

Regulatory Ecosystem Services of Forest Sacred Groves in comparison to Invasive vegetation in the urban and urban peripheries of a semi-arid region

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Abstract

Amidst anthropogenic pressures, certain forest relics in the urban and rural landscapes have been traditionally protected for centuries as sacred forest groves in the Asian regions, despite lying outside the protected area network. In the current context of climate change and ensuing disasters, these forest groves and similar kind of vegetative landscapes within urban and rural could potentially increase the resilience and buffering capacity of the surrounding environs, besides providing ecosystem services. This study attempted to evaluate 50 Sacred Groves Stands (SGS) and 50 *Prosopis juliflora* Stands (PJS) comprehensively for the floral diversity, carbon stock and dynamics, carbon-fixing traits, dendrochronology of trees, soil nutrient profiles, and soil erosion - deemed to be regulating ecosystem services. Structural Equation Model (SEM) was applied to derive the photosynthetic efficiency of eight dominant trees species using vital input parameters including eco-physiological, morphological, and biochemical characterization. Revised Universal Soil Loss Equation (RUSLE) model in conjunction with ArcGIS Pro and ArcGIS 10.3 was adopted to map soil loss. Among the 8 selected tree species, *Wrightia tinctoria* (SEM Estimated Coefficient: 1.28) > *Prosopis juliflora* (1.22) > *Acacia nilotica* (1.21) > *Albizia lebbek* (0.97) > *Azadirachta indica* (0.74) showed comparatively high carbon sequestering efficacy. SEM revealed species specific carbon sequestering functional traits (stomatal density, nitrogen fixing ability, RuBisCO and chlorophyll content) are evidently attributed to high carbon sequestration potential. Carbon source/sink determinations inferred through Net Ecosystem Productivity (NEP) assessments showed that mature SGS (0.06 ± 0.01 g C/m²/day) potentially acted as carbon sink, while matured PJS (-0.34 ± 0.12 g C/m²/day) as source. Soil erosion rates were significantly greater (29.5 ± 13.4 ton/ha/year) in SGS compared to PJS (7.52 ± 2.55 ton/ha/year).

1. Introduction

Beyond the protected area network, the biodiversity rich terrestrial ecosystems entailing minimal land area have been subjected indiscriminate anthropogenic exploitation in developing countries of Asian region since late Holocene. The extent of degradation hinges on the proximity of such ecosystems to the human habitations, urban areas and croplands (Chandran and Hughes, 1997; Chandran and Mesta, 2001; Gadgil and Vartak, 1976). In the current context of global change phenomenon and its tangible effects, as long as the biodiversity and the vegetative stratification in such high value ecosystems remains intact, the buffering potential of the adjoining area to the weather extremities are likely to be higher and the loss is minimal. However, human settlement and land use practices, which invariably involves non-native plants and animals, gradually contribute to loss of endemic biota and transformation of such native ecosystems (Devi et al., 2021; Douglass and Zinke, 2015).

Across the world, relics of few native forests are distributed along the urban peripheries and are safeguarded by the local community to a great extent over centuries, albeit anthropogenic interventions (Bhagwat et al., 2005; Cardelus et al., 2017; Kibet and Nyamweru, 2008; Mequanint et al., 2020; Nganso et al., 2012; Ormsby and Bhagwat, 2010; Wadley and Colfer, 2004). In Africa, South Asia and Southeast Asia, the motive of protecting these vegetation patches has deep socio-cultural linkages and are revered

as sacred forest grooves. However, whether such sacred forest grooves are fragmented remains of earlier forest stretches, or regenerated forests remain unclear, although a study from Western Ghats of India ascertains the phenomenon of regeneration driven by social, ecological and economic necessities, dating back to 400 Years Before Present (YBP) (Bhagwat et al., 2014). In addition, certain plants and animal species are protected due to religious and cultural taboos (Chandrashekara and Sankar, 1998). In fact, such an attitudinal shift towards protection of natural resource, had perhaps occurred few centuries ago due to comprehensive knowledge of ecosystem services.

Ecosystem services (ESS) are the indispensable benefits derived from natural ecosystems that serves as the basic life support system for humans either directly or indirectly (Balvanera and Cotler, 2007; Calzadilla et al., 2022; Gaudiano et al., 2022; Newbold et al., 2015). A wide spectrum of services including supporting, provisioning, regulating, and cultural services directly influence the life quality (Hernández-Morcillo et al., 2013; Li-Ping et al., 2010; MEa, 2005). Notwithstanding to the size, even a small systems like sacred groves are capable of delivering multiple ecosystem services including carbon sequestration, protection against flash floods, minimizing the urban heat island effect, attenuate noise pollution, and improve the overall environmental quality (Castro-Díez et al., 2019; Dearborn and Kark, 2010; Heinrich et al., 2023; Ke et al., 2023; Malsatar and Mehta, 2023; Trugman et al., 2019; Valentine et al., 2023). Apparently, certain regulating services like local climate regulation and soil erosion are significant (Larson et al., 1997; Parthasarathy and Naveen Babu, 2021). The role of sacred groves in replenishing the ground water is also reported (WITT, 2010). Indeed, sacred groves exhibit a complex and intricate web of species interactions that effectively controls the expansion of predatory parasitic pests (Brewer and Elliott, 2023; Ye et al., 2020).

India has a heritage of more than 100,000 sacred groove forests, overarching cultural taboos and religious beliefs of the local community (Ormsby, 2021). The tropical forests of Southern India are renowned for their rich and unique endemic flora, that in many cases, can trace its origins back to the end of the Mesozoic era approximately 65 million y ago (Ormsby and Bhagwat, 2010). Numerous scientific investigations had examined the regulating ecosystem services including carbon sequestration efficacy (Dar and Parthasarathy, 2023; Dar et al., 2019a; Kumar et al., 2021; Mgumia and Oba, 2003; Parthasarathy and Naveen Babu, 2021; Ray et al., 2014; Yadav et al., 2022) primary productivity, floral and faunal species richness (Bhagwat et al., 2005; Chandrashekara and Sankar, 1998; Devi Khumbongmayum et al., 2005; Kandari et al., 2014; Ramanujam and Praveen Kumar Cyril, 2003). Practically, these studies had a superficial approach in analyzing the values of ecosystem services and lack comprehensive assessment of functional traits of the vegetation. We attempted to understand the holistic function of the sacred groves in a semi-arid region of Southern India. Buoyed by the rapid economic growth in recent decades, the urban regions in India witness massive transformation and expansion, which has direct implications to the natural ecosystems in within its ambit and in peripheries. Such expansion drives had imposed considerable dent in the sacred grooves of the adjoining regions as well. Currently, in the fluvial plains of arid and semi-arid regions of India, other than the croplands and protected forests network, sacred forest groves and the landscapes invaded by the exotic vegetation (*Prosopis juliflora*) are the available green patches. Although, *Prosopis juliflora* infestation is widely

criticized for many ill effects, it is also credited for few ecosystem services like carbon sequestration and soil erosion control (Dey et al., 2020; Meena et al., 2022; Oduor and Githiomi, 2013). However, regulating eco-system services in such *Prosopis juliflora* Stands (PJS) like ground water regulation, floral and faunal richness remains low (Ayanu et al., 2015; Elfadl and Luukkanen, 2006; Garg, 1998; Tiessen et al., 2003). This study attempts to distinguish if there is any notable ecosystem services in these two type of vegetative stands and how significant is the difference. The investigations focused on species richness, soil nutrient availability, carbon stock, comparative photosynthetic efficiency of tree species including morphological and physiological functional traits, carbon flux dynamics in the dominant Sacred Grove Forests & *Prosopis juliflora* stands, and soil erosion control.

2. Materials and methods

2.1. Study area and sampling sites

Fifty Sacred Groves Stands (SGS), and another fifty sites representing invasive *Prosopis juliflora* stands (PJS) were chosen for the study in a typical semi-arid region. These study sites lie in the central districts of Tamil Nadu, India (Tiruchirappalli, Pudukkottai, Dindigul, Ariyalur, Thanjavur and Perambalur) spreading across 14,371 km² (10° 19' to 11° 26' North latitudes and 77° 30' to 79° 19' (Fig. 1). A portion of the study area falls under the Cauvery River Deltaic Region and the quaternary sediments are fluvial type (Goswami et al., 2019). The annual mean temperature of the study districts ranges between 27.5°C – 36.0°C, and the annual precipitation ranges from 286 to 880 mm (Fig. 2). At each site, soil physicochemical parameters, vegetation analysis including species richness and stand density, and other parameters representing the regulating ecosystem services were carried out.

<Insert Fig. 1. & Fig. 2.>

2.2. Soil physicochemical, vegetation characterization

Ecological survey

In all the 100 sites, four quadrants of dimensions 25 x 25m were laid for tree survey and parameters such as stand density, species richness, abundance, basal area and leaf area index were recorded. Characteristics such as Shannon diversity index, Simpson dominance index, and Pielou's evenness index were derived using R package #vegan. Litter fall in all the sites was recorded using typical rectangular baskets of dimensions 51*50 cm; all the accumulated litters were collected and calculated (Hero Saharjo and Watanabe, 2000). Leaf Area Index was estimated using Digital Hemispherical photographic technique; a digital camera (NIKON 7700D), with fisheye lens (Sigma EX-DC 4.5 mm) was erected vertically 1.5 m above the ground towards the forest canopy to capture canopy pictures. To classify the threshold between sky and canopy data, preprocessing was done using *Sidelook* software v1.1.01; subsequently, LAI was calculated in the software *Gap Light Analyzer* (Xie et al., 2023).

Soil nutrient analysis: In all the 100 sites (50: Sacred Grove Stands [SGS]; 50: *Prosopis juliflora* Stands [PJS]), composite soil samples were collected at depth 0–30 cm to determine nutrient profiling (N, P, K,

OC), bulk density, pH and electrical conductivity. Soil samples were dried in shade, sieved, and then stored in sterile containers under dark conditions for future analysis. The standard methodologies were followed for analyses of soil pH, electrical conductivity, bulk density (Black, 1965), organic carbon (Walkley and Black, 1934), available nitrogen content (Subbiah and Asija, 1956), available phosphorus content (Olsen, 1954), and available potassium content (Stanford and English, 1949).

2.3 Assessment of regulating eco-system services – Morphological, Eco-physiological, and Biochemical Carbon fixing functional traits of selected tree species

Morphological characterizations

Based on the eco-physiological characters and tree species abundance in the study sites, seven native trees from SGS and one invasive tree from PJS (*Prosopis Juliflora*) were selected for carbon fixing functional traits assessment. Morphological trait i.e. stomatal density in adaxial and abaxial side of the leaf was determined using leaf imprints method; clear nail polish was applied on the adaxial and abaxial sides of the mature leaf for the selected eight tree species; later dry nail polish layer was peeled off using clear tape and pasted in a clear sterile microscopic slide. Mounted specimens are observed under light microscope at 40x magnification using the software Image View; microscopic images of the stomata were captured using APTINA trinocular camera (Pathoumthong et al., 2023).

Eco-physiological characterization

Photosynthesis Rate ($\mu\text{mole CO}_2 \text{ m}^{-2}/\text{sec}$), Air temperature ($^{\circ}\text{C}$), Leaf intracellular CO_2 Concentration (ppm), Ambient Photosynthetic Active Radiation ($\mu\text{mole m}^{-2}/\text{sec}$), Transpiration rate ($\text{m. mole H}_2\text{O m}^{-2}/\text{sec}$) were determined for 50 tree species in SGS and PJS vegetation stands using Plant Photosynthesis system (Bio Base - BK 3051 C). All the aforesaid parameters were measured in top, middle, and low canopy leaves of the tree in triplicates to arrive a successive mean.

Biochemical characterization

Total chlorophyll content in leaves was determined following a methodology established by Arnon (1949). Fresh leaf samples (0.5 g) were ground with 10 ml of 80% acetone, centrifuged at 3000 rpm for 10 minutes and the supernatant containing the chlorophyll extract was collected for spectrometric analysis. Absorbance measurement were carried out at three specific wavelengths, namely 663 nm, 645 nm, and 470 nm, using a UV spectrophotometer. To calculate the amounts of chlorophyll a, chlorophyll b, and total chlorophyll, Arnon's equation was followed.

RuBisCO quantity and activity was determined following the methods described by Farquhar and Sharkey (1982) and Lilley and Walker (1974). Fresh leaf samples of selected trees of weight 0.5 g were homogenized in a pre-chilled mortar using an ice-cold extraction buffer solution. The extraction buffer solution consisted of 50 mM Tris-HCl (pH 7.5), 1 mM ethylene diamine tetra acetic acid (EDTA), 1 mM magnesium chloride (MgCl_2), 12.5% (v/v) glycerin, 10% polyvinylpyrrolidone (PVP), and 10 mM mercaptoethanol. Homogenized samples were filtered through four layers of Mira cloth and subsequently

centrifuged at 10,000 rpm for 10 minutes at 4°C. The resulting supernatant was collected and used for the enzyme assay. The initial RuBisCO activity was measured by adding 0.1 ml of an activation solution to the supernatant. The activation solution consisted of 33 mM Tris-HCl (pH 7.5), 0.67 mM EDTA, 33 mM MgCl₂, and 10 mM sodium bicarbonate (NaHCO₃). The mixture was incubated for 15 minutes, followed by the addition of RuBisCO enzyme. The initial absorbance was measured at 340 nm. To determine the total RuBisCO activity, the mixture was further incubated for 5 minutes, and the absorbance was measured at 340 nm after 90 seconds.

Assessment of carbon fixing functional trait of selected tree species using Structural Equation Model

Structural Equation Model (SEM) was constructed using a conceptual Meta model (Fig. S 2, Fig. 8. A & B.) With the vital input parameters (Eco-physiological, Morphological, Biochemical characterization) of selected tree species (seven native tree species and *Prosopis Juliflora*); the rationale behind the constructed model is described in Table S1. SEMs for the selected species was fitted using the *LAVAN* package (Rosseel, 2012). Significance and goodness of fit of the SEMs were tested using multiple model fit validation indices: i) the robust model chi-square (χ^2) with a non-significant p-value ($p > 0.05$) indicating that the model-implied covariance matrix equals the observed covariance matrix, ii) Comparative Fit Index (CFI), (best fit at CFI > 0.95), iii) Robust root Mean Square Error of Approximation (RMSEA) (best fit at RMSEA < 0.05), and iv) Standardized Root Mean squared Residual (SRMR) (best fit at SRMR < 0.08). The model with the complete best fit was arrived for the tree species. Each path in the final model was assessed for standardized coefficients, significant contribution, and explained variance (R^2) per response variable were calculated.

Carbon stock assessment

Above and Below Ground Biomass of SGS & PJS were estimated based on 1) tree height, 2) diameter at breast height (DBH), 3) wood density; AGB was estimated using general allometric Eq. 4 (Chave et al., 2014) in R package #BIOMASS. Furthermore, to assess the total carbon content of the selected tree species, stem, leaf, bark samples from selected tree species were collected and total carbon content was quantified under laboratory conditions using the following formula (Negi et al., 2003) Total carbon (%) = $100 - (\text{Ash weight}) + \text{Mole.wt of O}_2 (53.3) \text{ in C}_6 \text{H}_{12} \text{O}_6$.

Carbon dynamics

Plant respiration : Leaf nocturnal dark respiration measurements for 50 tree species of Sacred Groves Stands and *Prosopis juliflora* Stands were carried out on continuous basis for 24 hours in 3 days interval following the methodology established by Aspinwall et al., (2016) and Wohlfahrt et al., (2005). The rates of leaf dark respiration i.e. CO₂ efflux was quantified for the sampled leaves in triplicates using Plant Photosynthesis meter (Bio Base - BK 3051 C - standard leaf chamber area: 11 cm²); airflow rate and standard reference CO₂ was set at 400 $\mu\text{mol mol}^{-1}$ and 380 $\mu\text{mol mol}^{-1}$ (Collier et al., 2014).

Soil respiration

Soil Respiration was measured with a stratified random sampling design in each land use type to account for the spatial variability in soil properties and vegetation cover. A closed soil chamber of 962 cm³ in volume and 72 cm² area was used for soil respiration measurements; PVC chamber mount collars were inserted into the soil in prior (24 hours); measurement surface was kept free from autotrophic respiration by removing herbs and seedlings. Then the soil chamber was mounted on the PVC collar and locked. Before starting the experiment, initial concentration of CO₂ inside the respiration chamber was measured, then the increase in soil respiration under closed condition was measured using (IRGA) CO₂ sensor (GasAlertMicroIR5, BW Tech., Honeywell Inc., Charlotte, NC, USA). To avoid any high midday temperature, measurements were performed between 09.00 am to 11.00 am (Lou et al., 2004).

Dendrochronological assessment

Age of the tree was measured using incremental borer technique (Grissino-Mayer, 2003). Trees were bored twice, from the northern and the eastern side of the trunk. The bore was set at a right angle to the trunk. The depth of the drilling was equal to half of the premeasured DBH, with a margin of 5 to 10 cm, with the exception of trees with a diameter more than 70 cm, where the depth of the drilled hole was limited by the length of the boring bit. Based on the incremental borer survey data stepwise linear regression decision tree model was fitted. To increase the accuracy of the regression model, another set of field survey was conducted in 25 timber mills located in the study region; selected trees were spotted and subjected for vascular ring count, DBH and circumference measurements. A total number of 800 measurements were recorded; to construct a precise decision tree predication regressor model, R packages #mass and #Random Forest were used.

2.4. Soil erosion control

Revised Universal Soil Loss Equation (RUSLE) model in conjunction with ArcGIS Pro and ArcGIS 10.3 was adopted to map soil loss. Five factors were considered for soil loss estimation: rainfall erosivity (Fig. S 3), soil erodibility (Fig. S 4), slope steepness and length (Fig. S 5), crop management factor (Fig. S 6), and support practice for the RUSLE model (Fig. S 7). Datasets were prepared at varying resolutions (Fig. 3). The factors varied spatially and temporally, dependent on other factors. Aster DEM at 30m resolution and ESRI land cover data were used to compute the factors in ArcGIS Pro and ArcGIS 10.3. This method is based on quantitative analysis using the analytical tools of ArcGIS to assess the statistical properties of rainfall, soil erosion data, and digital elevation model (Behera et al., 2023). Kappa coefficient was used to validate to constructed RUSLE model for soil erosion (Table. S 11).

<Insert Fig. 3.>

Soil sampling, vegetation survey, field eco-physiological assessments, carbon dynamics measurements and respective laboratory and field experiments were carried out during Jan 2022 to May 2023. Eco-physiological assessments in tree species were carried out during clear sky ($PAR \geq 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the morning/forenoon when photosynthesis is likely to be at peak.

3. Results

3.1 Ecological diversity and soil physico chemical profile of Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS)

Tree species richness of SGS was found to high (34 ± 12) than PJS (9 ± 6). In SGS *Ziziphus jujuba* (32 ± 16 /ha) was found to be most abundant followed by *Vachellia leucophloea* (25 ± 15 /ha), *Borassus flabellifer* (27 ± 16 /ha), *Morinda coreia* (26 ± 16 /ha), *Acacia nilotica* (27 ± 11 /ha), *Ficus religiosa* (24 ± 14 /ha), *Diospyros ebenum* (21 ± 19 /ha), *Albizia amara* (21 ± 17 /ha), etc. Least abundant species was *Mimusops elengi* (4 ± 2 /ha), *Chloroxylon swietenia* (4 ± 1 /ha) (Fig. 4a). In PJS *Prosopis juliflora* (104 ± 36 /ha) was the most dominant tree followed by *Borassus flabellifer* (63 ± 38 /ha) and *Albizia lebbeck* (62 ± 21 /ha) etc (Fig. 4b). Moreover, family richness of the SGS also recorded high (range: 9–26), in contrast to PJS (range: 5–8). However, in both the vegetation types, Fabaceae family accounted to be the most abundant (Fig. 4c, d).

Our study comparing ecological indices between *Prosopis juliflora* Stands (PJS) and Sacred Groves Stands (SGS) revealed highly significant differences in both diversity and evenness; Shannon-Wiener diversity index values indicated high diversity (3.65 ± 0.52) in SGS when compared to PJS (0.46 ± 0.33) ($p < 0.01^{***}$ - Man-Whitney U Test) (Fig. 4e). Pielou's evenness index also demonstrated a significant contrast ($p < 0.01^{***}$ - Man-Whitney U Test), with SGS displaying higher evenness (0.81 ± 0.13) and PJS showing lower evenness (0.15 ± 0.08), which in turn indicates the dominance of *Prosopis juliflora* (Fig. 4f) and its implications in floral diversity of PJS.

<Insert Fig. 4.>

3.2. Soil Nutrient profile of Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS)

Soil nutrient profile viz. Available Nitrogen, Available Phosphorus, Available Potassium, Electrical Conductivity, pH, Bulk Density, Soil Organic Carbon, and Soil Moisture varied significantly (Kruskal- Wallis rank sum test - $p < 0.01^{***}$) between SGS and PJS. In PJS, comparatively high quantities of Available Nitrogen, Phosphorus, Potassium, Electrical Conductivity, pH and Organic carbon were recorded. Conversely, parameters i.e. Soil Bulk Density, Soil Moisture were observed to be high in SGS in comparison to in PJS (Fig. 5). Litter fall was found to be high in SGS (range: $1.6\text{--}5.0$ g/m²) than PJS (range: $1.1\text{--}3.6$ g/m²) (Fig. 5).

<Insert Fig. 5.>

3.3. Morphological, Biochemical and Eco-Physiological assessment in selected tree species

The mean adaxial and abaxial stomatal density among the tree species (selected for the experiment) showed significant variation ($p < 0.01^{***}$ in Kruskal-Wallis rank sum test) (Fig. 6a). *Azadirachta indica* exhibited the highest density at $1300 \pm 198 \text{ mm}^2$, while *Prosopis juliflora* displayed the lowest density at $287 \pm 148 \text{ mm}^2$ (Fig. S 1).

The mean total chlorophyll levels were found to be high in *Ficus religiosa* ($3.3 \pm 1.1 \text{ mg/g}$), while the species with the lowest chlorophyll content was *Acacia nilotica* ($1.3 \pm 0.87 \text{ mg/g}$). The higher proportion of chlorophyll in *Ficus religiosa* can be attributed to its greater demand for chlorophyll due to its larger mass and proportions (Fig. 6b). *Prosopis juliflora* exhibited highest mean plant Total Organic Carbon (leaf, stem, bark) followed by *Wrightia tinctoria*, *Acacia nilotica*, *Prosopis juliflora*, *Albizia lebbeck*, *Azadirachta indica*, *Ficus religiosa*, *Ficus benghalensis*, and *Terminalia arjuna*. The highest storage of organic carbon in *Wrightia tinctoria* can be attributed to its ability to fix larger proportions of organic carbon in its plant body (Fig. 6c).

The photosynthesis rates of selected tree species showed significant interspecific variation ($p < 0.01^{***}$) in the Kruskal-Wallis rank sum test. Among the trees, *Azadirachta indica* and *Prosopis juliflora* exhibited higher photosynthesis rates, measuring $8.1 \pm 2.0 \mu\text{mol CO}_2/\text{m}^2/\text{sec}$ and $8.0 \pm 1.86 \mu\text{mol CO}_2/\text{m}^2/\text{sec}$, respectively. The remaining species were ranked as follows: *Azadirachta indica*^a > *Prosopis juliflora*^b > *Terminalia arjuna*^c > *Wrightia tinctoria*^d > *Acacia nilotica*^e > *Ficus benghalensis*^f > *Albizia lebbeck*^h > *Ficus religiosa*^g. Kruskal-Wallis test and Pairwise comparisons using the Wilcoxon rank-sum test with continuity correction were conducted to assess the difference in mean photosynthesis rates of each species, results revealed species sharing different letter (in superscript) exhibited significant differences at $p < 0.05$. These findings underscore the variations in photosynthesis rates among the studied tree species, providing valuable insights into their relative photosynthetic capacities (Fig. 6d).

In the case of Stomatal Conductance, *Azadirachta indica*^a showed higher values ($0.42 \pm 0.15 \text{ milli mol/m}^2/\text{sec}$), followed by *Ficus religiosa*^b, *Ficus benghalensis*^d, *Prosopis juliflora*^c, *Albizia lebbeck*^e, *Wrightia tinctoria*^f, *Acacia nilotica*^g, and *Terminalia arjuna*^h. Kruskal-Wallis test and Pairwise comparisons using the Wilcoxon rank-sum test with continuity correction conducted to examine the difference in mean stomatal conductance rate of each species; species sharing different letter indicate significant differences at $p < 0.05$ (Fig. 6e).

The mean transpiration rate of tree species was found to be highest in *Ficus religiosa*^a, followed by *Azadirachta indica*^g, *Ficus benghalensis*^b, *Wrightia tinctoria*^c, *Prosopis juliflora*^d, *Acacia nilotica*^e, *Terminalia arjuna*^f, and *Albizia lebbeck*^g. Kruskal Wallis test and Pairwise comparisons using the Wilcoxon rank-sum test with continuity correction were employed to analyze the difference in mean transpiration rate of each species; results revealed species sharing the different letter (in superscript) exhibit significant differences at $p < 0.05$ (Fig. 6f).

Leaf intracellular CO_2 was observed to be higher in *Ficus religiosa*^a and *Ficus benghalensis*^b, followed by *Azadirachta indica*^c, *Wrightia tinctoria*^f, *Albizia lebbeck*^d, *Terminalia arjuna*^g, *Prosopis juliflora*^e, *Acacia*

nilotica^h. The higher intracellular CO₂ concentration in *Ficus religiosa* and *Ficus benghalensis* can be attributed to their greater leaf thickness compared to the other selected tree species. Kruskal Wallis test and Pairwise comparisons using the Wilcoxon rank-sum test with continuity correction were employed to analyze the difference in mean leaf intracellular CO₂ concentrations of each species; results revealed species sharing the different letter (in superscript) exhibit significant differences at $p < 0.05$ (Fig. 6g).

<Insert Fig. 6.>

Mean RuBisCO content within the selected 8 tree species was found to be very high in *Prosopis juliflora* (10.8 ± 1.08 micromole/m²) compared to other trees implying its higher efficiency in primary productivity. Within SGS, RuBisCO content varied in order: *Acacia nilotica* > *Albizia lebbeck* > *Azadirachta indica* > *Wrightia tinctoria* > *Ficus religiosa* > *Terminalia arjuna* > *Ficus benghalensis* (Fig. 7a). However, total RuBisCO activity among the selected species was found higher in *Wrightia tinctoria*^a > *Prosopis juliflora*^b > *Albizia lebbeck*^c > *Acacia nilotica*^d > *Azadirachta indica*^e > *Ficus benghalensis*^f > *Ficus religiosa*^g > *Terminalia arjuna*^h (Fig. 7b).

<Insert Fig. 7.>

3.4 Assessment carbon fixing Morphological, physiological functional traits of selected tree species (8) using Structural Equation Model

Based on the initial screening from Pearson's correlation, a best model fit was attained for the Structural Equation Model (SEM) testing the effects of environmental conditions, morphological, biochemical and physiological functional trait of selected trees on photosynthesis of the tree species (Fig. 8A, B). Exogenous variables such as stomatal density, ambient CO₂, ambient temperature, available soil nitrogen and soil moisture had significantly impacted (positive/negative) the endogenous variable photosynthesis.

Effects of exogenous and endogenous variables on photosynthetic rate of selected trees

SEM derived outputs on the effects of stomatal density on photosynthesis rate of tree species found a predominant negative relationship among the species with higher stomatal density. Higher stomatal density (Stomatal density ≥ 1000 mm²) showed a direct negative effect on photosynthesis rate of the following test species - *Azadirachta indica* (Estimated coefficient: -0.12), *Albizia lebbeck* (-0.09). However, in *Terminalia arjuna* (0.09), *Prosopis juliflora* (0.05), *Acacia nilotica* (0.10), *Wrightia tinctoria* (0.16), *Ficus benghalensis* (0.15), and *Ficus religiosa* (0.16), Stomatal density < 1000 mm² observed to have positive effect on photosynthetic rate (Fig. 8A, B).

Ambient CO₂ levels had an indirect and negative effect on the optimal photosynthetic rate in the case of *Azadirachta indica* (Estimated coefficient: -0.03) and *Albizia lebbeck* (Estimated coefficient: -0.01). However, other species exhibited indirect, neutral and positive relationships to ambient CO₂ levels (Fig. 8A, B). Ambient temperature between the morning hours ($32.5 \pm 2.02^\circ\text{C}$) had overall direct positive effect on photosynthesis rate of all the selected tree species, but photosynthesis rate of *Prosopis juliflora*

(Estimated coefficient: -0.09) and *Acacia nilotica* (-0.24) were indirectly affected by temperature through RuBisCO (Fig. 8A, B).

A positive direct effect was observed between soil nitrogen, chlorophyll and RuBisCO. Subsequently, a direct positive relation was witnessed between chlorophyll, RuBisCO and photosynthesis in all the eight species. In all the test species soil moisture observed to have a very positive effect on photosynthesis. Our findings advocate that the high carbon fixing efficiency of *Albizia lebbeck*, *Prosopis juliflora*, *Wrightia tinctoria*, and *Acacia nilotica* can be attributed to the trait of Fabaceae family, which enables them to fix nitrogen to the soil, and soil nitrogen is explained to have an indirect positive relation with photosynthesis. Furthermore, it is understood that the nitrogen availability plays a crucial role in supporting essential biosynthetic metabolic processes. SEM elucidated the carbon sequestering potential of selected tree species depicted following hierarchy: *Wrightia tinctoria* (estimated coefficient: 1.28) > *Prosopis juliflora* (1.22) > *Acacia nilotica* (1.21) > *Albizia lebbeck* (0.97) > *Azadirachta indica* (0.74) > *Ficus religiosa* (0.56) > *Ficus benghalensis* (0.37) > *Terminalia arjuna* (0.26) (Fig. 8A, B.).

<Insert Fig. 8A & B.>

Effects of endogenous physiological variables such as RuBisCO, Chlorophyll, and intracellular CO_2 on photosynthesis rate of eight selected tree species didn't exhibit uniformity. All the three endogenous variables exhibited a positive direct effect on photosynthesis in the following tree species *Prosopis juliflora* (Estimated coefficients: 0.39, 0.24, 0.07), *Acacia nilotica* (0.39, 0.24, 0.07), *Albizia lebbeck*, *Wrightia tinctoria*, *Terminalia arjuna* (0.04, 0.12, 0.11). But in case of *Azadirachta indica* (-0.05), *Ficus benghalensis* (-0.01) and *Ficus religiosa* (-0.09) leaf intracellular CO_2 tend to have a direct negative effect on optimal photosynthesis, also RuBisCO (*Azadirachta indica*: 0.46; *Ficus benghalensis*: 0.26; *Ficus religiosa*: 0.59) and chlorophyll (*Azadirachta indica*: 0.68; *Ficus benghalensis*: 0.02; *Ficus religiosa*: 0.40) observed to have direct positive relation (Fig. 8A, B.).

A negative relationship between temperature and RuBisCO was observed in *Prosopis juliflora* and *Acacia nilotica*. However, in *Ficus religiosa*, *Ficus benghalensis*, *Azadirachta indica*, *Albizia lebbeck*, *Wrightia tinctoria*, and *Terminalia arjuna*, temperature had no notable effects on RuBisCO. This trait could be attributed to the leaf thickness, as the leaf thickness lessens enzymes are susceptible to high temperature (Fig. 8A, B.).

SEM elucidated the carbon sequestering potential of selected tree species in the following hierarchy *Wrightia tinctoria* (estimated coefficient: 1.28) > *Prosopis juliflora* (1.22) > *Acacia nilotica* (1.21) > *Albizia lebbeck* (0.97) > *Azadirachta indica* (0.74) > *Ficus religiosa* (0.56) > *Ficus benghalensis* (0.37) > *Terminalia arjuna* (0.26) (Fig. 8A, B.).

3.5 Tree age prediction model using random forest algorithm and maximum life expectancy of selected tree species

Pearson's correlation analysis demonstrated a positive relationship between the circumference of trees and the number of their growth rings, based on the relation a decision tree model was constructed (Fig. S

8) for all the selected eight species. Among the trees selected for study, *Ficus religiosa* and *Ficus benghalensis* exhibited longer life spans, with recorded mean ages of 55 ± 45 years and 58 ± 42 years, respectively. On the other hand, *Prosopis juliflora* and *Terminalia arjuna* displayed shorter life spans, falling within the mean age of 25 ± 23 years and 25 ± 22 years, respectively (Fig. 9). While these trees thrive amidst the polluted urban environment, which significantly affects the lifespan of trees and increases mortality rate, these findings indicate that selected trees might possess the capability to acclimate to local polluted conditions and thrive despite environmental pressures. It's worth noting that trees with extended life spans can offer various ecosystem services to the surrounding urban environment (Fig. 9).

<Insert Fig. 9.>

3.6 Carbon stock estimation and carbon dynamics in Sacred Groves Stands (SGS) and Prosopis juliflora Stands (PJS)

Above and Below Ground Biomass proportions of Sacred Groves Stands (SGS) and Prosopis juliflora Stands (PJS)

Tree stand density in PJS stood at $1056 \pm 474/\text{ha}$, while in SGS it is comparatively low ($584 \pm 331/\text{ha}$). Similarly in SGS, the basal area ($25 \pm 11 \text{ m}^2/\text{ha}$) is also lower than PJS ($38 \pm 18 \text{ m}^2/\text{ha}$). Leaf area index of PJS was higher ($2.69 \pm 0.54 \text{ m}^2/\text{m}^2$) compared to SGS ($1.34 \pm 0.66 \text{ m}^2/\text{m}^2$). Concomitantly, Above Ground Biomass (AGB), Below Ground Biomass (BGB) and Carbon Stock (CS) was observed to be high in PJS (AGB = $56 \pm 35 \text{ tons/ha}$; BGB = $16.2 \pm 10.3 \text{ tons/ha}$; CS = $32 \pm 20.6 \text{ tons/ha}$) than SGS (AGB = $45 \pm 31 \text{ tons/ha}$; BGB = $9.6 \pm 8.8 \text{ tons/ha}$; CS = $27.3 \pm 22.4 \text{ tons/ha}$); Kruskal Wallis test determined the significance with $p < 0.05^*$ for AGB; $p < 0.05^*$ for BGB; and $p < 0.05^*$ for Carbon Stock between PJS and SGS (Fig. 10).

<Insert Fig. 10.>

Carbon dynamics in Sacred Groves Stands (SGS) and Prosopis juliflora Stands (PJS)

Within the PJS, the presence of young plants in young stands showed comparatively higher values of Net Ecosystem Productivity (NEP) and could possibly act as carbon sink ($0.0012 \pm 0.0004 \text{ g C/m}^2/\text{day}$). However, the matured stands within PJS, showed a shift towards carbon source, which is evident in the NEP value of $-0.0006 \pm 0.0003 \text{ g C/m}^2/\text{day}$; the old growth PJS records an NEP value of $-0.0034 \pm 0.0012 \text{ g C/m}^2/\text{day}$, clearly indicates the transition towards carbon source. In SGS among all the age groups Net Ecosystem Productivity values (Young: $0.07 \pm 0.02 \text{ g C/m}^2/\text{day}$, Mature: $0.13 \pm 0.02 \text{ g C/m}^2/\text{day}$, Old: $0.06 \pm 0.01 \text{ g C/m}^2/\text{day}$) identified the stands to be carbon sinks for a very prolonged period when compared to PJS (Fig. 11; Table.1).

<Insert Fig. 11; Table. 1.>

3.7. Soil erosion control in Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS)

RUSLE model revealed that soil erosion rates were significantly greater (29.5 ± 13.4 ton/ha/year) in SGS compared to PJS (7.52 ± 2.55 ton/ha/year) (Table. 2). This contrast difference between SGS and PJS might be attributed to the presence of a well-developed root system and higher soil organic carbon content and densely covered canopy in *Prosopis juliflora* Stands. These findings emphasize the importance of PJS in mitigating soil erosion and any restoration plans in such invasive vegetation stands should consider retaining this characteristic feature (Fig. 12).

<Insert Fig. 12. & Table. 2.>

4. Discussions

4.1 Ecological assessment and soil nutrient profile of Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS)

Field expeditions and analytical assessments conducted to examine the floral ecology of Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS), revealed distinct levels of floral diversity. SGS exhibited high floral diversity, whereas PJS displayed low floral diversity. Despite these differences, our study hints that both these vegetation types offer considerable regulating ecosystem services, though a previous research highlighted the pivotal role of biodiversity in governing and regulating, ecosystem services in forest ecosystems (Dar et al., 2019b). Earlier studies had observed that wherever the vegetation and the canopy is dense, such sacred grove like forest fragments rich in biodiversity are associated with substantial carbon stocks (Parthasarathy and Naveen Babu, 2021), nutrient-rich soils (Dar et al., 2019b), improved water quality (Oliveira et al., 2017), increased groundwater availability (Iftikhar Hussain et al., 2019), pathogen resistance (Quijas et al., 2010), and resistant against exotic taxa (Mace et al., 2012). And, once the floral diversity and species richness declines, it has negative implications on the relative ecosystem functions and eventually on the ecosystem services (Edrisi et al., 2020). Greater species richness is also linked to remarkable genetic diversity, which notably fosters ecosystem resilience against various biotic and abiotic factors exemplify climate resilient forests (Leakey et al., 2022). Such diverse ecosystems exhibit a variety of species population with diverse functional traits that contribute to sustainable ecosystem services over the course of their lifespans (Dar et al., 2019b). Where as in the *Prosopis juliflora* dominated vegetative stands, earlier studies elsewhere had documented monotonous ecosystem services (Holmgren, 2003; Kumar and Mathur, 2012; Mukherjee et al., 2017). In the arid and semi-arid regions, although PJS demonstrate high carbon stocks and nutrient-rich soils, its draws flak from the public due to groundwater depletion (Tomar et al., 2003). The current study noted the loss of floral diversity to due invasion of *Prosopis juliflora*, reinforcing the detrimental impact of this invasive species on ecosystem composition. Future reforestation and ecological restoration of invasive vegetation

needs to focus on selection of appropriate native trees that could potentially overcome the ill-effects induced to the landscape by invasive taxa.

In terms of nutrient enrichment, current research demonstrates that PJS exhibit higher soil nutrient proportions against SGS. The plant species of the family Fabaceae are known to have symbiotic associations between its nodulated roots and array of rhizobacteria (Joshi and Garkoti, 2020; Singh et al., 2019). In line with this phenomenon, plants in the study sites like *Prosopis juliflora*, *Albizia lebbeck*, *Wrightia tinctoria* etc. facilitates the process of nitrogen fixation, resulting in the enrichment of soil with biologically available nitrogen. Consequently, this nutrient enrichment stimulates the cycling of other nutrients, which further increases their invasion rate within the ecosystem (de Brito Damasceno et al., 2020). Earlier studies on this aspect have validated such an occurrence (Garg, 1998; Wakie et al., 2016) for instance, the levels of available nitrogen increased from 0.75 g/kg to 1.2 g/kg, while organic carbon content rose from 0.2 g/100 g to 1 g/100 g from 1981 to 1989 in the experimental plots of *Prosopis juliflora*. The dynamics include direct fixation of nutrients, deposition of organic matter through litter fall, promotion of root exudation and aeration in the root zone which facilitates the activity of mutualistic aerobic microorganisms, consequently enables nutrient cycling and enhance the overall soil nutrient pool (Tang et al., 2018). Nutrient enriched soil acts as a conducive substrate for the germinating seeds/saplings, also taxa which don't have the functional trait to generate its own nutrient island beneath its canopy, source its nutrients from other nutrient fixers which have the potential functional trait to fix nutrients (Joshi and Garkoti, 2020). The outcomes of this study suggests that transformation of PJS to forest groves using the apt native tree species could be a viable alternative, despite certain challenges. The major challenge confronting such an exercise could be recalcitrant nature of the soil, perhaps due to the presence of allelochemicals (L- tryptophan, 3-oxo-juliprosine) released by the *P.juliflora* (Nakano et al., 2004). And the native trees deemed to coexist or outcompete the invasive species in those landscapes can potentially be attempted for restoration. Nevertheless, the nutrient rich soil, as observed in the present study, could bolster the transformation and restoration of native vegetation.

4.2. Morphology, eco-physiology, biochemical characterization

Microscopic evaluation from the present investigation delved that stomatal density of the selected tree species varied significantly between the species; an early study hints that individual gene expression (STOMAGEN) and genetic imprint can have a significant role in the variations of stomatal densities within the tree species (Y. Tanaka et al., 2013). Similarly, in the present investigations, photosynthesis, transpiration, stomatal conductance, leaf intracellular CO₂, total chlorophyll plant total organic carbon and RuBisCO significantly varied between the selected species, which could also attributed to the specific genetic imprints respectively (Boudell, 2018; A. J. D. S. Negi et al., 2003; Porder, 2019; Seyyed and Haniyeh, 2013; Warren and Adams, 2004). In an attempt to unravel the ill-famed ground water depleting trait of *Prosopis juliflora* the present study compared transpiration rate of the eight selected species, and surprisingly *Prosopis juliflora* recorded only a medial position. Therefore, it may be interpreted that

despite a moderate transpiration in *Prosopis juliflora*, the large leaf area and dense canopy could be linked to the ground water depletion. This is in conjunction with another in arid and semiarid regions of Ethiopia which reports that a mature *Prosopis juliflora* tree consume 4.74 ± 1.97 L/day, while *Senegalia senegalia* (a native tree) consumes 6.46 ± 3.7 L/day; it also ascertains that *Prosopis juliflora* coppices at community scale with stand density of 1200–1600 trees consume 5688–7584 L/day/ha, whereas *Senegalia Senegal* (stand density : 400–600 trees) consumed 2584–3876 L/day/ha (Mbaabu et al., 2020; Shiferaw et al., 2023). Furthermore, the evergreen nature of *Prosopis juliflora* despite the aridity of the region, ostensibly necessitates high transpiration and water consumption, consequently depleting ground water (Shiferaw et al., 2023; T. Tanaka et al., 2013). On the other hand, most of the native trees in the arid and semiarid regions are deciduous in nature, and therefore transpiration per unit area is comparatively lower. The selected trees shows higher photosynthesis and its relative functional trait which determines its efficiency.

Assessment carbon fixing Morphological, Biochemical, physiological functional traits and carbon sequestering potential using SEM model

According to the SEM Model output, the morphological, biochemical, physiological functional traits play a pivotal role in determining the photosynthetic efficiency of different tree species. In the current study, stomatal density varied in order: *Azadirachta indica* > *Albizia lebbek* > *Ficus religiosa* > *Acacia nilotica* > *Ficus benghalensis* > *Wrightia tinctoria* > *Terminalia arjuna* > *Prosopis juliflora*. While relating the stomatal density to the photosynthetic efficiency, water availability is an important parameter to reckon in the semi-arid regions, and in such conditions such stomatal density is inversely proportional to photosynthetic efficiency. This phenomenon was previously explained by experimental studies in controlled conditions (heat/drought), where plants with high stomatal density tend to loose more water, which triggers stomata closing and eventually decreases photosynthesis rate (Hao et al., 2023; Karavolias et al., 2023). Even moderate water stress can limit photosynthesis by both stomatal resistance (closure) and carboxylation inhibition (Munne-Bosch and Penuelas, 2003; Schulze, 1986). Furthermore, when plants are exposed to water stress it produces ABA (abscisic acid), which signals the stomatal closure for regulating water loss (Gudesblat et al., 2007; Pei and Kuchitsu, 2005). This phenomenon of higher stomatal density > 1000 mm² implicates the lower photosynthetic rate in *Azadirachta indica* during water stress conditions in summer, while *Prosopis juliflora* showed comparatively higher photosynthetic rate in the present study.

Our field observations also indicated that ambient CO₂ levels fluctuations (398 ± 12 ppm) directly correlated with atmospheric temperature, affecting the photosynthesis rate. As the atmospheric CO₂ levels increases with increase in atmospheric temperature, the humidity decreases; and to replenish the reduced atmospheric humidity, the plants do transpire tremendously leading water loss in plant. In response, stomata gets closed to control the water loss and CO₂ intake via stomatal conductance gets reduced, which in turn diminishes the optimal photosynthesis rate of tree species (Haworth et al., 2023; Song et al., 2023; Xie et al., 2023; Xu et al., 2023; Yang et al., 2023; Yu et al., 2023). As the climate change impacts are becoming more tangible in India, the episodes of extreme summer and prolonged drought stress could potentially impact the photosynthetic rate of native tree species. Studies also speculate

certain native tree species can withstand shorter period of stress, however prolonged and extended summers could alter the photosynthesis while tree tends to put forth its energy for its survival rather than increasing productivity levels (Ghanbari et al., 2023; Rajesh and Goswami, 2023; Subramanian et al., 2023; Yuan et al., 2023). In that context, the outcomes of this study reveals native trees like *Terminalia arjuna*, *Wrightia tinctoria*, *Ficus benghalensis* are likely to perform and thrive well in the ensuing climate change scenarios in the semi-arid regions of India. This study also demonstrated that increase/decrease in other exogenous parameters such as soil moisture, intracellular CO₂, chlorophyll, RuBisCO, leaf water potential, stomatal conductance, and ambient temperature, tends to regulate photosynthesis rate in a positive/negative manner similar to earlier observations (Crafts-Brandner and Salvucci, 2000; De Souza, 2023; Feng et al., 2023; Kominami et al., 2008; Mao et al., 2023; Scafaro et al., 2023; Shirke, 2001; Xu et al., 2023). Particularly, the present study observed sensitivity of RuBisCO activity to heat especially for the species with very small leaf thickness. Earlier studies infer that high temperature limits photosynthesis by ceasing the activity of the enzyme RuBisCO activase (Crafts-Brandner and Salvucci, 2000; Kaur et al., 2023; Kumar et al., 2023), however the activity reversed upon cooling (Crafts-Brandner and Salvucci, 2004). This study also found the positive relationship between soil nitrogen availability and photosynthesis rate and its predominantly high in the taxa which had potential to fix nitrogen in soil, which is also substantiated by earlier investigations (Atkinson et al., 2016; Chtouki et al., 2022; Lachapelle and Shipley, 2012; Nasar et al., 2022). Decisively, the current investigation leads to the conclusion that high carbon-fixing potential of tree species is intricately linked to the presence of distinct adaptive functional traits, encompassing stomatal density below 1000 mm², nitrogen-fixing capability, the presence of chlorophyll, and the content of the RuBisCO enzyme; the following species (*Azadirachta indica*, *Prosopis juliflora*, *Wrightia tinctoria*, *Acacia nilotica*, and *Albizia lebbek*) exhibited to have higher productivity levels attributed to the possession of the aforementioned functional traits.

4.3. Dendrochronology and age of the trees

The current study found life expectancy of tree species like *Ficus religiosa* and *Ficus benghalensis* is high, probably due to their slow growth and genetic imprint. On the other hand, *Prosopis juliflora* and *Terminalia arjuna* were found to have comparatively shorter life span, which could plausibly be attributed to their fast growing nature. Many fast growing trees undergo rapid cell division, with each round of cell division telomeres of the chromosome gets shortened, and the cells enter replicative senescence stage, sooner or later senescent cell undergo apoptosis; however in the case of slow growing tree species, due to the critical intervals between cell division/cycle it takes prolonged time for the slow replicating cell to reach replicative senescence and apoptosis (Kirkwood and Holliday, 1979; Lorimer et al., 2001). In contrast, for tree species characterized by protracted intervals between cell division cycles, the progression toward replicative senescence and subsequent apoptosis is considerably protracted, largely due to their leisurely replicative rates (Kirkwood and Holliday, 1979; Lorimer et al., 2001). According to a study, slow growing species under go multiple rounds of mutation which enables them to live longer and adapt against prevailing environmental conditions; an experimental comparison of two tropical trees, *Shorea laevis* (slow-growing) and *S. leprosula* (fast-growing), found that the rate of somatic mutation accumulation per meter of growth was 3.7-fold higher in *S. laevis* than in *S. leprosula* (Satake et al.,

2023). In addition, the characters like bark thickness (which provide defense against disease causing pathogens), retention of meristematic cells to replace deformed or lost plant organ, synthesis of defensive compounds against pest and stress tolerant potential of tree species also determines trees life longevity (Bauman et al., 2022; Lorimer et al., 2001; Ohse et al., 2023).

4.4. Carbon stock

The current findings evinced that above ground biomass and below ground biomass was high in PJS (AGB = 56 ± 35 tons/ha; BGB = 16.2 ± 10.3 tons/ha) compared to SGS (AGB = 45 ± 31 tons/ha; BGB = 9.6 ± 8.8 tons/ha). Measurements of the current study with respect to basal area in PJS (38 ± 18 m²/ha) and SGS (25 ± 11 m²/ha) validate the above mentioned difference in AGB and BGB across PJS and SGS. Numerous have pointed that AGB and BGB are represently attributed to high basal area of the existing vegetation, carbon fixing potential of trees and robust growth of the tree species (Becknell and Powers, 2014; Ghosh and Mahanta, 2014; Návar Cháidez et al., 2005; Pragasan and Karthick, 2013; Shah et al., 2014; Shanmughavel and Francis, 1996). Current study found carbon stock in PJS, SGS to be 32 ± 20.6 tons/ha and 27.3 ± 22.4 tons/ha respectively. Findings of the current study are in line with recent previous study at deciduous forests (i.e. denoted as Sacred Groves Stands - Outside the protected area) across central Tamil Nadu in which mean carbon stock, ranged between 7.6 t ha^{-1} to 23.4 t ha^{-1} (Pragasan, 2022). While in the case of *Prosopis juliflora* stands, no authenticated information on carbon stock in India was reported, but a study in Ethiopia had recorded in the range from 85.8 ± 4.7 Mg/ha (in dense thickets) to 48.2 ± 4.4 Mg/ha (in sparse thickets) (Birhane et al., 2017).

4.5. Carbon dynamics

Present study revealed lower Photosynthetic Potential/Gross Primary Productivity of SGS when compared to PJS. Moreover, the present study articulated higher Gross Primary Productivity/Photosynthesis of taxon species of Fabaceae, Capparaceae, Moraceae, and Meliaceae, concomitantly contributing to the Net Ecosystem Production (NEP). Gross Primary Productivity (GPP) of vegetation stands are determined by individual photosynthetic potential of tree species, genetic imprint and its relative abundance (Dar et al., 2019a). The variation in carbon sequestration is also likely to be influenced by temperature, precipitation, atmospheric pressure, solar light availability and elevation (Lorenz and Lal, 2010). With respect to NEP, the current study recognized that during the young stage, both PJS and SGS are potential carbon sinks. As the transition occurs from young to mature, SGS acted like a sink while the PJS transformed as source. However, when PJS attains old-growth phase, it acted as potential CO₂ source; but in case of SGS even after the transition from mature to old-growth phase, the growth young saplings allowed the system to act partially as CO₂ sink. Such a phenomenon of younger vegetation acting as carbon sink and older trees as carbon source is presumably universal (Holtmann et al., 2021). Also, in the present study soil respiration in older stands was found to be high in PJS than SGS. Soil respiration increases with soil microbial load: an ecological study recorded 350 ± 121 /g microbial strains under the canopy soil of dense *Prosopis juliflora* stands (Vallejo et al., 2012); in case of SGS microbial diversity was recorded as 134 ± 87 /g (Pandey et al., 2010). Higher proportions of root exudate and

organic matter in the soil stimulates growth of soil micro biota, higher microbial population emits out higher proportions of CO₂ into the atmosphere via soil respiration.

4.6. Soil erosion

In the current investigation, PJS demonstrated notably reduced levels of soil erosion when compared to SGS. Subsequent analysis of soil nutrient composition within the present study indicated that the diminished soil erosion observed in PJS could be ascribed to its elevated soil organic carbon content. Consequently, these findings substantiate the postulation put forth in a prior study that delved into the pivotal functions of soil organic carbon within the rhizosphere of plants, particularly within the substantial reservoirs of soil. Furthermore, the study posited that carbon-rich root exudates betine and other polysaccharides, which functions as adhesive agents, effectively stabilizing the soil and mitigating soil erosion. Many earlier studies had ascertained the efficacy of this adhesive relationship in reducing soil erodibility (Bennett and Chapline, 2020; Jiao et al., 2009; Okacha et al., 2023; Sharma et al., 2023; Yan et al., 2023). A recent study in Dianchi watershed region of China, substantiated the relationship, in which it was observed that young forests with low soil organic carbon exhibited an annual soil erosion rate of 11.02 ± 4.77 tons per hectare, whereas mature forests high soil organic carbon exhibited a rate of 3.34 ± 1.88 tons per hectare (Sun et al., 2023). In India too, a research conducted in the forest landscape at Western Ghats region reported a controlled annual soil erosion rate of 68.26 tons per hectare due to the vegetation; while in open lands soil erosion rate was observed to be 89.36 tons per hectare (Chinnasamy and Honap, 2023).

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Tables

Table. 1 | Ecosystem productivity and carbon sinking efficiency and carbon dynamics for Young, Mature, Old Sacred Groves Stands (SGS) & *Prosopisjuliflora* Stands (PJS) across the study area.

	Young (15 - 25 years)		Mature (25 - 45 years)		Old (45 - 75 years)	
Productivity	PJS	SGS	PJS	SGS	PJS	SGS
GPP [Gross Primary Productivity] (g C / m² / Day)	0.0084 ± 0.0032	0.0038 ± 0.0014	0.0078 ± 0.0026	0.0067 ± 0.0011	0.0048 ± 0.0018	0.0055 ± 0.0015
Plant respiration – flux (g C / m² / Day)	0.0053 ± 0.0024	0.0022 ± 0.0011	0.0045 ± 0.0012	0.0032 ± 0.0004	0.0035 ± 0.0012	0.0037 ± 0.0007
NPP [Net Primary Productivity] (g C / m² / Day) <i>[NPP = GPP – PR]</i>	0.0031 ± 0.0014	0.0016 ± 0.0003	0.0033 ± 0.0014	0.0035 ± 0.0007	0.0013 ± 0.0004	0.0035 ± 0.0008
Soil respiration – flux (g C / m² / Day)	0.0019 ± 0.0007	0.0009 ± 0.0001	0.0039 ± 0.0011	0.0022 ± 0.0005	0.0047 ± 0.0016	0.0029 ± 0.0009
NEP [Net Ecosystem Productivity] <i>[NEP = NPP – SR]</i>	0.0012 ± 0.0004	0.0007 ± 0.0002	-0.0006 ± 0.0003	0.0013 ± 0.0002	-0.0034 ± 0.0012	0.0006 ± 0.0001
Mann Whitney U Test (P<0.05)	P < 0.05**		P < 0.01***		P < 0.01***	
Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1						
*If NEP is positive then the ecosystem is a sink, If NEP is negative the ecosystem is a source						

Table. 2 | Soil erosion rate in Sacred Groves Stands (SGS) & *Prosopis juliflora* Stands (PJS) across the study area

	Soil Erosion (ton / ha / year)	Kruskal Wallis Test (p<0.05)
PJS	7.52 ± 2.55	0.01***
SGS	29.5 ± 13.4	
Signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1		

Figures

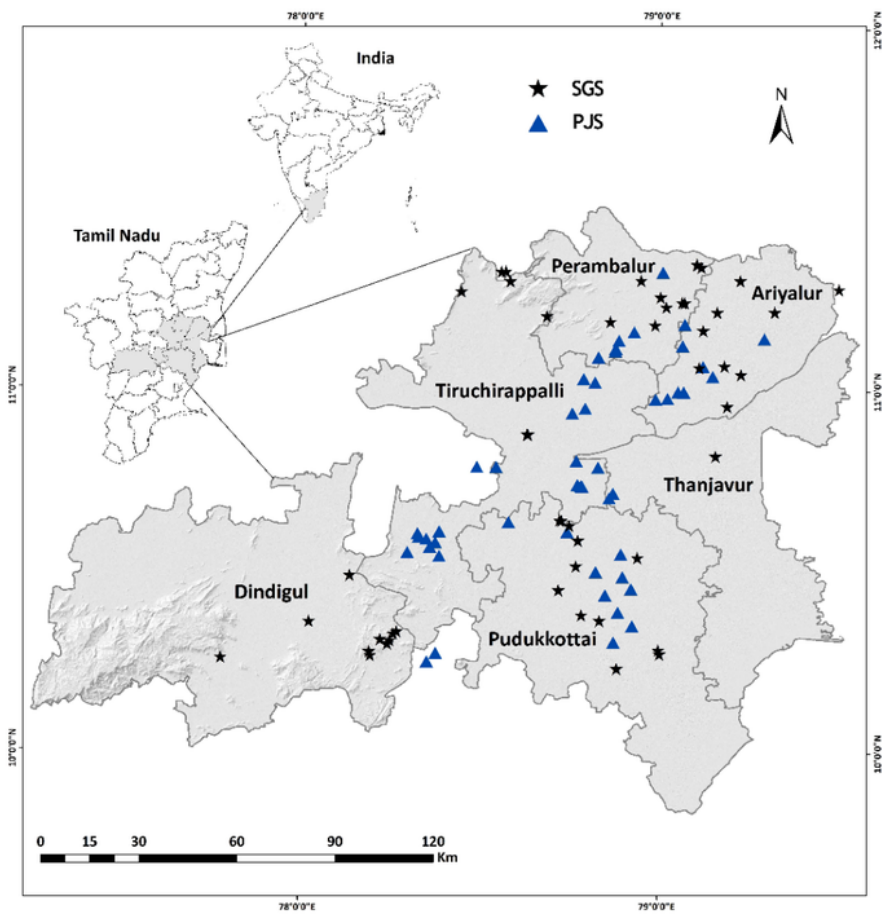


Figure 1

Study sites - Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS) across the central region of Tamil Nadu, India.

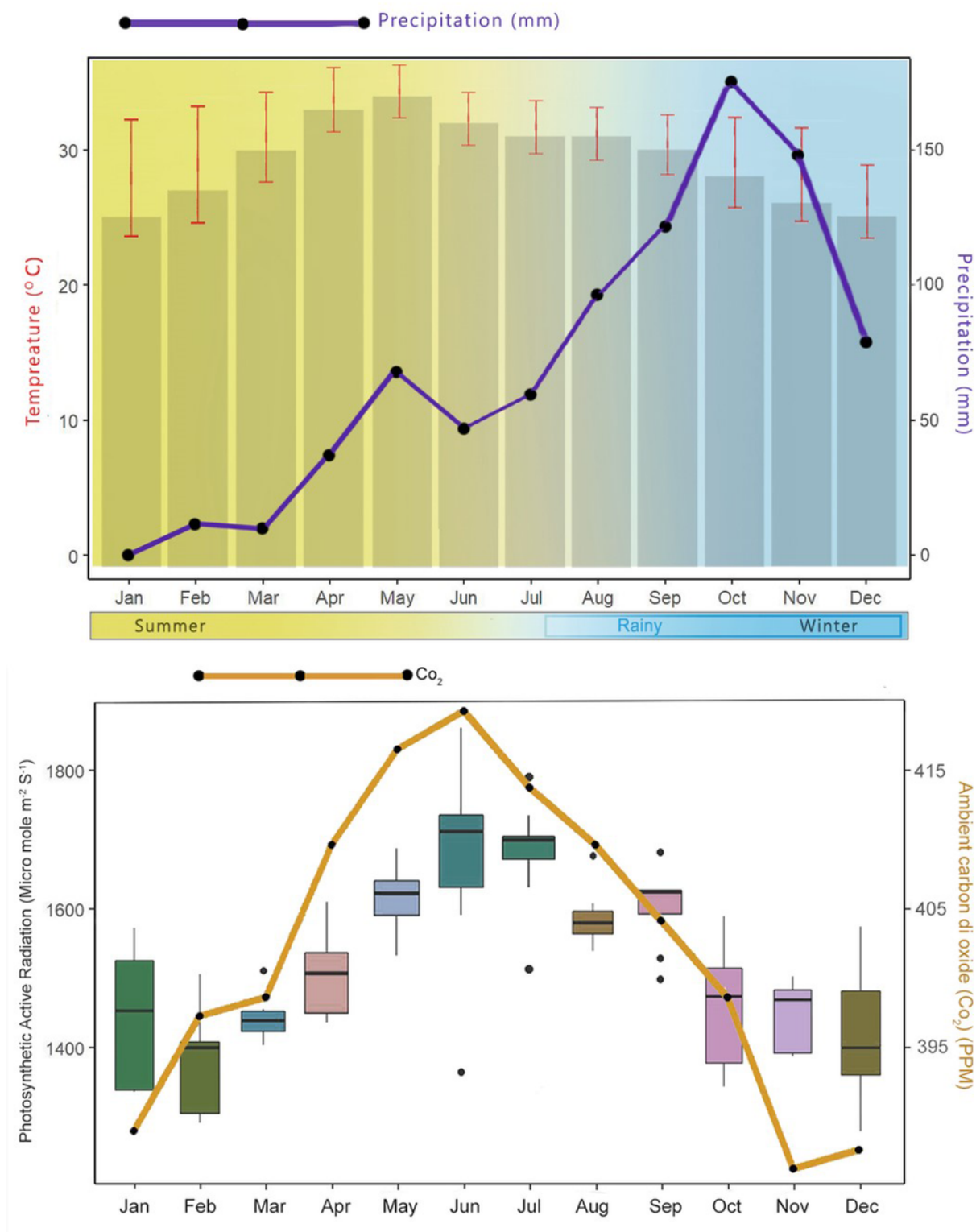


Figure 2

Annual (2022) Ambient environment condition across the study sites at central region of TamilNadu. a, Observed ambient temperature (°C), and mean precipitation levels (mm). **b,** Photosynthetic Active radiation (μ mole m⁻² s⁻¹) and mean ambient Carbon dioxide (ppm).

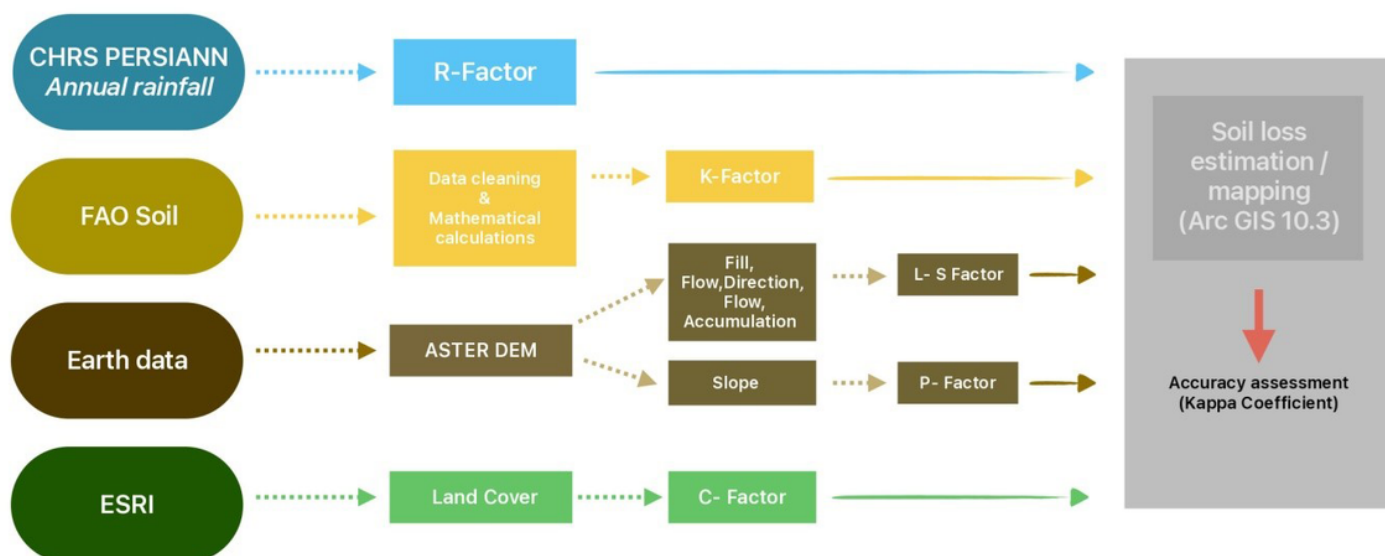


Figure 3

RUSLE soil erosion mapping methodology, RUSLE - model validation was attained using Kappa Coefficient with threshold limit > 90 %.

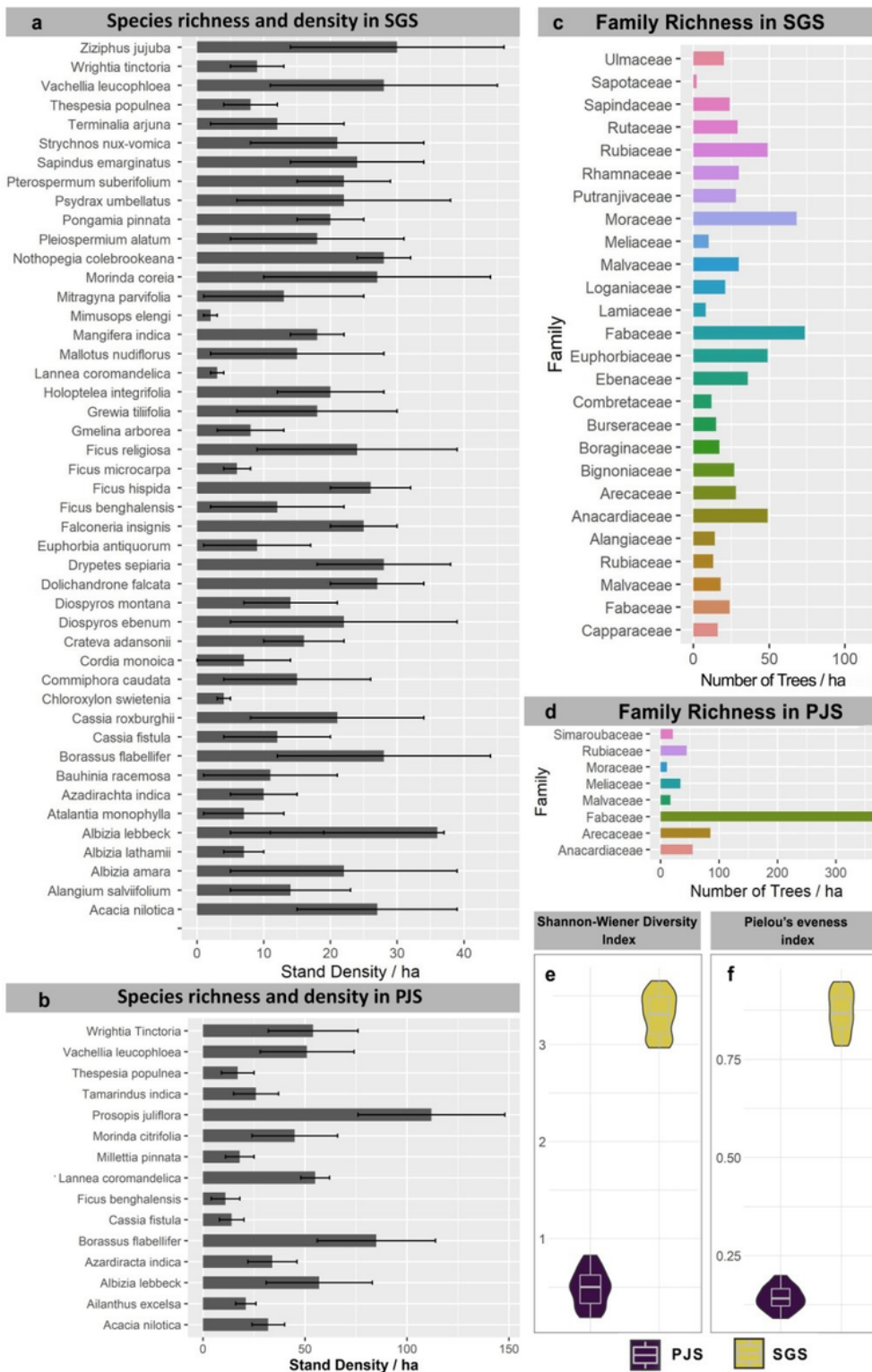


Figure 4

Ecological Profile of Sacred Groves Stands (SGS) & *Prosopis juliflora* Stands (PJS) located across the study region at central region of Tamil Nadu. a, Tree species richness and corresponding stand density / ha in SGS. **b,** Tree species richness and density / ha in PJS. **c,** Family richness in SGS. **d,** Family richness in PJS. **e,** Shannon wiener diversity index (H-index). **f,** Pielou's evenness index (E-index).

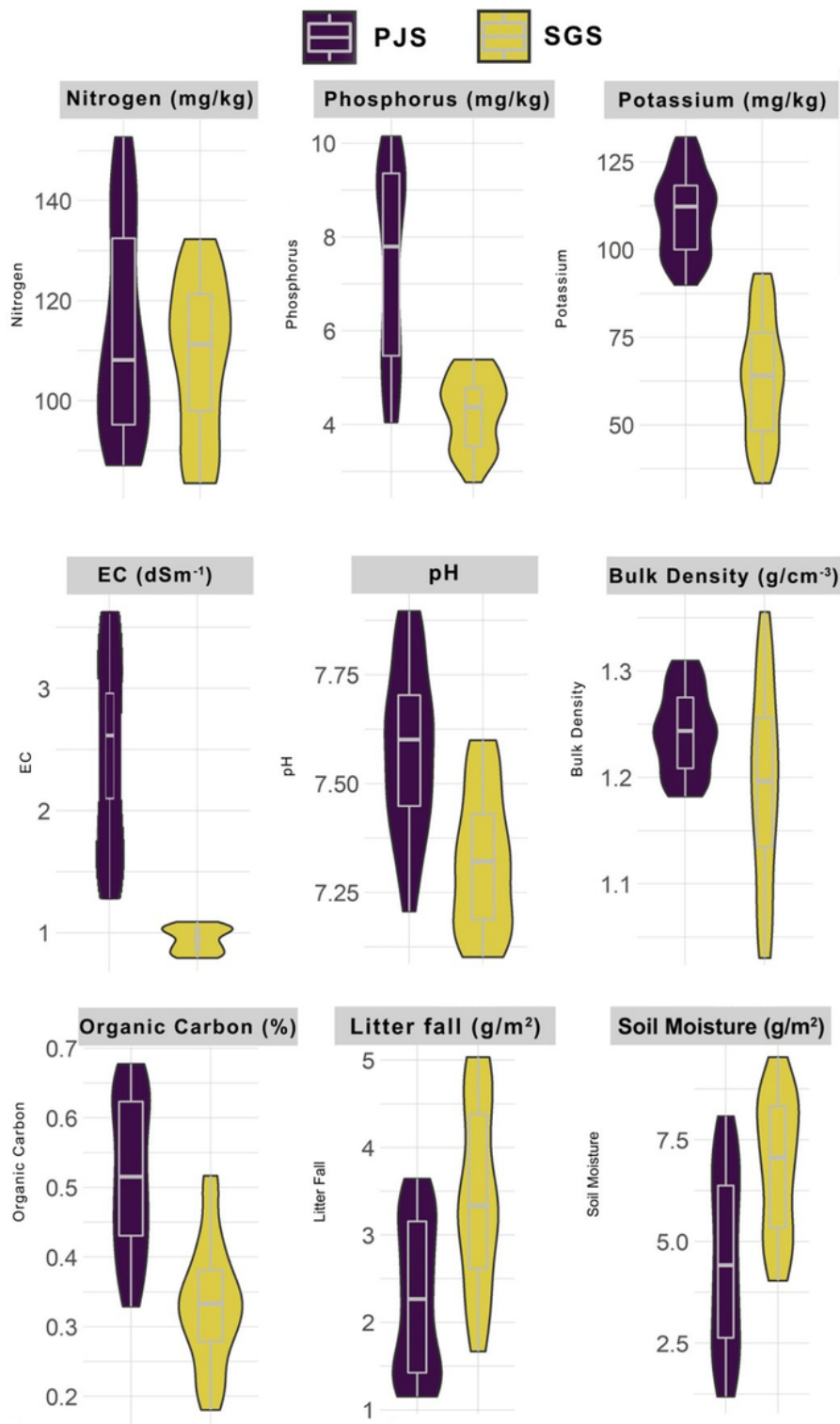


Figure 5

Soil nutrient profile of Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS) across the Central Region of Tamil Nadu.

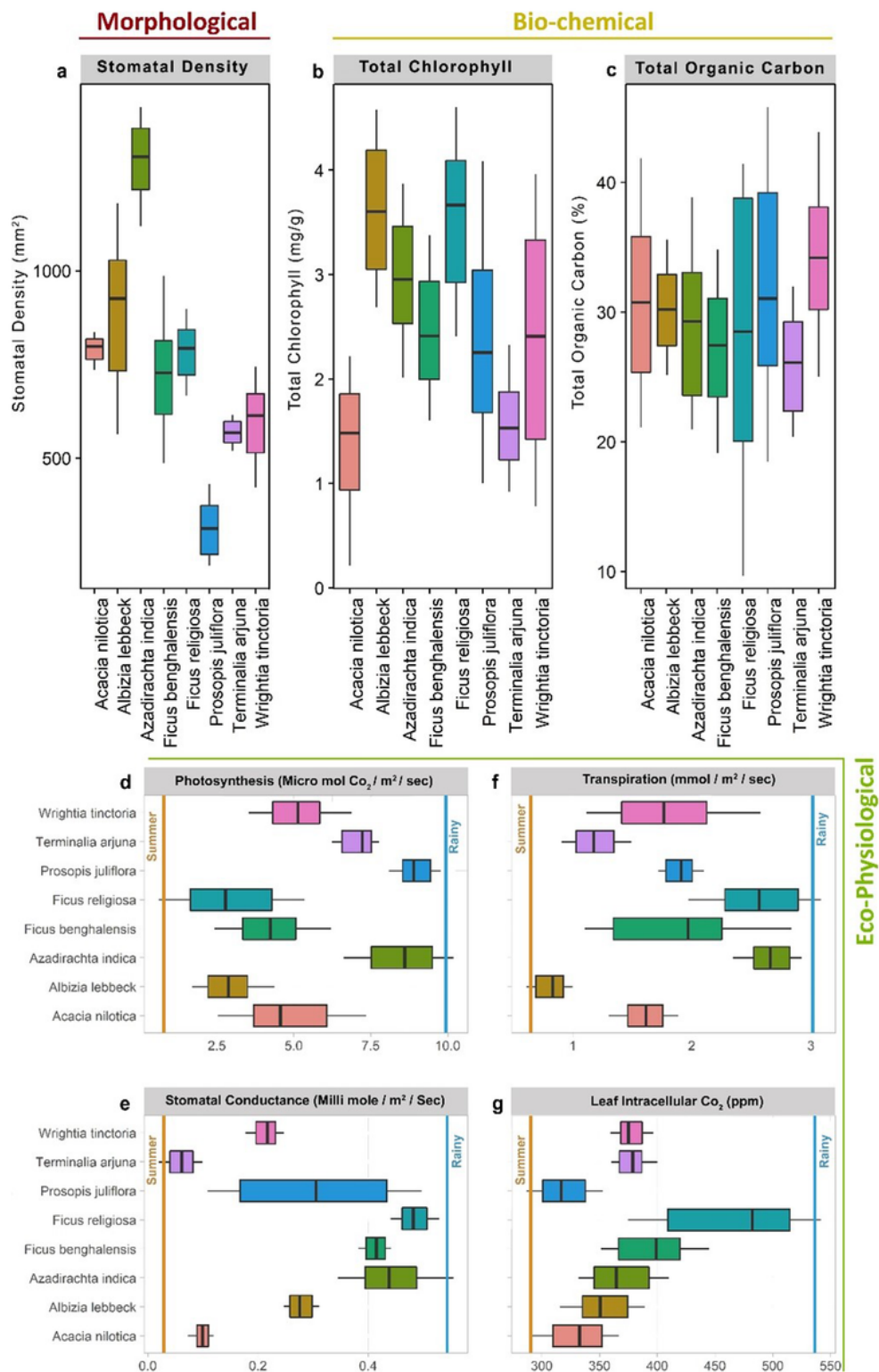


Figure 6

Morphological, Biochemical & Eco-physiological assessment in selected tree species in SGS and PJS across the central region of Tamil Nadu – a, Stomatal density. b, Total chlorophyll. c, Plant Total organic carbon. d, Photosynthesis. f, Transpiration, e, Stomatal Conductance. and g, Leaf Intracellular Co₂ levels.

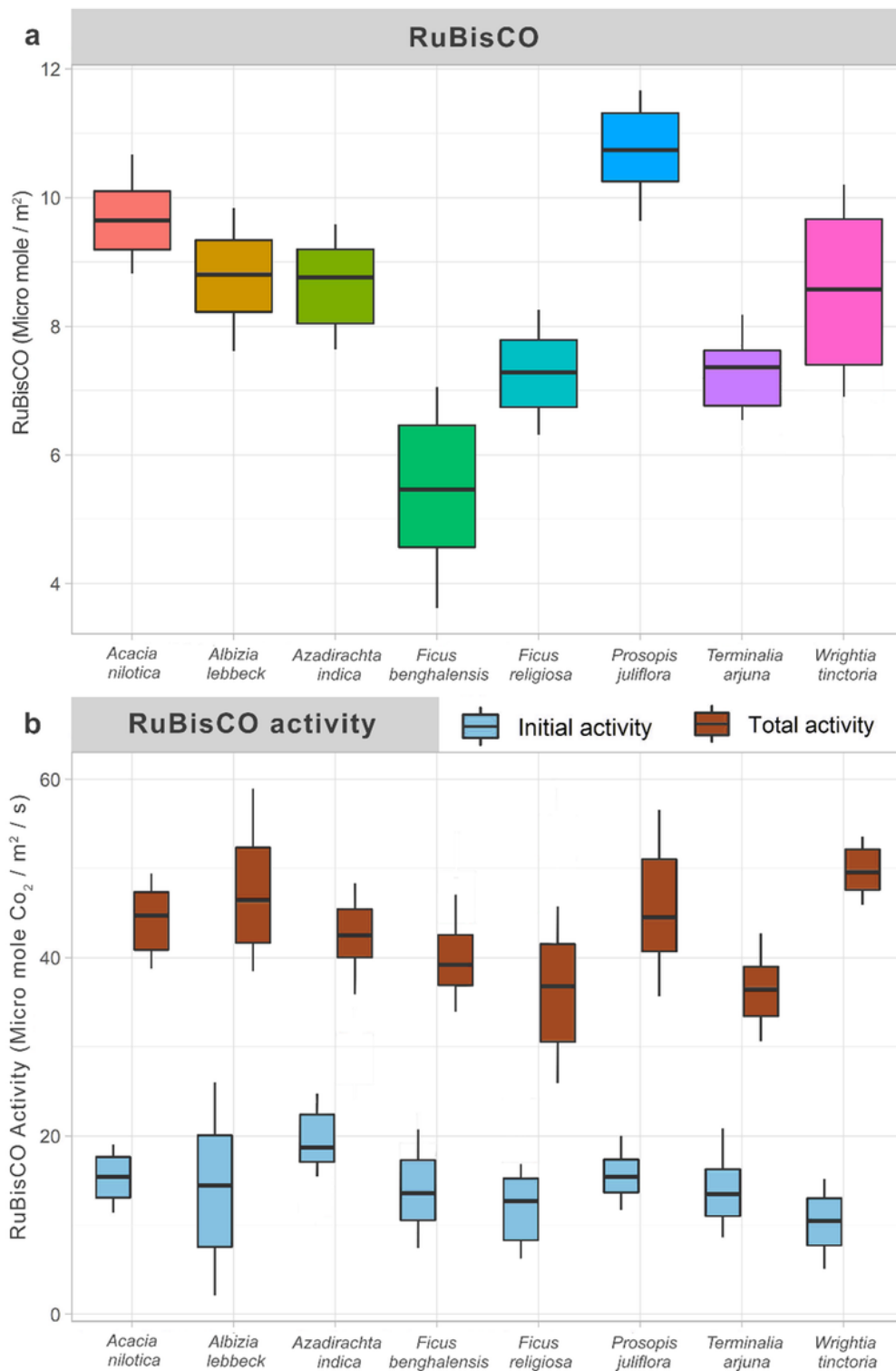
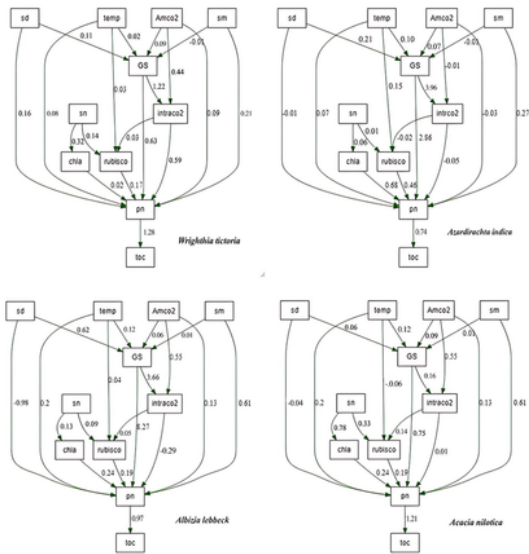


Figure 7

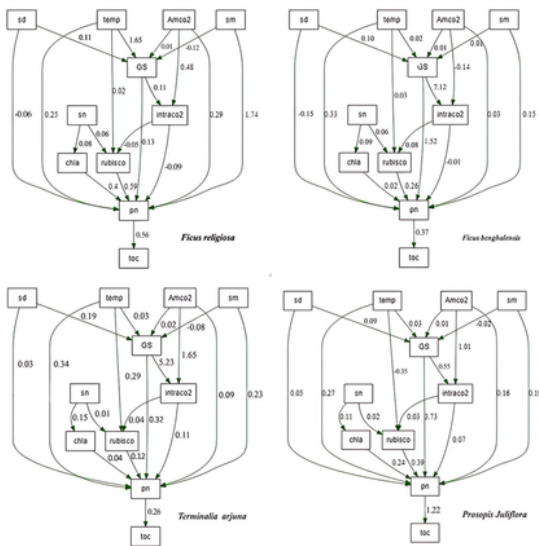
RuBisCO quantity and activity for selected tree species in Sacred Groves Stands (SGS) & *Prosopis juliflora* Stands (PJS) across central region of Tamil Nadu

sd - Stomatal Density temp - Temperature Amco2 - Ambient CO₂ sm - Soil Moisture GS - Stomatal Conductance
 sn - Soil Nitrogen intraco2 - Leaf Intra cellular CO₂ chla - Total Chlorophyll rubisco - RuBISCO
 pn - Photosynthesis TOC - Total Organic Carbon



a

sd - Stomatal Density temp - Temperature Amco2 - Ambient CO₂ sm - Soil Moisture GS - Stomatal Conductance
 sn - Soil Nitrogen intraco2 - Leaf Intra cellular CO₂ chla - Total Chlorophyll rubisco - RuBISCO
 pn - Photosynthesis TOC - Total Organic Carbon



b

Figure 8

A | Structural Equation Model (SEM) testing the effects of environmental, morphological and physiological functional trait of selected trees on photosynthesis and total organic carbon content of the tree species. Parameters of each SEM of the respective tree species were acquired using the multiple model validation indices - lowest Akaike information criterion (AIC) value, Comparative Fit Index (CFI) > 0.95, Tucker-Lewis index (TLI) > 0.90, model test chi square value $p > 0.05$, Root mean Square of

Appropriation (RMSEA) and Standardized Root Mean Square Residuals (SRMR) < 0.08. The numbers next to arrows in the model path diagrams denote the standardized coefficients for each path.

B | Structural Equation Model (SEM) testing the effects of environmental, morphological and physiological functional trait of selected trees on photosynthesis and total organic carbon content of the tree species. Parameters of each SEM of the respective tree species were acquired using the multiple model validation indices - lowest Akaike information criterion (AIC) value, Comparative Fit Index (CFI) > 0.95, Tucker-Lewis index (TFI) > 0.90, Model test chi square value $p > 0.05$, Root mean Square of Appropriation (RMSEA) and Standardized Root Mean Square Residuals (SRMR) < 0.08. The numbers next to arrows in the model path diagrams denote the standardized coefficients for each path.

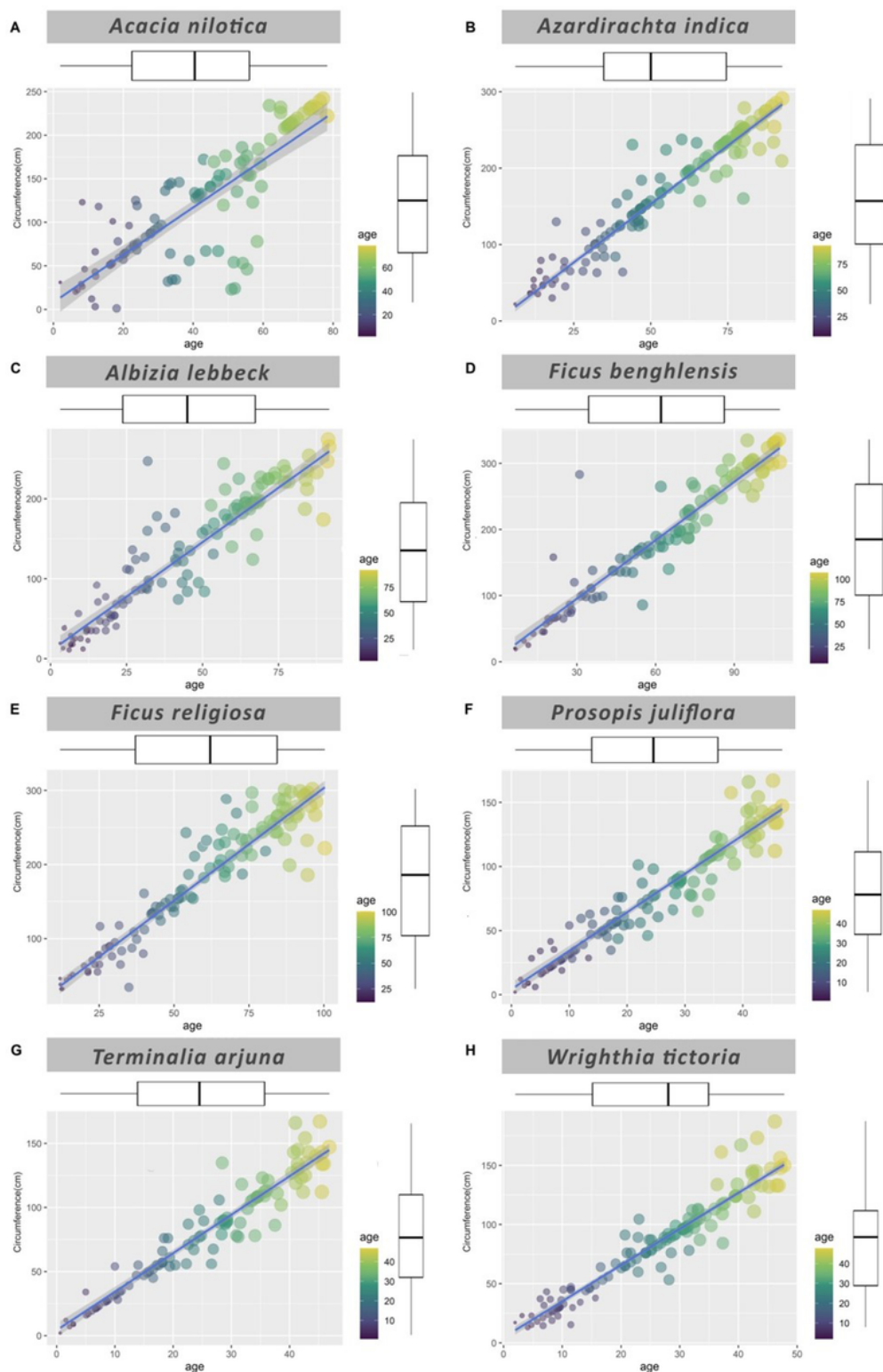


Figure 9

Tree age decision regressor model testing the effects on age of selected trees on variation with increase in stem circumference (cm) as a predictor variable. (Parameters based the decision tree model was achieved on the lowest Akaike information criterion (AIC) value.) (Grey bars in parallel with the regression line depict the 95% confidence interval).

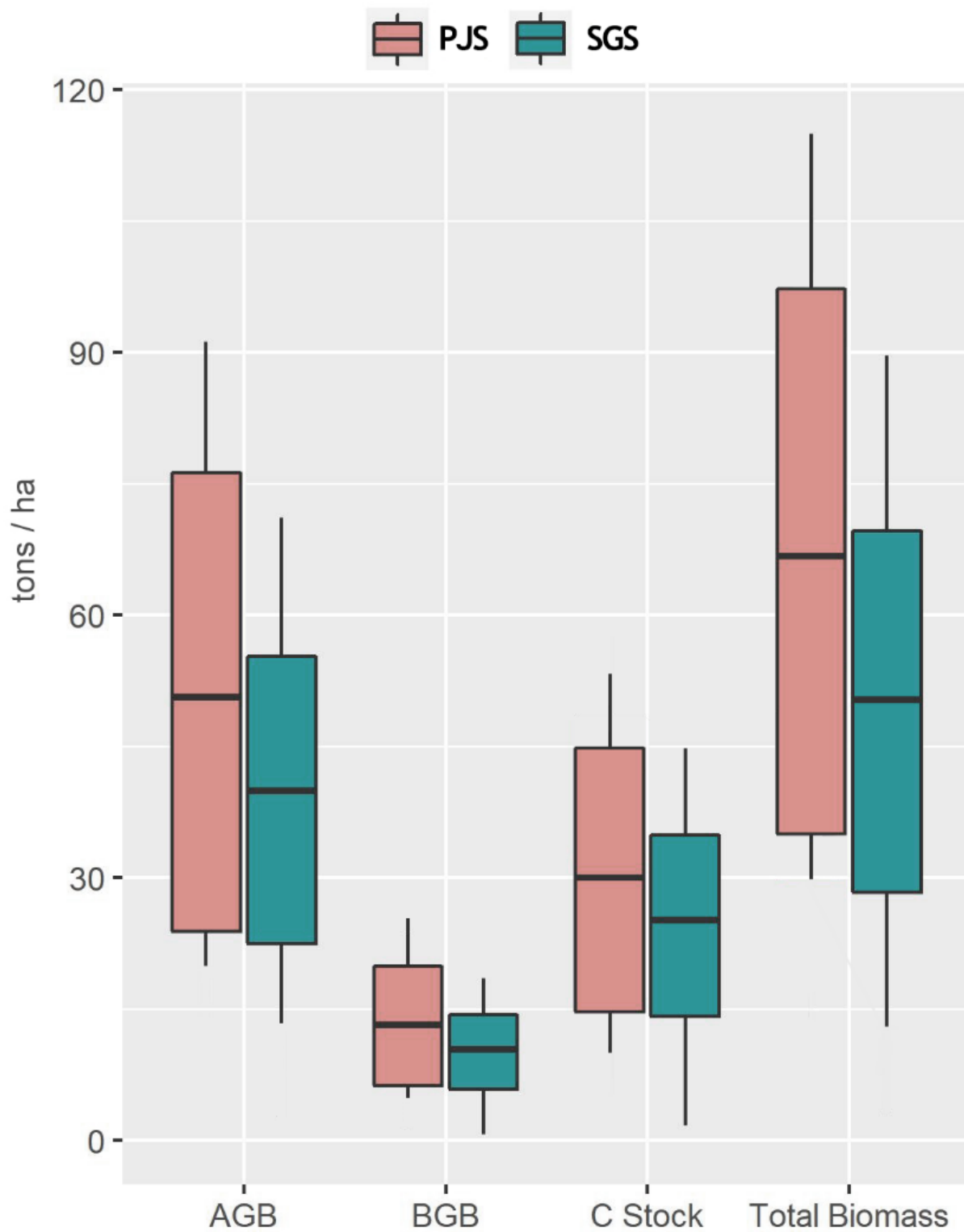


Figure 10

AGB, BGB, Total Biomass, and Carbon Stock of Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS) across the study area.

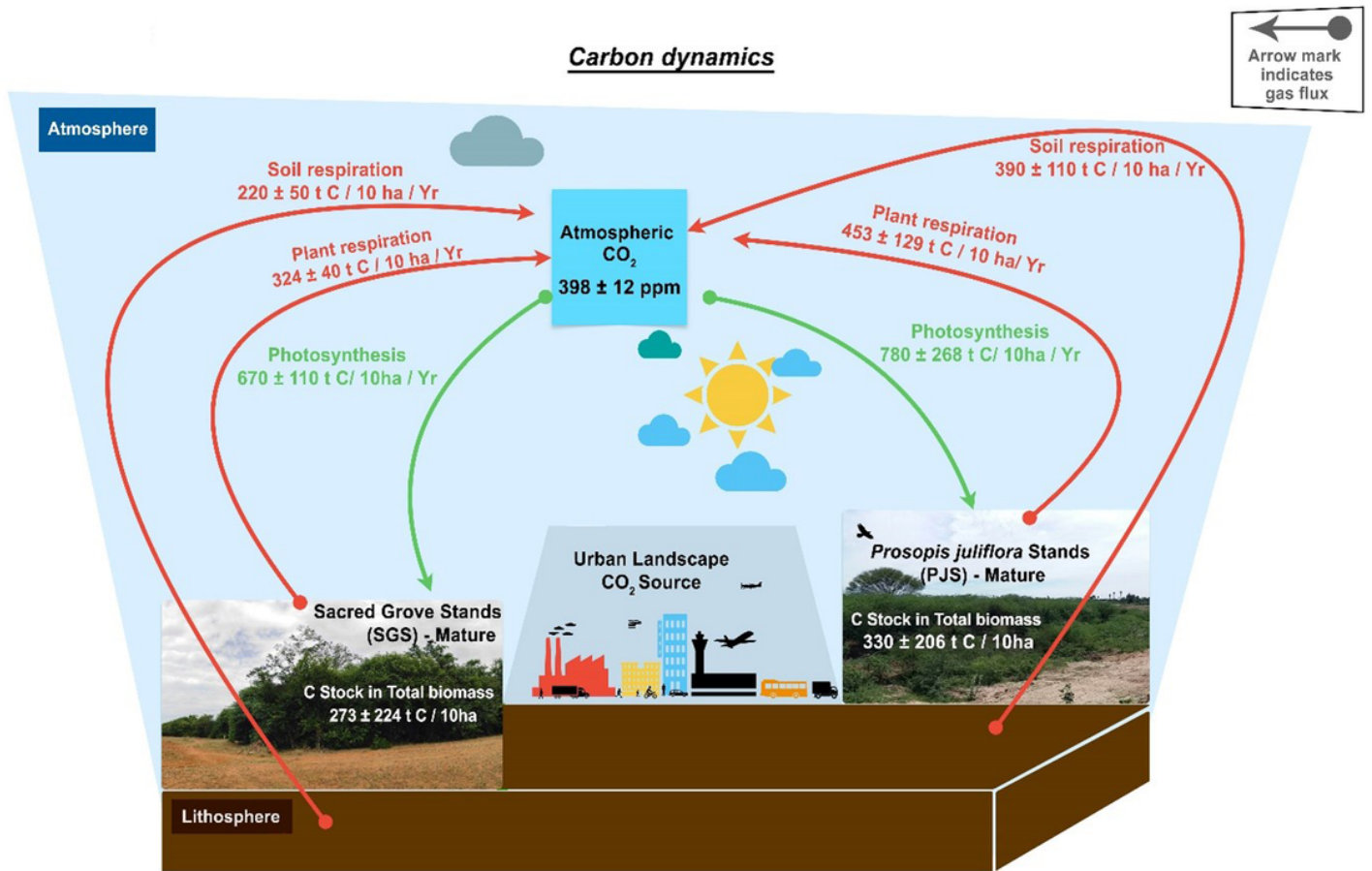
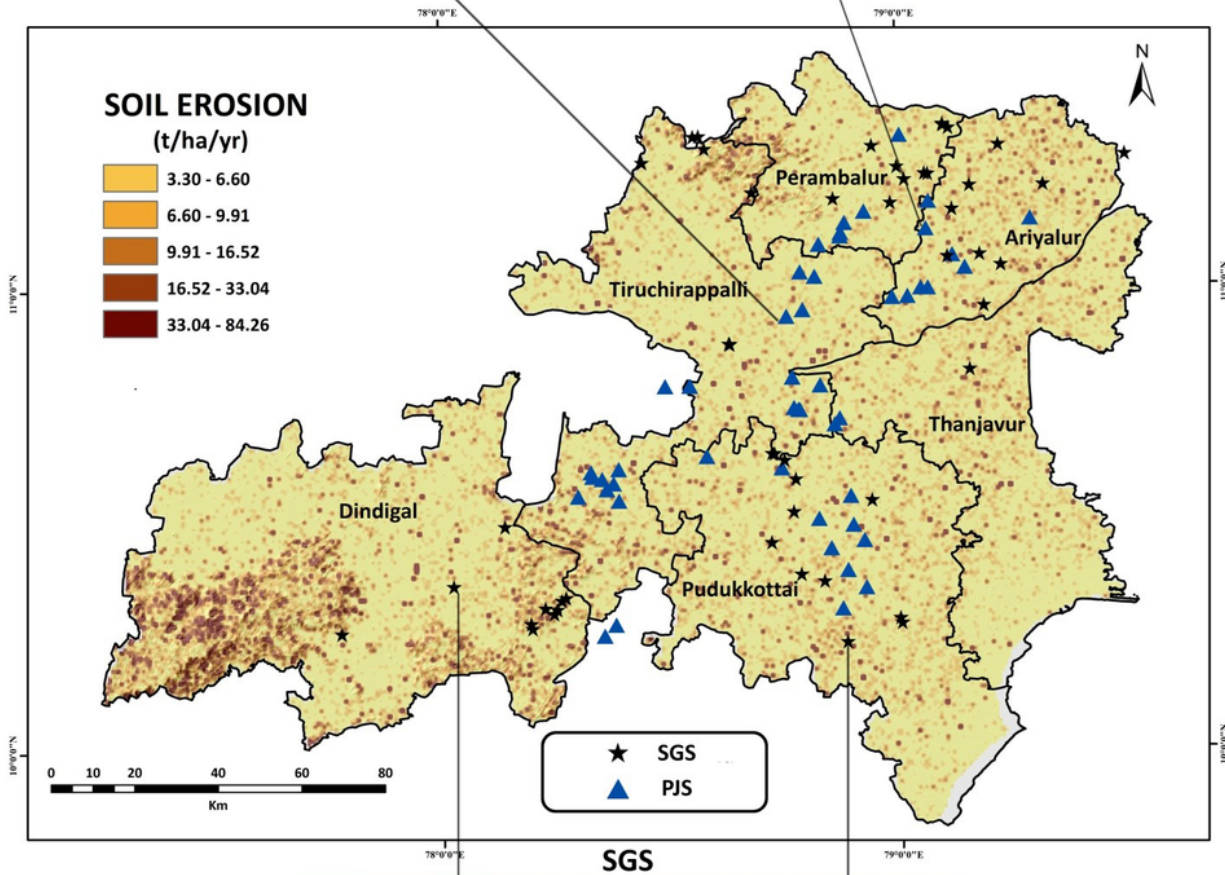
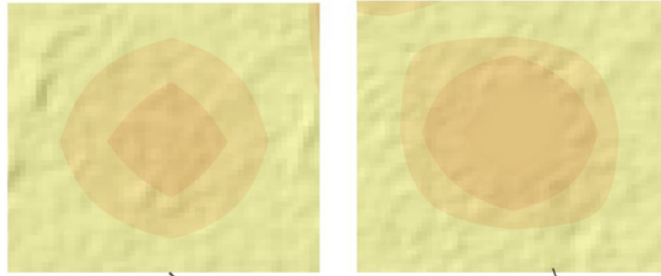


Figure 11

Carbon dynamics in Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS) across the study area.

PJS



SGS

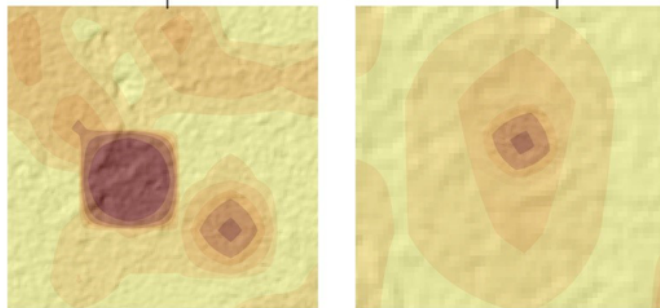


Figure 12

RUSLE model for soil erosion in Sacred Groves Stands (SGS) and *Prosopis juliflora* Stands (PJS) across the study area.

Supplementary Files

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