7). It has been observed that 980.83 km^2 area with potential for the *G. gigantea*. Most of the predicted areas are semi-evergreen and moist deciduous forests, which designates them as potential habitats. Nevertheless, the predicted areas also include patches of shifting cultivation fallows and degraded forests, indicating their potential as suitable habitats for *G. gigantea*. Field observations on the habitat status of the species revealed that the uplands experience recurrent disturbances in the form of tree lopping, grazing, fire, extraction of firewood and NTFPs, and invasive weeds compared to the glen habitats. On the other hand, about 2882.57 and 6435.23 km^2 areas of Tripura found with vulnerable and most vulnerable for *G. gigantea* (Fig. 7).

For future conservation planning of *G. gigantea* at the potential area, micro-level land use planning depicts that the eastern part of Tripura is the most potential. National Highway 108 passes the middle of the potential zone (Fig. 8). The most suitable habitat is located on the right bank of the river

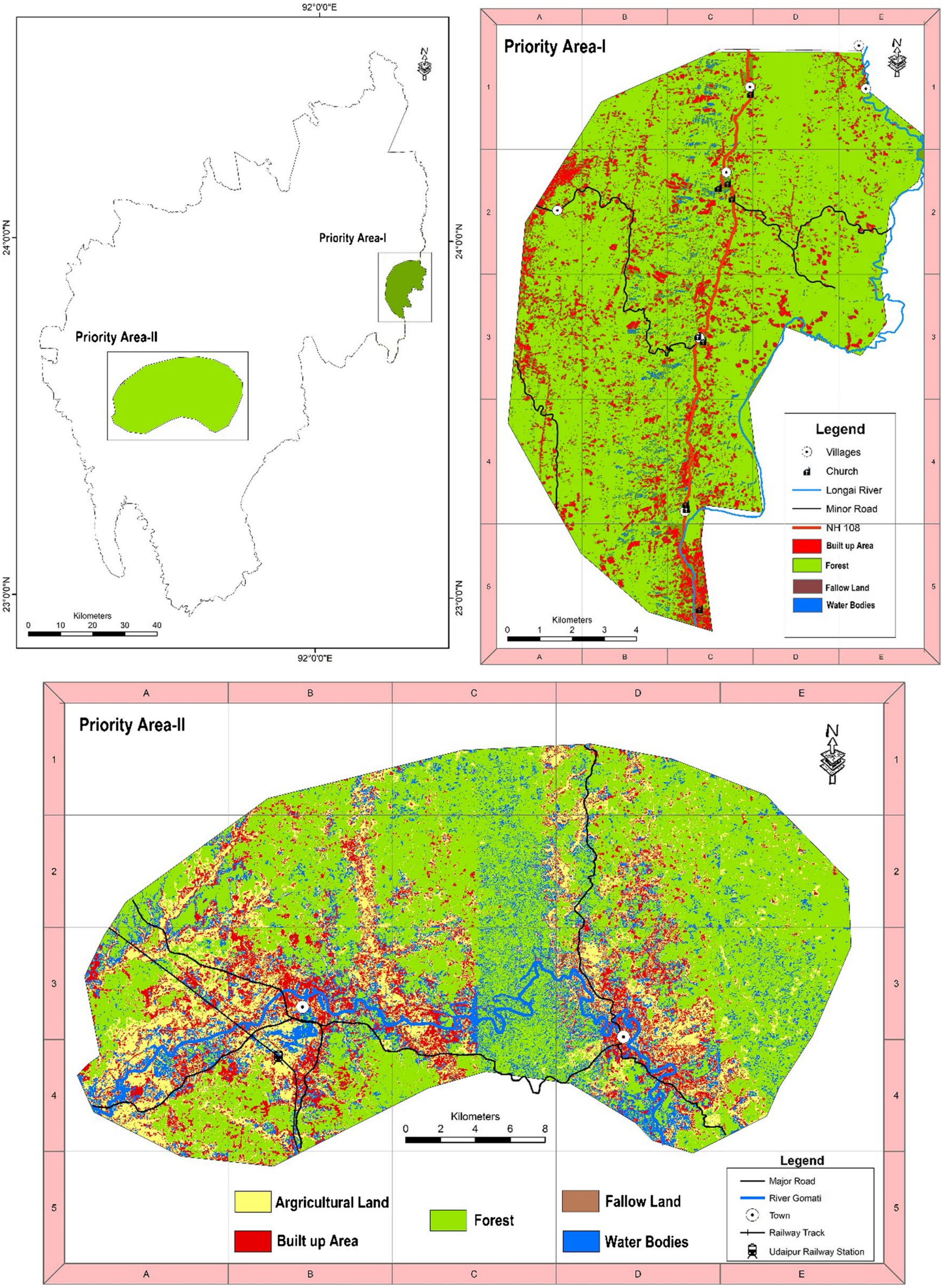


Fig. 8 Micro-level land use planning of potential suitable zones for future conservation implementation and reintroduction of *G. gigantea*

Longai. The 33.017-km-long Longai river flows from north to south which is the mainstream of the region. River Longai and its tributaries create favorable habitats for *G. gigantea.* Four major villages are located over here, namely Bangla, Tlangsang, Sabual, and Phuldungsei, and other villages of the area are Tumpanglui and Kahtobari. People's awareness and participation are very important for the conservation of *G. gigantea.* Administratively, these are located under the Jampui Rural Development Block as well as Local Panchayats should take the initiative to conserve *G. gigantea*. Socially, this region is occupant by Mizo and Reang (Bru) peoples, by believing they are Christian and Church has a significant impact on their lives which could use for conservation planning.

SWOT (Strength, Weakness, Opportunity, and Threat) proposed plan has been analyzed. With various positive factors, it has been observed that Jampui hill is located about 205 km away from Agartala, the capital city of the state. Even the district headquarter is situated 82.3 km away. Distance from the administrative warehouse is a crucial factor for policy implementation and policy intervention because implementing authorities and concerned experts are not able to visit frequently due to poor accessibility. Initial conservation policy needs the huge intervention of concern implanting authorities is required for training, awareness, marketing, and finance. In these circumstances, the second priority area, called priority area II, has also been proposed to conserve *G. gigantea*. The accuracy of the land use pattern of proposed conservation areas has been measured through Kappa coefficient, which depicts that the overall accuracy is 89.75%. The site of priority area II has located in the lower central part of the state under the upper Baramura Deotamura Reserve Forest. Agartala city is located about 53 km northwest of site B to conserve *G. gigantea.* The areas are well assessable by roadways and railways (Fig. 8). So, the administrative intervention will be easier in this region compared to the Jampui hill region. The site of priority area II has a mixed ethnic population concentration and implementing authorities would put extra effort into awareness and capacity building. With certain sort of positive and negative factors, both priority areas are viable for the conservation of *G. gigantea.*

Discussion

Habitat characteristics of *G. gigantea*

In the present study, we assessed habitat heterogeneity in terms of species association, their diversity, habitat environmental factors, and distribution of *G. gigantea* in a biodiversity hotspot region of North-eastern India. We also assessed how habitat environmental factors influence the overall abundance of *G. gigantea* in its habitats. This comprehensive study provides new insight into the distribution and abundance of *G. gigantea* across 19 populations. The habitats of *G. gigantea* dominated by a few tree species viz., *Tectona grandis, Bombax ceiba, Callicarpa arborea, Artocarpus chama*, *Albizia procera*, *Macaranga denticulata*, *Ficus auriculata*, *Artocarpus lacucha*, *Anogeissus acuminata*, and *Ficus hispida*. However, the observed differences in species composition and less habitat heterogeneity of *G. gigantea* study populations are possibly due to the differences in sampling methodology, forest age, geo-climatic and local habitat factors, and plot proximity. Because variations in forest structure are caused by formation series, edaphic variables, and yearly rainfall (Beard 1955). Rarefaction curves indicated that *G. gigantea*'s habitat association is substantially steeper, indicating a high species richness and failing to exhibit asymptote. The theory of intermediate disturbance suggests that the fragmented sites have a higher species richness (Connell 1978). As a result of species being recruited and established by increasing the number of species that are not present in managed areas due to disturbances (Banda et al. 2006), species richness in such fragmented forests grew fairly. In total, we recorded 183 tree species sampled (~ 95,000 sq. m or 9.5 ha) across the habitats of *G. gigantea* with a range of 19–61 tree species across the habitats from moist mixed deciduous to the semi-evergreen forest. The 183 species found in this inventory were greater overall than the stated number of species from some well-protected Indian forests, though (Pandey and Shukla 2003; Banda et al. 2006). In this study, the observed mean tree density was 256.435 trees ha^{-1} (ranging 134–514 trees ha^{-1}) falls well within the limit of tropical forests with a density of 245–859 trees ha^{-1} (Campbell et al. 1992). The diversity indices were also well within the reported range (0.83 to 4.1) for different Indian forests reported by Visalakshi (1995), Mishra et al. (2000), and Kumar et al. (2006). Moreover, the diversity index value varies from 1.5 to 3.5 and rarely cross the value of 4.5 (Kent and Coker 1992). Thus, the present assessment would play a vital role in the future understanding of diverse attributes of *G. gigantea* habitat for prioritization of suitable habitats. The total number of woody species (183 species) recorded in the present study was greater than 123 species (Devi and Yadava 2006) and 85 species (Chowdhury et al. 2000) previously reported from the tropical semi-evergreen forests of Indo-Burma Biodiversity hotspots region. High species richness in this forest type may be due to the complex biogeography of the Indo-Burma region due to a combination of factors (e.g., its age, unique plate tectonic, palaeoclimatic history, location at the confluence of distinct realms, i.e., Afrotropic, Palearctic, and Indo-Malay (Olson and Dinerstein 2002).

Furthermore, species richness rises as one moves from higher to lower elevations, both in complete floras and at smaller geographic scales (Korner 1992). However, the observed density of *G. gigantea* (about eight individuals ha^{-1}) in this study is much lower than recorded tree fern densities per 500 m^2 plot in primary forest (50, 36, to 66), secondary forest (83, 61, to 143), and open environment (83, 21, to 79) (Arens and Baracaldo 1998). *G. gigantea* was found in a tropical semi-evergreen forest in Assam (Sarkar and Devi 2014), with a similar low density (1 individual ha^{-1}), which could be due to the topographical effect of different patches and micro-climatic conditions that may prevail in different altitudes or different species composition. Likewise, overall density demonstrated a positive relationship with patch size, which was consistent with the results of Bach (1988) that patch size had a substantial impact on plant density and growth. Furthermore, the higher number of individuals recorded in the larger patch size could be due to the area, and availability of resources in time and space, as evidenced by Bach (1988), who found that plant longevity was significantly greater in larger patches (16 plants or greater) than in small patches of fewer than 16 plants (1 or 4 plants). However, Dauber et al. (2010) found that the impacts of flowering plant assemblage area and density were often stronger at the patch level than at the population level. Moreover, the disturbance history of tree ferns has a considerable influence on their adaptations to canopy disturbance, which is not ecologically similar (Bystriakova et al. 2011).

Effects of habitat environmental factors

Habitat features, topographic complexity, landscape-level phenological variations, and habitat environmental factors are the primary determinants of the distribution of viable habitats for *G. gigantea*, according to various studies and our comprehensive field investigations. Our results have shown the potential of NDWI and NDVI as a proxy indicator for species abundance. This further implies that both NDWI and NDVI are essential while assessing changes in species abundance over time. Some species tend to be succumbing to the environmental fluctuations influenced by climate change resulting in the changes in phenology, abundance, and distribution (Chapungu and Nhamo 2016). Considering our study species, a closed dependency with vegetation cover, adequate water availability, and moderate shade was encountered during the field survey. Similarly, our GLMs also predicted that the abundance of *G. gigantea* was largely influenced by remote sensing variables (NDVI and NDWI) (Table 4) compared to climatic, topographic, soil physicochemical, and other associated habitat level factors. Several studies have reported that satellite-driven ecosystem functioning attributes (EFAs) such as NDVI, NDWI, and landcover are more robust parameters in predicting species abundance than models based on topography and habitat-climatic variables (Arenas-Castro et al. 2018, 2019). Furthermore, satellite-driven EFAs are more advantageous because it is more frequently and easily updated compared to the variables collected from study populations. However, one of the most important limitations of this study was the occurrence data for the species (only 19 populations). Literature suggests that sample size effects become less critical above 50 occurrences (Li and Ding 2016). Another possible limitation of this study was the species occurrences that were confined to a small geographical area. While building models, it is important to incorporate geographically diverse samples and many habitat environmental factors of the species to minimize errors when predicting species distribution and habitat suitability mapping (Li and Ding 2016). The present findings also suggests that species occurrence data and other habitat environmental variables should be collected from a diverse geographical area, especially to predict habitat distribution and suitability mapping of rare and threatened fern species.

Studies have shown that the temperature, light, and moisture play a significant role in the growth and spore germination of ferns (Volkova et al. 2011; Nagano and Suzuki 2007). However, because topographic complexity has a crucial role in determining viable habitats for species and their distribution (Scherrer and Körner 2011), our findings highlighted some critical traits that largely contribute to the habitat requirements of this species. Because of the wide range of habitat environmental factors, findings based on these variables should be regarded with caution at the landscape level. Rare and threatened species are affected mostly by habitat heterogeneity variables than the common species. Thus, these species may face greater challenges in the future due to rising habitat degradation induced by habitat change and resource extraction (Liu et al. 2019). Changes in land cover and the loss of corridors between community patches could pose a severe threat to the conservation of rare and threatened species. The effects of area and density of blooming plant assemblages were often more significant at the patch level than at the population level, according to Dauber et al. (2010). Moreover, the disturbance history of tree ferns has a considerable influence on their reactions to canopy disturbance, which are not ecologically similar (Bystriakova et al. 2011). According to Ough and Murphy (2004), changes in forest structure caused by disturbances reduce the number of tree fern individuals, affecting local microclimates and forest processes.

Besides that, topographic variables such as elevation and slope and soil physicochemical factors such as soil pH, soil moisture content, bulk density, SOC, and SOC stock were found to have a significant impact on *G. gigantea* abundance (Table 3). This result is consistent with Ho et al. (2016) findings, which highlighted the optimum growth conditions of *Cyathea lepifera* at slopes of 20–30° because short steep slopes and moderately steep slopes are appropriate for vegetation growth since water can be retained in these locations. As per the hydrological principle, water tends to accumulate more in areas of gentle slopes or flat terrain, often referred to as areas of high topographic wetness quantified using a GIS-based approach as topographic wetness index (TWI) (Mattivi et al. 2019; Winzeler et al. 2022). Since the study species is more often found in neighboring small streams on gentle slopes, water availability is likely very crucial for *G.*

gigantea. While water can flow over steep slopes, the actual accumulation and potential for saturation are generally higher in areas of gentle slopes, as indicated by a high TWI.

The soil water, soil moisture, and soil temperature of slopes are indirectly influenced by the sun angle of incidence and wind action, which change on different slopes (Elliott and Kipfmueller 2010). As a result, the number of *G. gigantea* found on various slopes can be used to determine the soil water requirements for the growth and abundance of this species. To identify the most relevant factors influencing *G. gigantea* abundance and map optimal habitats for future protection, it is necessary to incorporate a variety of landscape and habitat data.

Conservation solutions for *G. gigantea* can be developed primarily by maintaining their natural habitats. Ho et al. (2016) focused on in situ conservation of threatened *Cyathea lepifera* by establishing specialized conservation areas and providing legal protection to its natural environment. By implementing conservation measures in the species' original habitats, this technique may also help to preserve their genetic diversity. The characteristics that influence the total abundance of *G. gigantea* can be used for future management and to discover other regions with ideal habitat conditions.

Habitat suitability mapping

According to the field surveys conducted for this study and further overlying LULC, the most suitable area was found on the right bank of the river Longai in the Jampui hill ranges in Tripura, which was a part of continuous tropical evergreen and semi-evergreen forest belts during the colonial era (Majumdar et al. 2019) and shares 24.4-km-long boundary of the state of Mizoram, India. Monoculture plantations, mainly citrus, coffee, and areca nut, have, however, resulted in the bulk of these forests being converted to degraded secondary moist deciduous forests. At present, habitat mapping revealed only 1.38% of the total geographical area of Tripura was found to be the most suitable habitat for the species, highlighting its habitat uniqueness and the necessity for protection. The preferable habitats of *G. gigantea* were discovered in glen and gentle upland settings. However, populations and regeneration states of this species were better in glen environments with suitable ecological conditions, where there were much more individuals. Canopies of plants growing in glen areas produce a microclimate of shade and moisture, allowing some species that do not grow on uplands to thrive (Peet 2000; Majumdar et al. 2019). As a result, the glen habitats have a higher density of *G. gigantea* and better recovery, suggesting important habitat corridors.

In the present study, the information obtained through SWOT analysis revealed the perception of stakeholders residing within the predicted priority areas and how the inhabitants could get involved in monitoring and conservation of *G. gigantea*. The involvement of local community along with the efforts from the Government (Department of Forest) might be essential to implement local-level conservation actions for this threatened species. Furthermore, to identify a priority conservation area, one should have general socio-environmental knowledge and the changes taking place during the course of development within that priority area ((Hockings 2003; Braun and Amorim 2014). The SWOT analysis is widely used globally that utilizes local socio-economic and environmental factors to identify conservation priority areas for the development of conservation strategies (Balram et al. 2004; Scolozzi et al. 2014; Braun and Amorim 2014; Dulić et al. 2020). The SWOT also provides supportive information on multiple scales towards identifying conservation priority areas and designing management strategies to ensure biodiversity conservation and ecosystem services provision (Scolozzi et al. 2014).

Moreover, additional data on meta-population size for effective gene flow can strengthen the suitability zonation map and reaffirm the conservation of threatened species through predictive model-based corridor planning (Majumdar et al. 2019), because successful restoration and conservation of threatened plants necessitate an understanding of their biology, geographic distribution, ecological niche, and suitable habitats (Adhikari et al. 2018). The prospective suitable habitat zonation map for *G. gigantea* would aid conservation planning, particularly for the Forest Department of the concerned state, which is actively involved in identifying diverse land uses for management objectives and discovering new populations utilizing population-level data. The map can also aid in the prioritization of efforts to restore the native habitats of this species to ensure its long-term survival.

Traditional forest conservation practices (e.g., sacred groves/forests) are seen in several areas in various forms. Here, we are proposing two priority areas for future conservation planning where local communities are predominantly inhabiting that area and they might play a crucial role in the conservation of this threatened species. In this context, community-level efforts in the form of long-held tradition of conserving specific land areas that have cultural as well as religious significance are in vogue (Wadley and Colfer 2004; Ormsby and Bhagwat. 2010). Furthermore, nature-culture relationships have been emphasized to promote traditional ecological knowledge as well as indigenous well-being for the preservation of biocultural diversity (Phatthanaphraiwan et al. 2022).

Furthermore, we believe that the present findings show promising results for identifying suitable habitats for associated threatened plants (e.g., *Canarium strictum*, *Gnetum montanum*, *Gynocardia odorata*, *Hydnocarpus kurzii*, *Saraca asoca*, *Entada phaseoloides*). Because these plants have common habitat requirements, the suitability area generated in this study may potentially aid in the identification of priority conservation areas. Though the present study was limited to the state of Tripura (a north-eastern state of India) due to time and resource restrictions, we feel that broadening the geographical scope will assist in the identification of appropriate habitats in other locations. As a result, a comprehensive study of the distribution and habitat mapping of this species is critical in identifying new priority locations for its conservation and reintroduction.

Conclusions

The natural populations of *G. gigantea* are threatened not only due to deforestation and habitat modifications but also influenced by the limited adaptability to the micro-environment of shade and moisture habitat. Landscape features and habitat requirements, i.e., habitat environmental factors, may influence the distribution and abundance of *G. gigantea*. Therefore, the conservation of this species and the associated threatened species will require an integrated landscape and local-scale habitat management strategies to protect the natural populations and enhance the distributional range of these species. The present study evaluated the influence of habitat environmental factors on the abundance of this threatened tree fern. Furthermore, to identify suitable habitats, the interpolation technique has been used. A SWOT approach was used with certain sort of positive and negative factors to make cost-effective priority areas settings for conservation and reintroduction. During field exploration throughout the state of Tripura, we encountered *G. gigantea* at 19 populations with altitude varying 59–747 m asl. Our PCA-based variable screening revealed 11 potential habitat environmental variables which may influence the abundance of this threatened species. However, GLMs analysis revealed that the two remote sensing variables viz., NDVI and NDWI as well as their combination significantly affect the abundance of *G. gigantea*. Based on SWOT analysis, we proposed two potential priority areas suitable for efficient conservation and future reintroduction of *G. gigantea*. Therefore, there is an urgent need to invest in habitat enhancement measures in the identified suitable areas for the conservation of this tree fern. Furthermore, populations of this species are under threat of habitat modification and fragmentation due to slash-and-burn agricultural practices (*Jhum cultivation*), deforestation, and rubber monoculture plantations. Such threats should be minimized to mitigate the loss of natural populations and to promote the natural regeneration of this species. We further recommend urgent administrative interventions to implement conservation measures to protect this threatened species in this biodiversity-rich region.

Here, we evaluated the relationships between habitat environmental factors and abundance of *G. gigantea* based on the data collected from 19 representative populations. Moreover, utilizing statistical methods, EWHI, and SWOT analysis, we identified two priority areas for possible distribution and population establishment of *G. gigantea* in the future considering the climate change scenarios. Furthermore, sufficient ecological data considering a larger geographical area and potential site of occurrences should be used for the prediction of distribution changes of rare and threatened species. Therefore, the full application of our current findings of *G. gigantea* is limited. Though the current study was confined to a small geographical area because of time and resource constraints, we strongly believe that extending the site of occurrence of this species for future studies might help identifying the potential distributional range in this biodiversity-rich region. Furthermore, improvements in our analytical approach may aid in the successful mapping of habitat distributional range for the conservation and reintroduction of rare and threatened species. Thus, we suggest future studies should be undertaken using more advanced machine learning tools to determine the possible geographical range for the conservation of this species.

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Data Availability The data supporting the findings of this study are presented in the published article and in the online supplementary files.

Declarations

Competing interests The authors declare no competing interests.

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