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Assessment of habitat features modulated carbon sequestration strategies for drought management in tropical dry forest fragments

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HIGHLIGHTS

- Species and functional diversity significantly reduced with decreasing edge distance
- Functional richness strongly increased C-sequestration for drought avoiding strategy
- C-sequestration for drought tolerants was mainly attributed by Shannon diversity
- Fire index was critical for declining C-sequestration for drought avoiding strategy
- Drought index critically decreased C-sequestration for drought tolerant strategy

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ABSTRACT

Habitat features, such as species diversity, functional diversity, tree size, disturbances and fragment sizes have differential impacts on carbon (C) storage and C-sequestration in forest ecosystems. Present study attempted to understand the tree strategies for modulating C-sequestration capacity across tropical dry forest fragments with variable edge distances. We evaluated the differences between drought strategies (*i.e.*, drought avoiding and drought tolerant) for variations in stem density, relative growth rate (RGR), C-storage and C-sequestration, species diversity, functional diversity, tree size and disturbance indicators along edge distance gradient, besides analyzed the differences between drought strategies for responses of C-storage and C-sequestration to variations in species diversity, functional diversity, tree size and disturbance indicators. Various traits and functional indices were analyzed using standard statistical techniques. For total trees and for the two drought strategies, generalized linear modeling results showed a significant decline in stem density, RGR, C-stock, C-sequestration, species diversity, functional diversity and tree size indicators, while a considerable increase in disturbance indicators, along decreasing edge distance across the fragments. The drought strategies exhibited a high degree of variation in the slope of associations for above variables with edge distance across fragments. For predicting C-sequestration, structural equation modeling results showed highly significant influence of functional diversity indicators for drought avoiding strategy, while species diversity indicators were strongly significant for drought tolerant strategy. Moreover, fire index and drought index were critical predictors for C-sequestration for drought avoiding and drought tolerant strategies, respectively. This study provide inputs to understand the largely ignored processes of C-storage and C-sequestration in fragmented forests, which are currently prevalent due to heavy anthropogenic pressures. Our findings are useful for forest managers to understand vegetation responses to interactions of species diversity, functional diversity, tree size and disturbance indicators, for predicting the stability of larger fragments and for planning restoration of smaller fragments.

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1. Introduction

Forests are economical approach for climate change mitigation due to their capacity to fix atmospheric CO_2 and transforming it as biomass carbon (Pan et al., 2011; Cook-Patton et al., 2020). However, uncertainty still exists, on how tree strategies and habitat features interact to modulate the carbon sequestration capacity of the forest ecosystems. The carbon storage in forests is partly determined by species diversity (Li et al., 2019; Osuri et al., 2020), while functional traits are also considered as the advanced way of understanding forest functional dynamics (Wright et al., 2010). Currently, loss of natural habitats and climate change are threatening structural and functional diversity of forest ecosystems (Aquilué et al., 2020), therefore critical assessment of the associations of forest carbon storage and sequestration with important habitat features, *i.e.*, species diversity indicators (*viz.*, species richness, Shannon diversity and species evenness), functional diversity indicators (*viz.*, functional richness, functional dispersion and functional evenness), tree size indicators (*viz.*, height, canopy depth and canopy cover) and disturbance indicators (*viz.*, harvest, fire and drought), and their inter-relationships is highly warranted.

Species diversity is associated with productivity and carbon storage (Diaz et al., 2009; Poorter et al., 2015; Liang et al., 2016; Ammer, 2019), however to what extent species diversity determines carbon storage in various ecosystems is still uncertain (Bunker et al., 2005; Liu et al., 2018; Ammer, 2019). Among several mechanisms demonstrating impact of species diversity on ecosystem productivity or carbon balance, the most suitable explanation for understanding biodiversity-ecosystem functioning relationships are based on selection effects, niche complementarity, and biotic and abiotic facilitation (Hooper et al., 2005). The selection effect was hypothesized to result from differences in the fundamental productivities of species, as revealed in monocultures, and from the greater likelihood that a more productive species would be present (“selected”) at higher diversity (Tilman et al., 2014). However, niche complementarity hypothesis indicates facilitative interactions or niche differentiation between species, which suggests that relative to monoculture, species mixture promotes resource-use and nutrient retention by partitioning of resources, leading to increase in productivity (Williams et al., 2017). Under biotic and abiotic facilitation, species or the improved environmental conditions in a plant community enhance the performances of another species (Wright et al., 2017).

The functional diversity has been described as “the value and range of functional traits of the organisms present in a given ecosystem” (Diaz and Cabido, 2001, pp. 654), indicating intricate associations between species diversity and functional diversity which determines carbon storage. Consequently, the significance of species diversity and functional diversity for influencing carbon storage in different ecosystems are increasing in debates, while recent empirical studies have emphasized that they act complementarily, and species diversity promotes carbon storage through functional diversity and functional dominance (Mensah et al., 2016). For this argument, the niche complementarity hypothesis assumes that the increasing species diversity leads to the production of a variety of functional traits which provide opportunities for efficient use of resources by the species, leading to an increase in ecosystem functions (Diaz and Cabido, 2001). While, the selection effects hypothesis suggests that highly diverse ecosystems have greater chances of having dominant species or traits influencing ecosystem functions (Mensah et al., 2016). However, the recent reviews have also reported controversies in the relationships between species diversity and functional diversity and suggested that the relationships could also be affected by habitat alterations or disturbances and species pool (Mayfield et al., 2010; Mouchet et al., 2010; Cadotte et al., 2011).

Together with species diversity and functional diversity, forest structural attributes, such as tree size indicators also strongly determine resource capture, productivity and forest biomass (Poorter et al., 2015; Fotis et al., 2018). Moreover, the variations in tree size indicators are significantly associated with species diversity and carbon storage in natural forests (Enquist et al., 2009; Zhang and Chen, 2015) through adjustments in spatial packing of crown cover for better utilization of light (Yachi and Loreau, 2007; Rödig et al., 2018).

Tropical dry forest is the most widely distributed forest type in the tropics, covering approximately 42 % of tropical forests worldwide (Murphy and Lugo, 1986), however determinants of aboveground carbon in these forests are still debatable (Portillo-Quintero et al., 2015; Mesa-Sierra et al., 2022). These forests experience a long dry period ranging from 5 to 7 months, each year, and are subjected to anthropogenic disturbances, such as harvesting and fire (Chaturvedi et al., 2024). Harvesting reduces the carbon stock, while fire and drought redistribute the carbon stock from live pools into the dead pools, which also mechanically damages the retaining trees and may change the demography of tree communities (Collins et al., 2019). Consequently, the trees exhibit survival strategies against fire and drought which widely vary among species (Chaturvedi et al., 2021, 2024). For drought strategies, trees can be categorized according to their capacity to avoid or tolerate drought, or as per the Grime's model for competitive (C), stress tolerance (S) and ruderal (R) strategies, while other disturbances may also be linked with the drought avoiding and drought tolerant strategies for disturbed ecosystems (see Chaturvedi et al., 2024).

Earlier studies, mainly focused on the influence of tree species and/or functional diversity on carbon storage, in intensively managed forests with very few species (Erskine et al., 2006; Piotto, 2008), or in stands with high species richness (Ruiz-Jaen and Potvin, 2011; Wardle, 2016; Poorter et al., 2016; Sullivan et al., 2017). However, evaluation of the impacts of structural and functional diversity, tree size and disturbances on carbon storage in tropical dry forest fragments have not been documented. In this study, we examined the relationships of carbon storage capacity in tropical dry forest fragments with species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators. We are particularly interested in understanding factors explaining variations in carbon storage capacity of tree communities or functional strategies in fragmented tropical dry forests, to explore the role of these habitats in decreasing atmospheric CO_2 concentration. We classified tree species across tropical dry forest fragments into drought avoiding and drought tolerant strategies to answer the questions: (1) What are the differences between drought strategies for variations in stem density, relative growth rate (RGR), carbon storage and sequestration, species diversity, functional diversity, tree size and disturbance indicators along edge distance gradient in a tropical dry forest? (2) What are the differences between drought strategies for responses of carbon storage and sequestration to variations in species diversity, functional diversity, tree size and disturbance indicators? We hypothesize that, for both drought strategies, stem density, RGR, carbon storage and sequestration, species diversity indicators, functional diversity indicators and tree size indicators will decline on decreasing edge distance across the forest fragments, whereas, the disturbance indicators will increase on decreasing edge distance. Besides, due to the dominance of drought avoiding trees along smaller fragments, and the dominance of drought tolerant trees along larger fragments (Chaturvedi et al., 2024), niche complementarity and selection effects at larger fragments will support more to drought tolerants, while along smaller fragments, they will favor more to drought avoidants. Therefore, the slope of responses for above variables along decreasing edge distance will be more steep for drought tolerant strategy compared to drought avoiding strategy. Further we hypothesize that the effects of species diversity, functional diversity, tree size and disturbance indicators on carbon storage and sequestration will be variable for the two drought strategies. Species diversity and functional diversity indicators will be common influencers for the two drought strategies, however, due to the large tree size of drought tolerants, the tree size indicators will strongly influence their carbon storage and sequestration, and since drought avoidants are more exposed to disturbances, the disturbance indicators will highly determine their carbon storage and sequestration.

2. Materials and methods

2.1. Study sites

Our investigation was conducted in 45 forest fragments or patches or study sites in Vindhyan highlands, located in the Sonebhadra district of Uttar Pradesh, India (Fig. 1, Table S1). The selected fragments cover around a 50 km radius, and the distance between the two nearest fragments is around 2 km. The largest fragment occupies 92.4 ha land area, while that of the smallest fragment covers 1.5 ha area. The patch perimeter ranged from 0.4 to 4.0 km, and the edge distance varied from 0.07 to 0.4 km. The altitude for these fragments ranges from 231 to 350 m asl. The selected sites contain naturally established old-growth forests. The forest area was exposed to anthropogenic disturbances mainly by the local villagers in the form of extraction of forest resources, illegal harvesting, and occasional burning, however for the past three decades government policies have been engaged in forest conservation and controlling disturbances, particularly in large-sized fragments. The idea behind site selection was to get greater variations in habitat properties, such as edge distance and disturbances, to cover the maximum possible tree species diversity and functional diversity of the region. The area experiences a tropical monsoon climate. We collected monthly climatic and weather data for 12 years, starting from January 2008 to December 2019 from the website, www.worldweatheronline.com. The data include minimum, average and maximum temperatures, rainfall, and relative humidity. The average temperature during this period ranged from 10.5 °C, in January to 42.5 °C, in May. The average annual rainfall was 662.3 mm, with a minimum rainfall of 2.69 mm in November to a maximum of 208.7 mm in July. The study region experienced >80 % of the total annual rainfall during only three months (July–September), and the remaining 20 % in the other nine months. Similar to rainfall, relative humidity in the study region was also higher (>70 %), during the July–September period, where the minimum and maximum relative humidity during this period was 22.0 % in April, and 76.4 % in August. A more detailed description of the study region is given in Chaturvedi (2010).

2.2. Sampling design

We established three rectangular plots (50 m × 20 m) randomly, in the central region of each forest fragment for periodical measurements. The distance from the forest edge for each plot was recorded in four directions, and the average value was considered as the edge distance. For fragments whose edge distance was ≥200 m, the three plots inside the fragment were separate from each other by a distance of at least 50 m, while for the fragments whose edge distance was <200 m, we tried to keep a distance of at least 25 m between the plots. We counted the stems and measured their diameter at breast height (DBH) for all tree species inside each plot using a measuring tape, and identified all individuals ≥10 cm DBH for further measurements. In each plot, growth measurements were recorded for the five years, starting from September 2010 to August 2015. Increases in girth for all individuals ≥10 cm DBH, inside

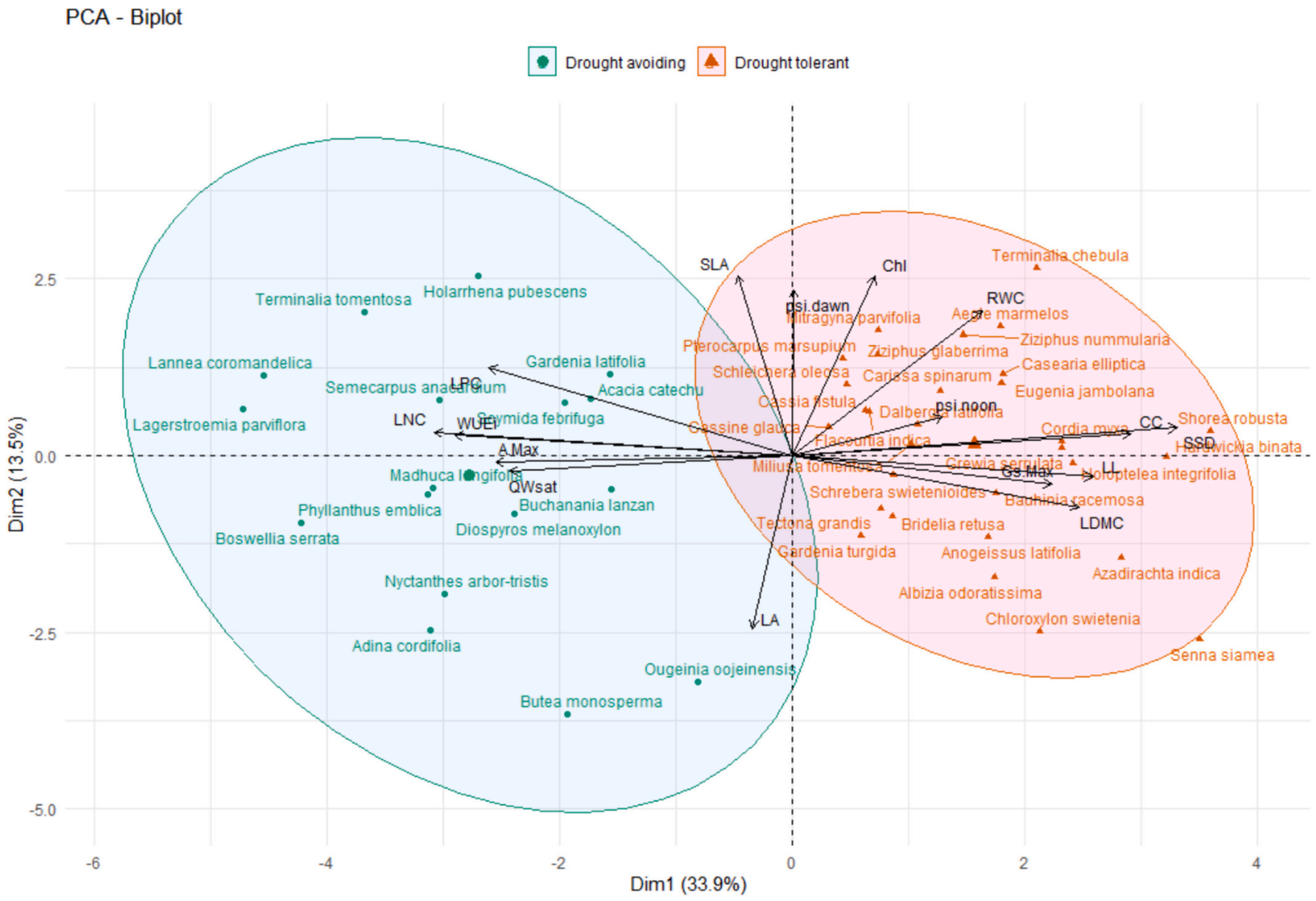

Fig. 1. PCA biplot showing grouping of tree species into two functional types, *viz.*, drought avoiding (blue colored eclipse), and drought tolerant (pink colored eclipse) based on HCPC analysis on 16 functional traits. SSD, stem specific density; QWsat, stem water storage capacity; CC, canopy cover intensity; SLA, specific leaf area; RWC, relative water content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; Gs_{max}, maximum saturated stomatal conductance; A_{max}, maximum saturated photosynthesis; WUEi, intrinsic water use efficiency; psi.dawn, leaf water potential at dawn; psi.noon, leaf water potential at noon; Chl, chlorophyll content; LL, leaf life-span; LA, leaf area.

each plot were measured annually with the help of metal dendrometer bands fitted at 1.37 m height (Chaturvedi et al., 2011a, 2017). We also measured height increments for each individual ≥10 cm DBH, inside each plot with the help of a 15 m graduated measuring pole for individuals up to 15 m height (one person holding the pole, a second acting as "spotter" to assess the mark on the pole which reached the level of the top of the crown), and for taller individuals trigonometric method was applied. For the measurement of functional traits, including whole plant traits, wood traits, and leaf traits, we marked at least five individuals, ≥ 10 cm DBH, for each tree species inside the three rectangular plots, at each fragment. For a few species, whose individuals were less than five inside the three plots, we marked the remaining individuals outside the plot boundary. Sampling for most of these measurements were made in September 2013, however, a few rare species which were not sampled in the year 2013, were covered in 2014.

Soil moisture content (SMC) at a depth of 10 cm was measured every month for two years, starting from September 2012 to August 2014, by a theta probe instrument (type ML 1, Delta-T Devices, Cambridge, UK), as percentage by volume under the canopy, at four sides of the main trunk, at a distance of one meter from each marked individual tree species.

2.2.1. Functional trait data

We selected 16 functional traits considered important for tropical dry forest trees (Chaturvedi et al., 2011b), including one whole plant trait, *viz.*, tree foliage cover intensity/canopy cover intensity (CC), two wood traits, *viz.*, wood specific gravity (WSG) and saturated stem water content (QWsat), six morphological leaf traits, *viz.*, leaf size or leaf area (LA), specific leaf area (SLA), relative water content (RWC), leaf dry matter content (LDMC), leaf water potential at dawn (Ψ_{dawn}), and leaf water potential at noon (Ψ_{noon}), six physiological leaf traits, *viz.*, leaf nitrogen content (LNC), leaf phosphorus content (LPC), maximum saturated stomatal conductance (Gs_{max}), maximum saturated photosynthetic rate (A_{max}), intrinsic water use efficiency (WUEi), and chlorophyll content (Chl), and one phenological leaf trait, *viz.*, leaf life-span (LL).

The tree CC was recorded for all marked individuals of each species, monthly for two years, starting from September 2012 to August 2014. For this observation, we tagged 20 to 50 terminal twigs on the four sides of each marked individual. We recorded the date of leaf budding or leaf flushing, and leaf shedding (including the time of yellowing, browning, and partial or total leaf shedding) for each marked individual, at each plot, and at each forest fragment. During these observations, we also recorded the leaf life-span (LL), and the proportion of leaves in the canopy under a particular phenophase or phenological event. For estimation of the intensity of phenological event (*viz.*, CC), we followed Fournier (1974), and quantified the phenophases for each individual from zero to four (Fournier intensity index). Among these five indices, zero represents the absence of phenophase, one indicates the intensity of phenophase between 1 and 25 %, two between 26 and 50 %, three between 51 and 75 %, and four between 76 and 100 %. We calculated the intensity of phenophases for foliage cover, for each species at each forest fragment by the formula:

$$Phenophase\ intensity = \left(\frac{\sum Fournier\ intensity}{4N}\right) \times 100$$

where, ∑Fournier intensity is the sum of Fournier intensity for all individuals of a species, and N is the number of individuals of the species.

WSG was measured for the five healthy individuals ≥10 cm DBH, for each tree species inside the three plots, each at the 45 forest fragments, following protocol given in Chaturvedi et al. (2010). The individuals selected for the measurement of WSG were different from those which were marked for the measurement of tree growth and samples were collected from the trees outside the plots. The wood samples were collected from trees outside the plots to protect the trees inside the plots from injuries, which could lead to their mortality. We took wood samples from the main trunk at the height of 1.4 m, up to the radial depth, with the help of a stem borer. The wood samples were sealed in plastic bags separately and brought to the laboratory. The volumes of fresh wood samples, after removing bark were estimated by the water displacement method, and the wood samples were dried in an oven at 80 °C till constant weight. The values of WSG are expressed as g cm^{-3}. For determining the amount of saturated stem water (QWsat, %), we collected stem samples from the same five individuals which were selected for WSG measurement for each species. The volume and dry weight of stem samples were estimated after removing the outer bark, by following the same method which was applied during the measurement of WSG, however, before measuring volume, stem samples were soaked in water overnight. The formula for obtaining QWsat was, according to Borchert (1994):

$$QWsat = \left(\frac{Stem\ weight_{(water\ saturated)} - Stem\ weight_{(dry)}}{Stem\ weight_{(dry)}}\right) \times 100$$

Leaf traits were measured on the same trees which were marked for the study of phenology. While, we measured LA, SLA, LDMC, LNC, LPC, A_{max}, Gs_{max}, WUEi, Ψ_{dawn}, and Ψ_{noon} according to Pérez-Harguindeguy et al. (2013), RWC was measured according to Tanentzap et al. (2015). For the measurement of LA, SLA, LDMC, RWC and Chl, 10 to 20 fully expanded, mature, and sun-facing leaves were collected from each marked individual of each tree species. Fresh leaf weights for all leaves were recorded just after collection, at the field site, by portable electronic weighing balance. After weighing, leaves were wrapped separately in the moist paper for rehydration, sealed in separate plastic bags, and brought to the laboratory. All measurements were made within 24 h of bringing the samples to the laboratory. Chlorophyll was analyzed by crushing 0.1 g of the leaf in 10 ml of 80 % acetone (Aron, 1949). The absorbance (D) of the extract was then measured at 645 and 663 nm using 80 % acetone as blank. The concentrations of Chl_a and Chl_b were calculated from the following expressions (Aron, 1949):

$$Chl_a\left(mg\,g^{-1}\right) = \left([12.7 \times D_{663}] - [2.60 \times D_{645}]\right) \times \frac{volume\ of\ acetone\,(10\,ml)}{weight\ of\ leaf\ tissue\,(0.1\,g)}$$

$$Chl_b\left(mg\,g^{-1}\right) = \left([22.9 \times D_{645}] - [4.68 \times D_{663}]\right) \times \frac{volume\ of\ acetone\,(10\,ml)}{weight\ of\ leaf\ tissue\,(0.1\,g)}$$

$$Chl\ \left(mg\,g^{-1}\right) = Chl_a\ \left(mg\,g^{-1}\right) + Chl_b\ \left(mg\,g^{-1}\right)$$

After Chl measurement, the remaining fresh leaves were rehydrated, weighed on electronic balance, and scanned on a table scanner, and their dimensions were determined with the help of Image-J programme (Abramoff et al., 2004) for the measurement of LA. After LA measurements, all leaf samples were dried in separate paper bags in the oven at 70 °C till constant weight. After recording the leaf fresh weight, leaf rehydrated fresh weight and leaf dry weight, we calculated SLA, LDMC and RWC by using the following equations (Chaturvedi et al., 2024):

$$SLA = \frac{Leaf\ area}{Leaf\ dry\ weight}$$

$$LDMC = \left(\frac{Leaf\ dry\ weight}{Leaf\ rehydrated\ fresh\ weight}\right) \times 100$$

$$RWC = \left(\frac{Leaf\ fresh\ weight - Leaf\ dry\ weight}{Leaf\ rehydrated\ fresh\ weight - Leaf\ dry\ weight}\right) \times 100$$

LNC and LPC were measured by micro-Kjeldahl (acidic) digestion, followed by colorimetric (flow-injection) analysis.

For measurement of A_{max} (μmol m^{-2} s^{-1}), Gs_{max} (mol m^{-2} s^{-1}), Ψ_{dawn} (MPa), and Ψ_{noon} (MPa), we sampled twigs from each marked tree species, at mid-canopy height, having full sun exposure for at least part of the day, with healthy and fully expanded leaves. Measurements for

A_{max} and Gs_{max} were made immediately after collecting the samples using an LC Pro Console Photosynthesis meter (model EN11 ODB, ADC Bioscientific Ltd., UK) between 09:30 h and 12:30 h (solar noon). The WUEi was determined as the ratio of A_{max} and Gs_{max}, and expressed as μmol mol^{-1}. For the measurement of leaf water potential (Ψ), we used a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Ore.). Measurements of Ψ_{dawn} for each species at each fragment started at 04.30 h and finished before sunrise, while Ψ_{noon} was generally measured between 12.30 h to 13.30 h.

2.2.2. Tree size data

Under tree size, we selected tree height to DBH ratio (HTDBH), crown depth to DBH ratio (CDDBH), and crown cover to DBH ratio (CCDBH). Crown depth for each individual tree was measured at four sides of the tree as length along the main axis from the top of the tree to the base of the crown. Similarly, the crown cover for each tree was measured as the area covered by the vertical projection of the perimeter of the crown.

2.2.3. Disturbance data

We recorded tree mortality and recruitment in each plot annually and averaged the data for the three plots for each site. Under mortality, we recorded the number of trees that died due to harvesting by humans, fire and drought, each year, while recruitment was considered as the number of trees attaining 10 cm DBH within the year. To get getting more accuracy, these data were recorded every month for five years, where harvested tree was identified by tree stumps, fire-killed trees were recorded by observing fire scars, while drought killed trees were categorized when the tree died with no external harvesting sign or fire scar. The annual mortality index (MI, %) for harvest, fire and drought indices were calculated as:

$$MI = \left(\frac{T_D}{T_F + T_N}\right) \times 100$$

where, T_D is the number of newly died trees within a year, T_F is the number of trees during the first measurement of the year, and T_N is the number of newly recruited trees in a year.

2.3. Statistical analysis

The statistical analyses were done in R version 4.4.1 (R Foundation for Statistical Computing, Vienna, AT). By using species count data in each plot, we calculated species richness, Shannon diversity, and species evenness, and for this we used "vegan" R-package (Oksanen et al., 2019). By using the average value of species trait data and the species count data for each plot, we calculated functional richness, functional dispersion and functional evenness, and for this, we used "fundiversity v.0.2.1" R-package (Gruson and Grenié, 2022).

Stem biomass was obtained by using the equation given by King et al. (2006) as:

$$Stem\ biomass = 0.5 \times (\pi/4) \times WSG \times (DBH)^2 \times H$$

where, 0.5 is the form factor, defined as the ratio of stem volume to the volume of a cylinder with the height (H, m) and diameter at breast height (DBH, cm) of the tree. We validated the estimates from this equation against those obtained by using species-specific as well as multi-specific allometric equations relating destructively measured tree biomass and the DBH, for tropical dry forest tree species, as well as actually measured biomass of harvested trees (Chaturvedi et al., 2010). We also compared the estimates of stem biomass of two dominant species obtained by the CBH-based equation and observed that the estimate from the WSG-based equation was closer to the directly measured biomass ($R^2 = 0.97$, $P < 0.001$), as compared to the CBH-based equation ($R^2 = 0.83$, $P < 0.001$). We calculated biomass per unit stem basal area, as well as per unit stand area. The biomass accumulation capacity for each tree species was calculated as the rate of change in biomass per unit basal area (*i.e.*, relative growth rate, RGR). The aboveground carbon content for each tree was calculated by multiplying the aboveground biomass by the default IPCC carbon fraction value of 0.47 (IPCC, 2006). For calculating carbon stock at each plot, we divided the carbon content (expressed in tons) of all trees inside the plot by the area of plot (expressed in hectares, ha).

For estimating carbon sequestration, we used mass ratio of the photosynthetic reaction equation:

$$\underset{(264)}{6CO_2} + \underset{(108)}{6H_2O} \rightarrow \underset{(180)}{C_6H_{12}O_6} + \underset{(192)}{6O_2}$$

Based on the above equation, 180 g of biomass ($C_6H_{12}O_6$) is produced by using 264 g of CO_2. Therefore, for determining carbon dioxide sequestration, we can use the formula:

$$CO_2\ sequestration = \frac{264}{180} \times Biomass = 1.4667 \times Biomass$$

We used likelihood ratio tests (LRTs) for testing interactions and main effects. We also used Wald tests for evaluating the parameter estimates. The data normality was checked by Shapiro–Wilk test and the data exhibiting non-normal distribution (*viz.*, functional richness and functional dispersion) was log-transformed before statistical analysis.

We observed species groupings as functional types, by using the 16 traits data for each species through PCA, hierarchical clustering, and partitioning clustering particularly through the k-means method by HCPC (hierarchical clustering on principal components). According to Kassambara (2017), HCPC is a robust tool for multivariate data analysis, where it allows three techniques (*viz.*, hierarchical clustering, k-means partitioning, and PCA) in combination for extracting information from the data and summarizing results in the best possible format. The HCPC basically uses Euclidean distances to define the distance between individuals, while the hierarchical tree is constructed by Ward's agglomeration method (Husson et al., 2010; Husson et al., 2011). According to Husson et al. (2010), the categories of cluster variables are represented by the categories of the categorical variables. The HCPC generates a list of species groups in ascending order of *P*-value, which shows the order of impact of the categorical variables. HCPC also develops V-test values which are reported to be associated with the *P*-values (Husson et al., 2011). Moreover, the order of over represented positive V-test values exhibits categories of categorical variables according to their influence on the cluster variables (Husson et al., 2011). Our analysis was based on the average value of functional traits for all individuals of each species across the 45 forest fragments. We showed the clusters of tree species in the form of a PCA biplot. The clustering of tree species was based on the shared set of functional traits. Based on the identity of functional traits in each cluster, we classified the total tree species into two functional types [*viz.*, drought avoiding and drought tolerant]. For this analysis, we used the R package "FactoMineR" and "factoextra" (Kassambara and Mundt, 2016). We used functions prcomp() and PCA(), "FactoMineR" package for PCA analysis.

We observed the trends of vegetation attributes (*viz.*, stem density, RGR, carbon density and carbon sequestration), species diversity indicators (*viz.*, species richness, Shannon diversity and species evenness), functional diversity indicators (*viz.*, functional richness, functional dispersion and functional evenness), tree size indicators (*viz.*, HTDBH, CDDBH and CCDBH), and disturbance indicators (*viz.*, harvest, fire and drought) in the form of response variables, with a generalized linear model (GLM, Nelder and Wedderburn, 1972), where we defined edge distance as the explanatory variable. We used an autoregressive moving average model for accounting temporal autocorrelation. This model structure was required to appropriately account for the temporal autocorrelation caused by repeated measurements of biomass and biomass accumulation capacity for the same individuals of each tree species.

We performed a redundancy analysis (RDA) to assess the response of

RGR, carbon stock and carbon sequestration to species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators, and to check whether such response was specific to edge distance. To account for relatedness to edge distance, we included edge distance across the forest fragments as a covariate (*i.e.*, in RDA, the RGR, carbon stock and carbon sequestration are standardized response variables, the species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators are explanatory variables, while the edge distance is a covariate). We conducted a Monte Carlo permutation test based on 999 random permutations for testing the significance of the eigenvalues of the canonical axes and the marginal and conditional significance of explanatory variables. For RDA, we used the function rda() and anova.cca(), respectively, both from the package "vegan" (Oksanen et al., 2019). We also checked multicollinearity, and dropped the traits with VIF > 10 (Borcard et al., 2018) from the final RDA. For plotting RDA projections, we used "ggvegan" package (Simpson, 2019). We performed RDA separately for the tropical dry forest, and the two functional types.

To assess the distinct effects of species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators on site-level carbon sequestration, we fitted structural equation models using the package "lavaan" (Rosseel, 2012). To obtain the best-fitting model, we used stepwise regression and removed the non-significant and weak links. Under structural equation modeling, our aim was to (i) identify non-significant *P*-values of the Chi-squared (χ^2) test, which reflected the probability of failing to reject the model for the given data, (ii) maximize the Comparative Fit Index (CFI) and Tucker-Lewis Index (TLI), and (iii) reduce sample size-adjusted Bayesian Information Criterion and the Root Mean Square Error of Approximation (RMSEA) (Bollen et al., 2014). We performed the structural equation modeling separately for the tropical dry forest, and the two functional strategies.

3. Results

3.1. Drought strategies

Table S1 summarizes habitat features across the study sites, including location, altitude, patch size, patch perimeter, edge distance, species richness, stem density, and dominant species. Across the study sites, patch size varied from 1.47 to 92.4 ha, while the edge distance ranged from 66 to 408 m. Based on HCPC analysis, tree species were grouped into two drought strategies, where 17 tree species were categorized as drought avoiders and 30 tree species were classified as drought tolerators (Figure 1, Table S2). Although, tree species were greater for drought tolerators, the number of individuals were higher for drought avoiders (63% trees), with increasing dominance towards lower sized fragments.

3.2. Trends along edge distance gradient

3.2.1. Vegetation attributes

Across the forest fragments, the average stem density was 404 trees ha^{-1}, ranging from 150 to 800 trees ha^{-1}. The average RGR was 0.05 kg cm^{-2} yr^{-1}, ranging from 0.02 to 0.11 kg cm^{-2} yr^{-1}. The average carbon density was 58.9 t ha^{-1}, ranging from 27.0 to 112.9 t ha^{-1}. Average carbon sequestration was 1.96 t ha^{-1} yr^{-1}, ranging from 0.78 to 3.68 t ha^{-1} yr^{-1}. Stem density, RGR, carbon density and carbon sequestration exhibited significant decline towards decreasing edge distance, for total trees as well as for the two different communities of drought strategies (Fig. 2, Table S3). We observed significant variations of all vegetation attributes among drought strategies for their relationships with edge distance, except for the association of RGR of drought tolerant strategy with edge distance, although the interaction of edge distance with drought tolerant strategy showed significant variations for RGR (Table S3).

Across the forest fragments, we observed greater average stem

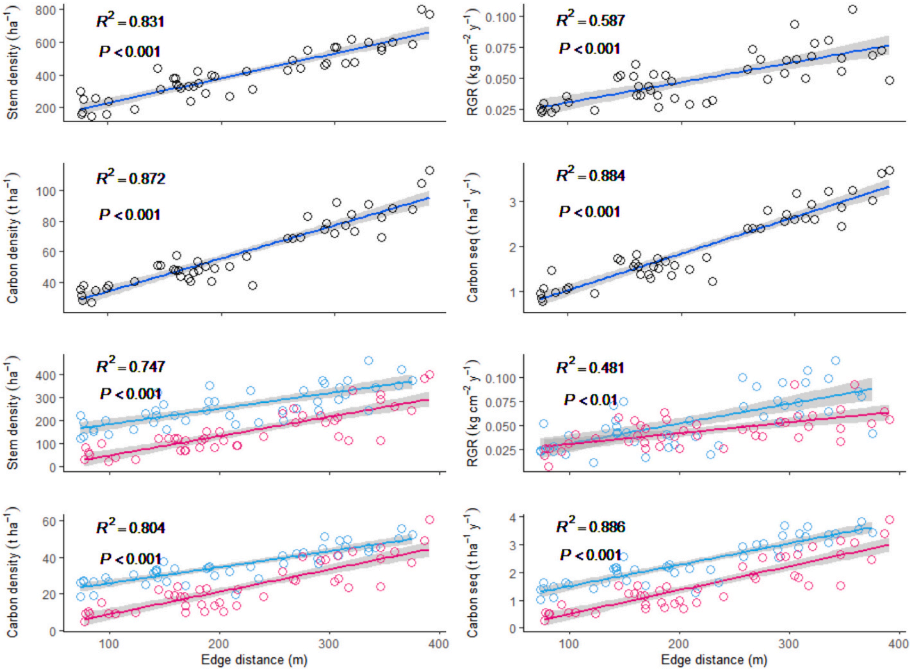

Fig. 2. Generalized linear model trend lines for the vegetation attributes of the total trees (black points and regression lines), drought avoiding (blue points and regression lines) and drought tolerant (pink points and regression lines) functional types along the gradient of edge distance across 45 forest fragments. Upper two panels represent total trees, and lower two panels represent drought strategies. The model accuracy is determined by adjusted R^2. The statistical results are summarized in table S3. RGR, relative growth rate.

density (257 trees ha^{-1}), RGR (0.05 kg cm^{-2} yr^{-1}), carbon density (35.5 t ha^{-1}) and carbon sequestration (2.37 t ha^{-1} yr^{-1}) for the drought avoiding strategy compared to the drought tolerant strategy (stem density, 150 trees ha^{-1}; RGR, 0.04 kg cm^{-2} yr^{-1}; carbon density, 23.9 t ha^{-1} and carbon sequestration, 1.56 t ha^{-1} yr^{-1}) (Fig. 2). However, along declining edge distance, the decline in vegetation attributes for the drought tolerant strategy was steeper compared to the drought avoiding strategy, except for RGR, where the decline was steeper for drought avoiding strategy compared to the drought tolerant strategy (Fig. 2).

3.2.2. Species diversity indicators

Across the forest fragments, the average species richness was 20 species ha^{-1}, ranging from 10 to 34 species ha^{-1}. The average Shannon diversity was 2.5, ranging from 2.0 to 3.0, while the average species evenness was 0.85, ranging from 0.80 to 0.91. Among the species diversity indicators, a significant decline in species richness and Shannon diversity along with decreasing edge distance gradient was observed for the total trees as well as the drought strategies, across the forest fragments (Fig. 3, Table S4). However, species evenness showed a non-significant trend for total trees, while a significant trend for the drought strategies. Although, the drought tolerant strategy showed a non-significant trend for species evenness, the interaction of edge distance with drought tolerant strategy was significant (Table S4).

Across the forest fragments, the average species richness (10 species ha^{-1}), Shannon diversity (2.0) and species evenness (0.87) for drought avoiding strategy was greater compared to the drought tolerant strategy (species richness, 9 species ha^{-1}; Shannon diversity, 1.4; species evenness, 0.74). We found a steep decline in species richness and Shannon diversity for drought tolerant strategy along the declining edge distance gradient, compared to the drought avoiding strategy (Fig. 3). Besides, the decline in species evenness along the decreasing edge distance was only significant for drought avoiding strategy.

3.2.3. Functional diversity indicators

Across the forest fragments, the average functional richness was 3.1, ranging from 1.9 to 3.6. The average functional dispersion was 4.78, ranging from 4.26 to 5.76, while the average functional evenness was 0.49, ranging from 0.28 to 0.70. For the total tree species as well as for the two drought strategies, functional richness, functional dispersion and functional evenness exhibited significant decline along the decreasing edge distance gradient (Fig. 4, Table S5). We observed higher average functional richness (3.6) for drought avoiding strategy compared to drought tolerant strategy (3.3), however the average functional dispersion (4.51) and functional evenness (0.42) for drought avoiding strategy were lower compared to the drought tolerant strategy (functional dispersion, 4.68; functional evenness, 0.61). Besides, the two drought strategies exhibited significant variations in their responses for their functional diversity indicators along the edge distance gradient,

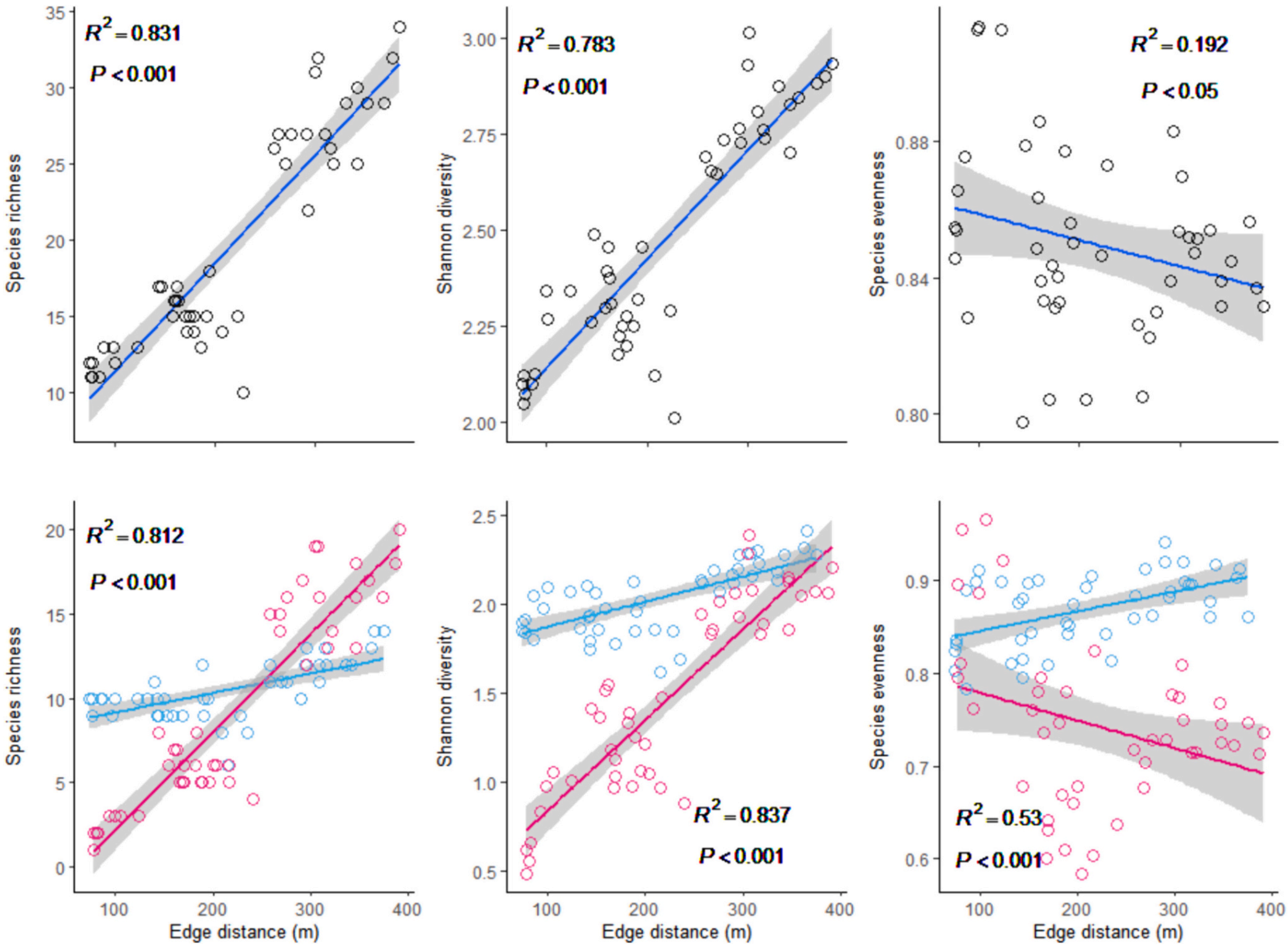

Fig. 3. Generalized linear model trend lines for the species diversity indicators of the total trees (black points and regression lines), drought avoiding (blue points and regression lines) and drought tolerant (pink points and regression lines) functional types along the gradient of edge distance across 45 forest fragments. Upper panel represents total trees, and lower panel represents drought strategies. The model accuracy is determined by adjusted R^2. The statistical results are summarized in table S4.

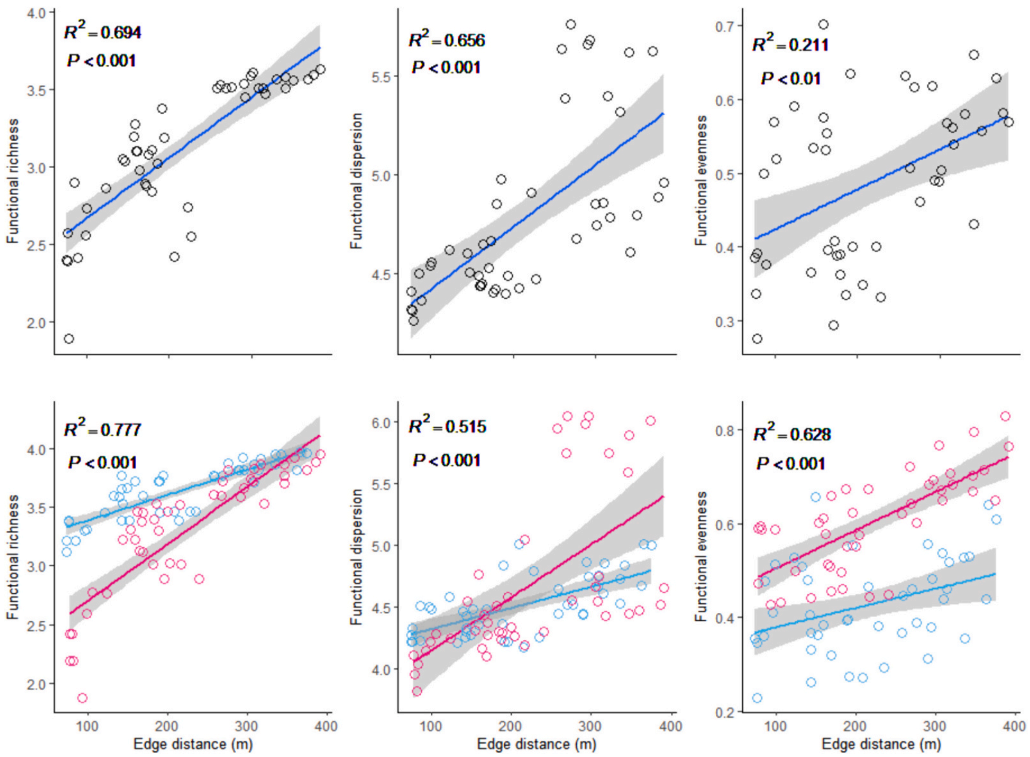

Fig. 4. Generalized linear model trend lines for the functional diversity indicators of the total trees (black points and regression lines), drought avoiding (blue points and regression lines) and drought tolerant (pink points and regression lines) functional types along the gradient of edge distance across 45 forest fragments. Upper panel represents total trees, and lower panel represents drought strategies. The model accuracy is determined by adjusted R^2. The statistical results are summarized in table S5.

where we observed a steep decline in functional richness, functional dispersion and functional evenness for the drought tolerant strategy, as compared to the drought avoiding strategy.

3.2.4. *Tree size indicators*

Across the forest fragments, the average HTDBH was 0.49, ranging from 0.37 to 0.58. The average CDDBH was 0.24, ranging from 0.15 to

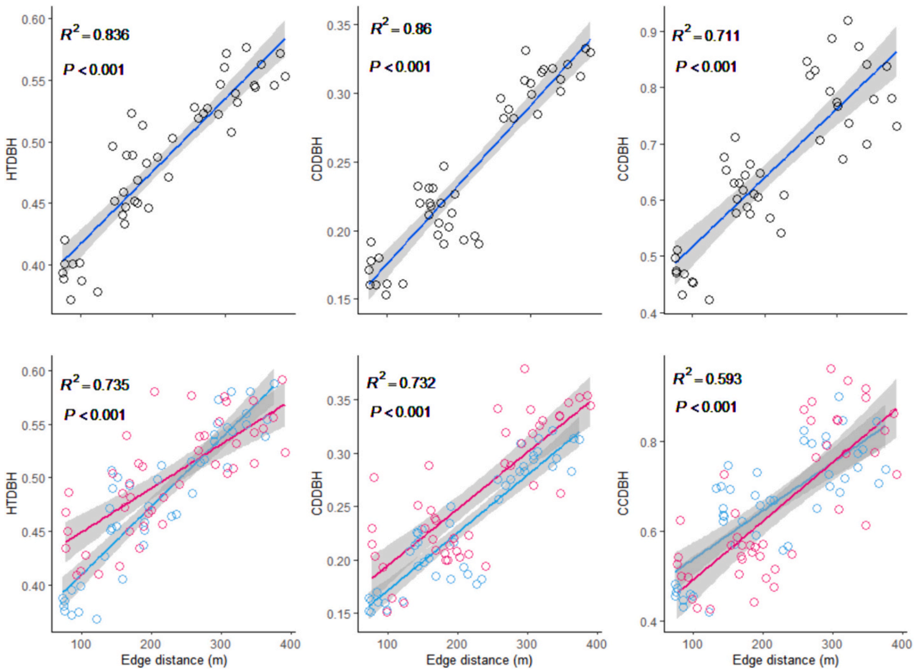

Fig. 5. Generalized linear model trend lines for the tree size indicators of the total trees (black points and regression lines), drought avoiding (blue points and regression lines) and drought tolerant (pink points and regression lines) functional types along the gradient of edge distance across 45 forest fragments. Upper panel represents total trees, and lower panel represents drought strategies. The model accuracy is determined by adjusted R^2. The statistical results are summarized in table S6. HTDBH, tree height to diameter at breast height (DBH) ratio; CDDBH, crown depth to DBH ratio; CCDBH, crown cover to DBH ratio.

0.33, while the average CCDBH was 0.66, ranging from 0.42 to 0.92. The tree size indicators, including HTDBH, CDDBH and CCDBH exhibited a significant decline towards decreasing edge distance gradient across the forest fragments for the total trees as well as for the two drought strategies (Fig. 5, Table S6). Across the forest fragments, average HTDBH (0.48) and CDDBH (0.23) were lower for drought avoiding strategy compared to drought tolerant strategy (HTDBH, 0.50; CDDBH, 0.26), however average CCDBH for drought avoiding strategy (0.66) was higher compared to the drought tolerant strategy (0.65). For the two drought strategies, responses along the edge distance gradient differed only for HTDBH and CCDBH, whereas responses of CDDBH for the two strategies did not show considerable differences. Towards decreasing edge distance gradient, the decline in HTDBH was greater for the drought avoiding strategy, compared to the drought tolerant strategy, whereas the decline in CCDBH was greater for the drought tolerant strategy, compared to the drought avoiding strategy (Fig. 5).

3.2.5. *Disturbance indicators*

Across the forest fragments, the average harvest index was 3.9, ranging from 1.2 to 6.3. The average fire index was 0.58, ranging from 0.0 to 1.6, while the average drought index was 0.03, ranging from 0.0 to 0.08. Towards decreasing edge distance gradient, we observed a significant increase in disturbance indicators, including harvest index, fire index and drought index, for total trees, as well as for the two drought strategies (Fig. 6, Table S7). Across forest fragments, the average harvest index (2.3) for drought avoiding strategy was lower compared to the drought tolerant strategy (2.5), the fire index (0.36) for drought avoiding strategy was higher compared to the drought tolerant strategy (0.33), while drought index for drought avoiding strategy (0.02) as well as drought tolerant strategy was similar (0.02). The two drought strategies showed considerable variations in their responses to disturbance indicators to edge distance. For harvest and fire indices, the drought avoiding strategy exhibited greater increases towards declining edge distance gradient, compared to the drought tolerant strategy, whereas for drought index, the drought tolerant strategy showed a higher increase towards declining edge distance, compared to the drought avoiding strategy (Fig. 6).

3.3. *Responses of RGR, carbon stock and carbon sequestration to species diversity, functional diversity, tree size and disturbance indicators*

Fig. 7 shows projections of RGR, carbon stock and carbon sequestration and habitat features including species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators for total tree species and the two functional strategies, across 45 forest fragments in RDA space, with edge distance as a co-variate. Below we describe the results of this analysis for the total tree species and the two functional strategies.

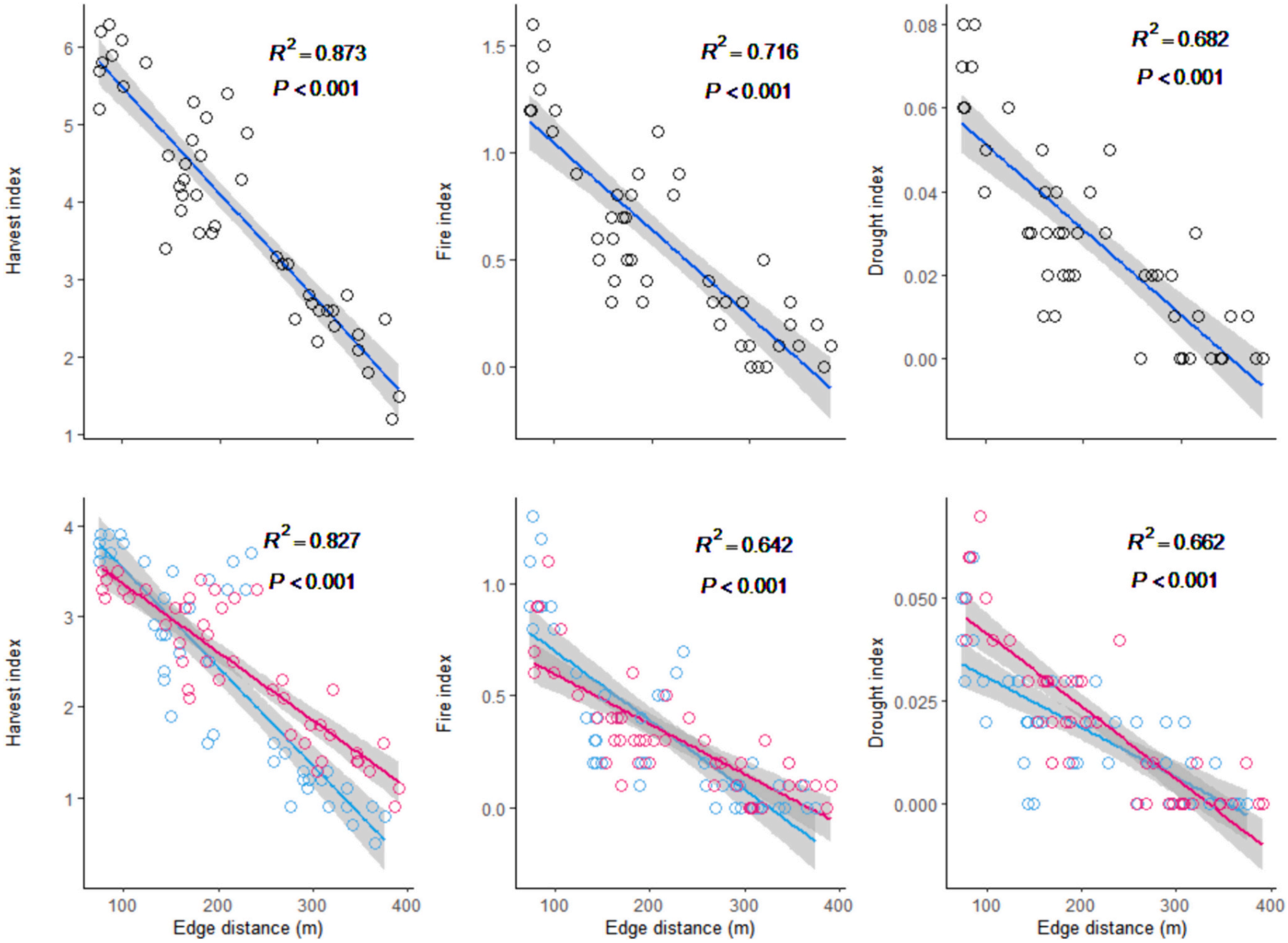

Fig. 6. Generalized linear model trend lines for the disturbance indicators of the total trees (black points and regression lines), drought avoiding (blue points and regression lines) and drought tolerant (pink points and regression lines) functional types along the gradient of edge distance across 45 forest fragments. Upper panel represents total trees, and lower panel represents drought strategies. The model accuracy is determined by adjusted R^2. The statistical results are summarized in table S7.

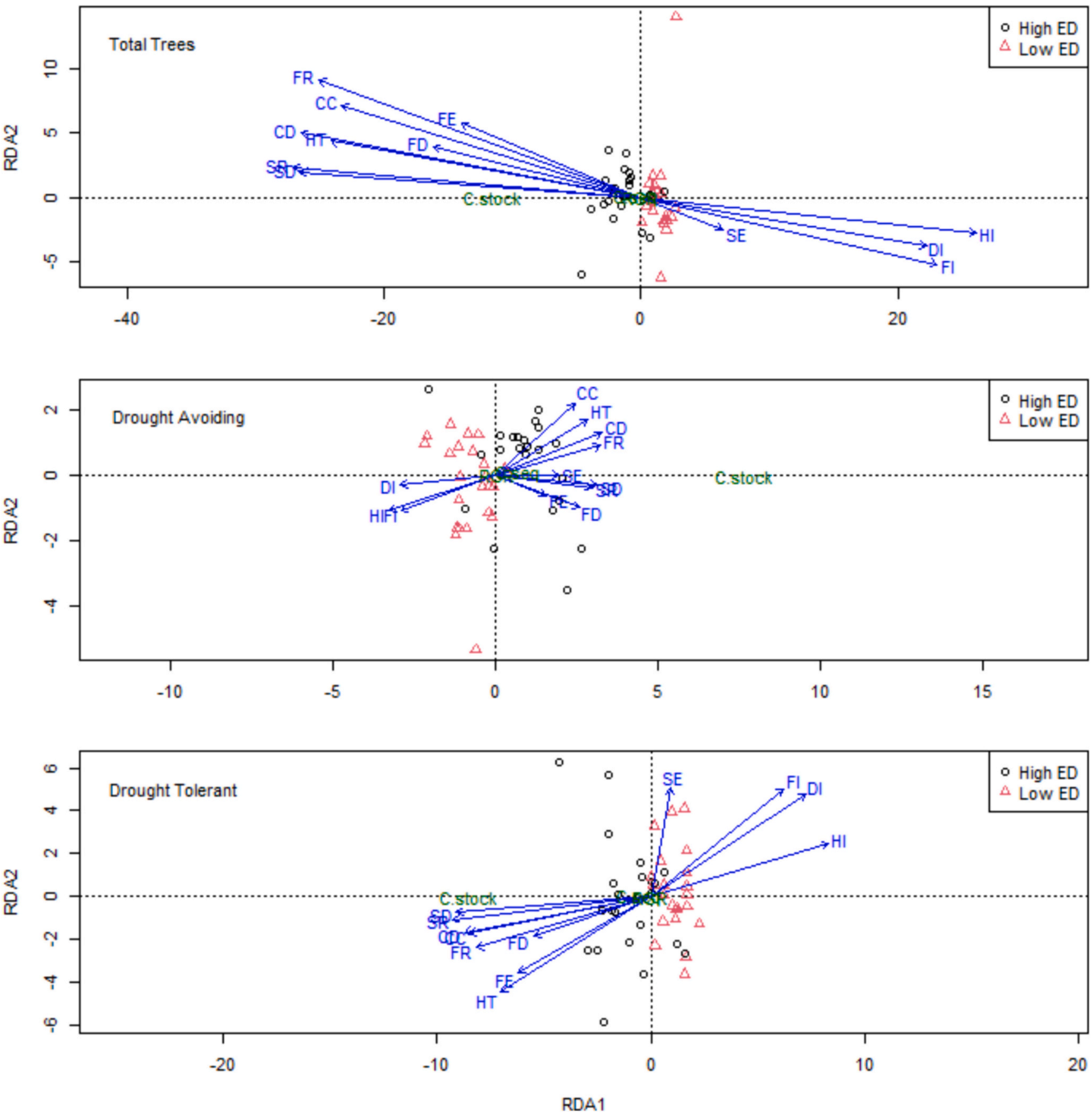

Fig. 7. Projection of the relative growth rate (RGR), carbon stock (C stock) and carbon sequestration (C seq), and species diversity, functional diversity, tree size and disturbance indicators across 45 forest fragments in RDA space, with edge distance (ED) as covariate, for total trees (TDF), Drought Avoiding and Drought Tolerant strategies. SR, species richness; SD, Shannon diversity; SE, species evenness; FR, functional richness; FD, functional dispersion; FE, functional evenness; HT, tree height to diameter at breast height (DBH) ratio; CD, crown depth to DBH ratio; CC, crown cover to DBH ratio; HI, harvest index; FI, fire index; DI, drought index.

3.3.1. *Total tree species*

For the total tree species combined (*i.e.*, for all TDF species), the eigenvalue for the first and second constrained axes was 436.2 and 0.0, respectively, while the first and second constrained axes explained 93.9 % and 0.0 % of the total variation, respectively (pseudo-F = 41.0, $P < 0.001$). The results of Pearson's correlations between habitat features and linear combinations of constraining variables along RDA axes showed that the first axis was strongly correlated with species richness ($R = -0.978$, $P < 0.001$), CDDBH ($R = -0.956$, $P < 0.001$) and Shannon diversity ($R = -0.958$, $P < 0.001$), while the second axis showed significant relationship with functional richness ($R = 0.328$, $P < 0.05$). Moreover, the Pearson's correlation showed the strongest relationship of RGR with CDDBH ($R = 0.831$, $P < 0.001$), carbon stock with species richness ($R = 0.948$, $P < 0.001$), and carbon sequestration also with species richness ($R = 0.955$, $P < 0.001$).

3.3.2. *Drought avoiding strategy*

For drought avoiding strategy, the eigenvalue for the first and second constrained axes were 82.7 and 0.01, respectively, while the first and second constrained axes explained 94.0 % and 0.0 % of the total variation, respectively (pseudo-F = 42.1, $P \leq 0.001$). The results of Pearson's correlations between habitat features and linear combinations of constraining variables along RDA axes showed that the first axis was strongly correlated with harvest index ($R = -0.914$, $P < 0.001$), CDDBH

($R = 0.905$, $P < 0.001$) and functional richness ($R = 0.895$, $P < 0.001$), while the second axis showed strong relationship with CCDBH ($R = 0.618$, $P < 0.001$), HTDBH ($R = 0.481$, $P < 0.01$) and CDDBH ($R = 0.364$, $P < 0.05$). Moreover, the Pearson's correlation showed the strongest relationship of RGR with CDDBH ($R = 0.802$, $P < 0.001$), carbon stock with harvest index ($R = -0.886$, $P < 0.001$), and carbon sequestration with functional richness ($R = 0.903$, $P < 0.001$).

3.3.3. Drought tolerant strategy

For drought tolerant strategy, the eigenvalue for the first and second constrained axes were 146.8 and 0.0, respectively, while the first and second constrained axes explained 83.7 % and 0.0 % of the total variation, respectively (pseudo-F = 13.2, $P \leq 0.001$). The results of Pearson's correlations between habitat features and linear combinations of constraining variables along RDA axes showed that the first axis was strongly correlated with species richness ($R = -0.974$, $P < 0.001$), Shannon diversity ($R = -0.956$, $P < 0.001$) and CDDBH ($R = -0.913$, $P < 0.001$), while the second axis showed strong relationship with species evenness ($R = 0.533$, $P < 0.001$), fire index ($R = 0.528$, $P < 0.001$) and drought index ($R = 0.502$, $P < 0.001$). Moreover, the Pearson's correlation showed strongest relationship of RGR with Shannon diversity ($R = 0.657$, $P < 0.001$), carbon stock with species richness ($R = 0.891$, $P < 0.001$), and carbon sequestration also with species richness ($R = 0.901$, $P < 0.001$).

3.4. Interacting influence of habitat features on carbon sequestration

Fig. S1 illustrates a conceptual framework exhibiting the mutually interacting influence of habitat features, including species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators on carbon sequestration across the forest fragments. Table S8 summarizes parameter estimates of the structural equation model (SEM) exhibiting variances in the habitat features, explaining significant variance in carbon sequestration of the total trees, and drought avoiding and drought tolerant strategies. We observed non-significant χ^2 test results for total trees ($\chi^2 = 0.001$, Df = 2, $P = 0.999$), drought avoiding ($\chi^2 = 0.050$, Df = 2, $P = 0.975$) as well as the drought tolerant ($\chi^2 = 0.000$, Df = 2, $P = 1.000$) strategies, which indicated good agreements between the implied models and the variance-covariance matrices observed. The goodness-of-fit statistics also showed optimal values for total trees (CFI = 1.000, RMSEA = 0.000, SRMR = 0.000), drought avoiding (CFI = 1.000, RMSEA = 0.000, SRMR = 0.001), and the drought tolerant (CFI = 1.000, RMSEA = 0.000, SRMR = 0.000) strategies. Several regression coefficients between latent variables were also non-significant, however we have shown only significant interactions. Table S8 also summarizes the path coefficients of the models, while the visual description of path models are illustrated in Fig. 8 for total trees, drought avoiding, and drought tolerant strategies, respectively.

For total trees, SEM indicated significant influence of all habitat features, *i.e.*, species diversity indicators, functional diversity indicators, tree size indicators and disturbance indicators on carbon sequestration across the study sites (Fig. 8). We observed a direct positively significant influence of species richness, Shannon diversity, functional richness and HTDBH on carbon sequestration, whereas CCDBH and harvest index showed an indirect significant impact on the carbon sequestration (Fig. 8). The associations among the habitat features were mostly positive, except the impacts of harvest index on species richness, Shannon diversity, functional richness and CDDBH, which were significantly negative (Fig. 8). The SEM results for drought avoiding strategy showed dominating influence of functional diversity indicator, tree size indicators and disturbance indicators on carbon sequestration across the forest fragments, whereas the significant impacts of species diversity indicators on carbon sequestration were not observed (Fig. 8). Results showed a direct significantly positive influence of functional richness, HTDBH and CDDBH on carbon sequestration, while harvest index and fire index exhibited an indirect significantly negative impact (Fig. 8). The covariance of functional richness with CDDBH, and the covariances of harvest index with functional richness and fire index were significantly positive, whereas the covariance of fire index with CDDBH was significantly negative. The SEM results for drought tolerant strategy showed dominating influence of species diversity indicators, tree size indicators and disturbance indicators on carbon sequestration across the forest fragments, however the significant impacts of functional diversity indicators on carbon sequestration was not observed (Fig. 8). Results showed a direct significantly positive influence of Shannon diversity and CCDBH on carbon sequestration, whereas harvest and drought indices exhibited a direct significantly negative impact on carbon sequestration. Moreover, the species richness and CDDBH exhibited an indirect significant impact on carbon sequestration (Fig. 8).

4. Discussion

On decreasing edge distance across the forest fragments, we observed a significant reduction in stem density, RGR, carbon stock, carbon sequestration, and habitat features including species diversity, functional diversity and tree size indicators, while the considerable increase in disturbance indicators. Besides, the responses of the drought avoiding and drought tolerant strategies exhibited high differences for the majority of variables. Studies have shown that forest fragmentation is mainly due to the persistence dependence of human livelihood on forest and forest products, leading to a decline in ecosystem structure and functional diversity (Wood et al., 2000; Chaturvedi et al., 2024). However, a few studies also reported positive aspects of fragmentation for conserving biodiversity (Fahrig, 2017; Fahrig et al., 2019), and argued that compared to larger fragments, a network of smaller fragments can potentially conserve more plant species and carbon stocks mainly through functional diversity influences and management interventions (Ziter et al., 2013). Although fragmentation modifies the physical environment and resource availability by altering the structural and functional diversity of forest ecosystems (RamõÂrez-Marciala et al., 2001), the impact and consequences of fragmentation highly depend on ecosystem properties and species composition (Haddad et al., 2015).

Across the forest fragments, we found greater stem density, RGR, carbon density and carbon sequestration for the drought avoiding strategy compared to the drought tolerant strategy. Besides, the decline in stem density, carbon density and carbon sequestration towards decreasing edge distance was greater for the drought tolerant strategy, while the decline in RGR towards decreasing edge distance was higher for the drought avoiding strategy. Further, we observed that the dominant functional traits associated with drought avoiding strategy were LNC, WUEi, A_{max}, QWsat and LPC, while the traits associated with drought tolerant strategy were SSD, CC, LDMC, Gs_{max}, LL and RWC, which indicates that the drought avoiding type follow acquisitive strategy, and the drought tolerant type follow conservative strategy (see Wright et al., 2004). Under acquisitive strategy, plants exhibit fast growth and acquire resources available for a limited period, where LNC, A_{max} and LPC support the fast growth, while WUEi and QWsat are important for surviving in water limited conditions (Poorter et al., 2021; Chaturvedi et al., 2021). For conservative strategy, plants conserve resources and sustain growth for a longer period, where higher SSD is needed for supporting large sized trees with greater CC, while greater LDMC is required to support leaves with higher LL and RWC (Poorter et al., 2021; Chaturvedi et al., 2021). Our study sites experience extreme dry weather during post-winter and summer seasons for more than six months, while the favorable wet season is only for three months. The drought avoiding strategy is successful in lower sized fragments, since these trees have greater ability to avoid low water stress, and a higher capacity to acquire resources during the short wet season (Chaturvedi et al., 2024). The greater decline in stem density for drought tolerant strategy towards smaller sized fragments might be due to low availability of resources, and lower resistance to disturbances, such as

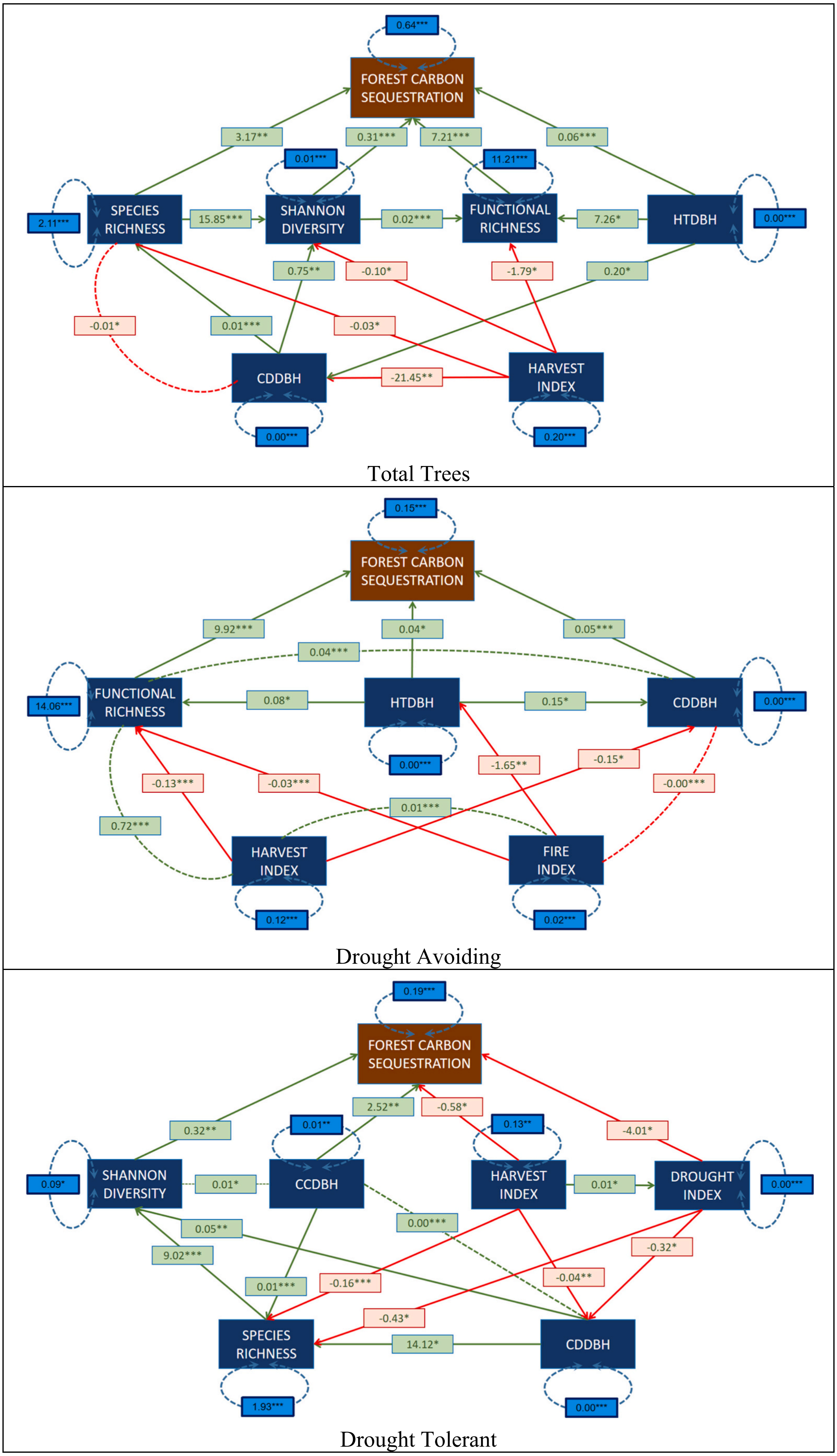

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Fig. 8. Structural equation model representing relations of carbon sequestration in forest fragments, with species diversity, functional diversity, tree size and disturbance indicators. Positive and negative significant links are represented by green and red arrows, respectively. The error covariance is represented by dotted arrows, while the variance for each variable is shown by the spiral blue dotted arrows. The numbers next to each arrow are standardized coefficients. See Table S8 for the model results summary. HTDBH, height to DBH ratio; CDDBH, canopy depth to DBH ratio; CCDBH, canopy cover to DBH ratio. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

drought and fire (Fauset et al., 2012). Moreover, compared to the drought tolerant strategy, a greater increase in RGR for drought avoiding strategy towards larger fragments indicates that this strategy is competitively superior in acquiring resources at favorable conditions, while the higher decline in RGR for drought avoiding strategy towards smaller fragments indicates that at unfavorable conditions, this strategy avoids investing limited resources for growth, but conserves them for survival (Markesteijn and Poorter, 2009).

The regression trends for stem density, carbon stock and carbon sequestration predict that at larger fragments, the drought tolerant strategy has the capacity to out compete for drought avoiding strategy, since the drought tolerant trees are large sized with greater canopy extension and do not allow small sized shade intolerant drought avoiding trees to survive under their canopy (Markesteijn and Poorter, 2009). This is evident when we observed a lower increase in species richness and species diversity for drought avoiding strategy towards larger fragments compared to the drought tolerant strategy, where the drought tolerant trees exhibited a huge increase, ultimately out competing the drought avoiding trees from those fragments. Moreover, we found contrasting patterns for species evenness for drought avoiding and drought tolerant strategies, where species evenness for drought avoiding strategy was increasing towards larger fragments, while species evenness for drought tolerant strategy was increasing towards smaller sized fragments. The declining evenness indicates the existence of a few very common species and several uncommon and rare species. For drought tolerant strategy, towards increasing fragment size, a few common species are competitively superior and reduce resources for others (competitive effect) (Aarssen, 1983). They increase their population, while uncommon species have the ability to tolerate a reduction in resources (competitive response) and exhibit a decline in population (Mulder et al., 2004). Regarding drought avoiding strategy, due to smaller size compared to drought tolerant species at larger fragments, these species need to modify shape (*e.g.*, leaf morphology, stem architecture and root morphology) to acquire light and other resources, therefore they differ more in shape and exhibit greater niche differentiation (Harper, 1977). The higher differences in shape lead to lower asymmetrical interspecific competition, thereby increasing species evenness and productivity (Hooper and Vitousek, 1998).

We observed considerable differences between the two strategies for functional diversity indicators. Among functional diversity indicators, the functional richness explains the amount of niche space the species occupies within a community, functional dispersion shows the variance in a species traits in the trait space, whereas functional evenness indicates the distribution of species abundance in the niche space (Mason et al., 2005; Schleuter et al., 2010). Consequently, greater functional diversity of the community allows better exploitation of the available niche space, leading to greater resource use and biomass production (Loreau et al., 2002). In our study, the trends of functional diversity indicators along the edge distance gradient suggest that compared to drought tolerants, drought avoiding strategy has the capacity to better exploit the available resources in smaller fragments, whereas compared to drought avoidants, the drought tolerant strategy has the ability to better exploit the available resources in large sized fragments.

Based on the RDA results, we observed that RGR, carbon stock and carbon sequestration for total trees across forest fragments were strongly influenced by species diversity, functional diversity and tree size indicators. For drought avoiding strategy, RGR, carbon stock and carbon sequestration were strongly affected by functional diversity, tree size and disturbance indicators, whereas the drought tolerant strategy exhibited a stronger impact of species diversity, tree size and disturbance indicators. The SEM results for total trees showed that the response of carbon sequestration was significantly influenced by species diversity, functional diversity, tree size and disturbance indicators (Singh and Pandey, 2024). For drought avoiding strategy, carbon sequestration was significantly affected by functional diversity, tree size and disturbance indicators, whereas the drought tolerant strategy exhibited a significant impact of species diversity, tree size and disturbance indicators. These results indicate that the analysis based on total species across the forest fragments is not able to precisely capture the critical habitat features explaining carbon dynamics (see Lavorel et al., 1997). Moreover, after categorizing tree species across the fragments into drought strategies, both RDA and SEM clearly differentiated the habitat features explaining carbon dynamics between drought avoiding and drought tolerant trees.

For the two drought strategies, tree size and disturbance indicators were common habitat features explaining carbon sequestration, however at one side functional diversity indicators were significant for drought avoiding strategy, at the other side species diversity indicators were strongly determining carbon sequestration for drought tolerant strategy. The functional diversity indicators represent diversity of traits and also explain the diversity of species niches or functions (McGill et al., 2006; Petchey and Gaston, 2006). Besides, they help understanding the relationships of species diversity indicators to ecosystem function and their responses to environmental disturbances (Petchey et al., 2004; Suding et al., 2008; Flynn et al., 2011; Cadotte et al., 2011). In our study, we observed that the drought avoiding strategy is better adapted along smaller fragments exhibiting greater disturbance, while drought tolerant strategy is better adapted along large sized fragments showing lower disturbance. Supporting our findings for drought avoiding strategy, studies have suggested that for disturbed forests functional diversity indicators are directly linked to recovery and productivity compared to species diversity indicators, as they better represent species assemblage and function (Cadotte et al., 2011; Schmitt et al., 2020). Moreover, in support of drought tolerant strategy, the study of Biswas and Mallik (2011) reported a positive relationship between species diversity and functional diversity indicators and emphasized that species diversity indicators are a better predictor of the stability of the ecosystem, although, it depends on environmental conditions and disturbance history of the ecosystem. Since functional diversity is positively correlated with species diversity, functional richness could also be replaced by species richness at certain conditions (Tilman et al., 1997). Besides, Song et al. (2014) suggested that correlations between functional diversity and species diversity could be positive, negative or neutral, and emphasized that species diversity could be higher or lower than functional diversity in natural communities depending on niche overlap among species and intraspecific variations. The larger fragments are comparatively stable, containing higher resources, leading to lower niche overlap and lesser intraspecific variations (Chaturvedi et al., 2024), and this might be the probable reason for the greater predictive efficiency of species diversity indicators, compared to functional diversity indicators.

Disturbances such as harvesting, fire and drought in tropical dry forest are linked with shifting species diversity and productivity (Williams-Linera and Lorea, 2009). According to our SEM models, we observed significant impacts of disturbance indicators on species diversity, functional diversity and tree size indicators, leading to a considerable influence on carbon sequestration across the fragments. Among the disturbance indicators, harvest index was a common disturbance indicator for total tree species, as well as for the two drought strategies. However, fire index was the critical predictor for drought avoiding strategy, while drought index was the important explanatory factor for drought tolerant strategy. The drought avoiding trees shed their leaves for longer duration during the drought period, leading to accumulation of a thick litter layer acting as a fuel for fire, particularly in smaller fragments. Consequently, these fragments experience frequent fire, therefore plants exhibit fire resistance traits for avoiding harmful impacts of fire (Bär et al., 2019). Besides, the drought tolerant trees contain leaves with longer life-span and larger canopies, which rarely allow fire to burn the ground layer (Bond and van Wilgen, 1996). However, these trees are more vulnerable to drought induced mortality due to presence of wider conduits which are susceptible to embolism (Hartmann, 2011; Stovall et al., 2019).

5. Conclusion

Present study provide inputs to the differences between tree drought strategies for variations in vegetation attributes, including stem density, relative growth rate (RGR), carbon stock and carbon sequestration, as well as habitat features, *viz.*, species diversity, functional diversity, tree size and disturbance indicators across the tropical dry forest fragments, along edge distance gradient. Besides we evaluated differences between drought strategies for responses of carbon storage and carbon sequestration to variations in species diversity, functional diversity, tree size and disturbance indicators. Across the forest fragments, we observed greater average species diversity, stem density, RGR, carbon density and carbon sequestration for drought avoiding strategy compared to the drought tolerant strategy. Functional richness was higher for drought avoiding strategy, while functional dispersion and functional evenness were greater for the drought tolerant strategy. HTDBH and CDDBH were higher for drought tolerant strategy, while CCDBH was greater for drought avoiding strategy. Although, drought index was similar for the two drought strategies, harvest index was greater for drought tolerant strategy, whereas fire index was higher for drought avoiding strategy. Generally, the declining edge distance across forest fragments, led to a significant reduction in vegetation attributes, as well as habitat features, except disturbance indicators which significantly increased. We observed considerable variations between the two drought strategies for the slope of associations of vegetation attributes and habitat features with edge distance across fragments. For explaining carbon sequestration across forest fragments, functional diversity indicators were highly significant for drought avoiding strategy, while species diversity indicators were strong predictors for drought tolerant strategy. Moreover, for both drought strategies, tree size and disturbance indicators were common habitat features explaining carbon sequestration. Among the disturbance indicators, the SEM results indicated fire index and drought index, as the critical predictors for carbon sequestration in drought avoiding and drought tolerant strategies, respectively. Since, forest fragments in tropical dry forests are largely ignored for ecological evaluations of carbon dynamics, our findings are novel and would be a reference for forest managers. Moreover, the present study will also provide insights into studies exploring vegetation responses to interactions of species diversity, functional diversity, tree size and disturbance indicators for predicting stability of larger fragments and for planning restoration of smaller fragments.

CRediT authorship contribution statement

R.K. Chaturvedi: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anshuman Tripathi:** Writing – review & editing, Resources, Investigation, Data curation. **Rajiv Pandey:** Writing – review & editing, Methodology, Formal analysis. **A.S. Raghubanshi:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Conceptualization. **J.S. Singh:** Writing – review & editing, Visualization, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175703.

References

Aarssen, L.W., 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. Am. Nat. 122, 707–731. https://doi.org/10.1086/284167.

Abramoff, M.D., Magalhaes, P.J., Ram, S.J., 2004. Image processing with ImageJ. Biophot. Internat. 11 (7), 36–42.

Ammer, C., 2019. Diversity and forest productivity in a changing climate. New Phytol. 221 (1), 50–66. https://doi.org/10.1111/nph.15263.

Aquilué, N., Filotas, É., Craven, D., Fortin, M.J., Brotons, L., Messier, C., 2020. Evaluating forest resilience to global threats using functional response traits and network properties. Ecol. Appl. 30 (5), e02095 https://doi.org/10.1002/eap.2095.

Aron, D., 1949. Copper enzymes isolated chloroplasts, polyphenoloxidase in *Beta vulgaris*. Plant Physiol. 24, 1–15. https://doi.org/10.1104/pp.24.1.1.

Bär, A., Michaletz, S.T., Mayr, S., 2019. Fire effects on tree physiology. New Phytol. 223 (4), 1728–1741. https://doi.org/10.1111/nph.15871.

Biswas, S.R., Mallik, A.U., 2011. Species diversity and functional diversity relationship varies with disturbance intensity. Ecosphere 2(4), 1–0. doi:https://doi.org/10.1890/ES10-00206.1.

Bollen, K.A., Harden, J.J., Ray, S., Zavisca, J., 2014. BIC and alternative Bayesian information criteria in the selection of structural equation models. Struct. Equ. Model. Multidiscip. J. 21 (1), 1–9. https://doi.org/10.1080/10705511.2014.856691.

Bond, W.J., van Wilgen, B.W., 1996. Fire and Plants. Chapman & Hall, New York.

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology with R, 2nd ed. Springer Switzerland, Cham, Switzerland.

Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75, 1437–1449. https://doi.org/10.2307/1937467.

Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M., Naeem, S., 2005. Species loss and aboveground carbon storage in a tropical forest. Science 310, 1029–1031. https://doi.org/10.1126/science.1117682.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48 (5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x.

Chaturvedi, R.K., 2010. Plant Functional Traits in Dry Deciduous Forests of India. Ph.D Thesis.. Banaras Hindu University, Varanasi, India.

Chaturvedi, R.K., Pandey, S.K., Tripathi, A., Goparaju, L., Raghubanshi, A.S., Singh, J.S., 2024. Variations in the plasticity of functional traits indicate the differential impacts of abiotic and biotic factors on the structure and growth of trees in tropical dry forest fragments. Front. Plant Sci. 14, 1181293. https://doi.org/10.3389/fpls.2023.1181293.

Chaturvedi, R.K., Raghubanshi, A.S., Singh, J.S., 2010. Non-destructive estimation of tree biomass by using wood specific gravity in the estimator. Nat. Acad. Sci. Lett. 33, 133–138.

Chaturvedi, R.K., Raghubanshi, A.S., Singh, J.S., 2011a. Carbon density and accumulation in woody species of tropical dry forest in India. For. Ecol. Manag. 262, 1576–1588. https://doi.org/10.1016/j.foreco.2011.07.006.

Chaturvedi, R.K., Raghubanshi, A.S., Singh, J.S., 2011b. Plant functional traits with particular reference to dry deciduous forests: a review. J. Biosci. 36, 963–981. https://doi.org/10.1007/s12038-011-9159-1.

Chaturvedi, R.K., Raghubanshi, A.S., Tomlinson, K.W., Singh, J.S., 2017. Impacts of human disturbance in tropical dry forests increase with soil moisture stress. J. Veg. Sci. 28, 997–1007. https://doi.org/10.1111/jvs.12547.

Chaturvedi, R.K., Tripathi, A., Raghubanshi, A.S., Singh, J.S., 2021. Functional traits indicate a continuum of tree drought strategies across a soil water availability gradient in a tropical dry forest. For. Ecol. Manag. 482, 118740 https://doi.org/10.1016/j.foreco.2020.118740.

Collins, L., Bradstock, R., Ximenes, F., Horsey, B., Sawyer, R., Penman, T., 2019. Aboveground forest carbon shows different responses to fire frequency in harvested and unharvested forests. Ecol. Appl. 29 (1), e01815 https://doi.org/10.1002/eap.1815.

Cook-Patton, S.C., Leavitt, S.M., Gibbs, D., Harris, N.L., Lister, K., Anderson-Teixeira, K. J., Briggs, R.D., Chazdon, R.L., Crowther, T.W., Ellis, P.W., Griscom, H.P., 2020. Mapping carbon accumulation potential from global natural forest regrowth. Nature 585 (7826), 545–550. https://doi.org/10.1038/s41586-020-2686-x.

Diaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2.

Diaz, S., Hector, A., Wardle, D.A., 2009. Biodiversity in forest carbon sequestration initiatives: not just a side benefit. Curr. Opin. Environ. Sustain. 1, 55–60. https://doi.org/10.1016/j.cosust.2009.08.001.

Enquist, B.J., West, G.B., Brown, J.H., 2009. Extensions and evaluations of a general quantitative theory of Forest structure and dynamics. Proc. Natl. Acad. Sci. USA 106, 7046–7051. https://doi.org/10.1073/pnas.0812303106.

Erskine, P.D., Lamb, D., Bristow, M., 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? Forest Ecol. Manag 233, 205–210. https://doi.org/10.1016/j.foreco.2006.05.013.

Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. Annu. Rev. Ecol. Evol. Syst. 48 (1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612.

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A., Koper, N., 2019. Is habitat fragmentation bad for biodiversity? Biol. Conserv. 230, 179–186. https://doi.org/10.1016/j.biocon.2018.12.026.

Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G., Hamer, K.C., Swaine, M.D., 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. Ecol. Lett. 15 (10), 1120–1129. https://doi.org/10.1111/j.1461-0248.2012.01834.x.

Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I., Naeem, S., 2011. Functional and phylogenetic diversity as predictors of biodiversity-ecosystem function relationships. Ecology 92 (8), 1573–1581. https://doi.org/10.1890/10-1245.1.

Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2018. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. J. Ecol. 106 (2), 561–570. https://doi.org/10.1111/1365-2745.12847.

Fournier, L.A., 1974. Un método cuantitativo para la medición de características fenológicas en árboles. Turrialba 24, 422–423.

Gruson, H., Grenié, M., 2022. Fundiversity: Easy computation of functional diversity Indices. 7360757 https://doi.org/10.5281/ZENODO.

Haddad, N.M., Brudvig, L.A., Clobert, J., et al., 2015. Habitat fragmentation and its lasting impact on earth' s ecosystems. Sci. Adv. 1, 1–9. https://doi.org/10.1126/sciadv.1500052.

Harper, J.L., 1977. Population Biology of Plants. Academic Press.

Hartmann, H., 2011. Will a 385 million year-struggle for light become a struggle for water and for carbon?–how trees may cope with more frequent climate change-type drought events. Glob. Chang. Biol. 17 (1), 642–655. https://doi.org/10.1111/j.1365-2486.2010.02248.x.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75 (1), 3–35. https://doi.org/10.1890/04-0922.

Hooper, D.U., Vitousek, P.M., 1998. Effects of plant composition and diversity on nutrient cycling. Ecol. Monogr. 68, 121–149. https://doi.org/10.1890/0012-9615(1998)068[0121:EOPCAD]2.0.CO;2.

Husson, F., Josse, J., Pagès, J., 2010. Principal Component Methods - Hierarchical Clustering - Partitional Clustering: Why Would we Need to Choose for Visualizing Data? Technical Report - Agrocampus Ouest.

Husson, F., Lê, S., Pagès, J., 2011. Exploratory Multivariate Analysis by Example Using R. Chapman & Hall, CRC.

IPCC, 2006. Guidelines for National Greenhouse Inventories, prepared by the National Greenhouse gas Inventories Programme. Ed: Eggleston, H.S., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., Japan: IGES. http://www.ipcc-nggip.iges.or.jp.

Kassambara, A., 2017. Practical Guide to Principal Component Methods in R (Multivariate Analysis Book 2). CreateSpace Independent Publishing Platform, Scotts Valley, CA.

Kassambara, A., Mundt, F., 2016. Factoextra: extract and visualize the results of multivariate data analyses, pp. 1–74.

King, D.A., Davies, S.J., Tan, S., Noor, N.S., 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. J. Ecol. 94 (3), 670–680. https://doi.org/10.1111/j.1365-2745.2006.01112.x.

Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol. Evol. 12 (12), 474–478. https://doi.org/10.1016/S0169-5347(97)01219-6.

Li, Y., Bao, W., Bongers, F., Chen, B., Chen, G., Guo, K., Jiang, M., Lai, J., Lin, D., Liu, C., Liu, X., 2019. Drivers of tree carbon storage in subtropical forests. Sci. Total Environ. 654, 684–693. https://doi.org/10.1016/j.scitotenv.2018.11.024.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., de-Miguel, S., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354, 6309. https://doi.org/10.1126/science.aaf8957.

Liu, X., Trogisch, S., He, J.S., Niklaus, P.A., Bruelheide, H., Tang, Z., Erfmeier, A., Scherer-Lorenzen, M., Pietsch, K.A., Yang, B., Kühn, P., 2018. Tree species richness increases ecosystem carbon storage in subtropical forests. Proc. R. Soc. B 285 (1885), 20181240. https://doi.org/10.1098/rspb.2018.1240.

Loreau, M., Naeem, S., Inchausti, P., 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford Univ, Press.

Markesteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought-and shade-tolerance. J. Ecol. 97 (2), 311–325. https://doi.org/10.1111/j.1365-2745.2008.01466.x.

Mason, N.W., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111(1), 112–118. doi:https://doi.org/10.1111/j.0030-1299.2005.13886.x.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S., Vesk, P.A., 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Glob. Ecol. Biogeogr. 19, 423–431. https://doi.org/10.1111/j.1466-8238.2010.00532.x.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002.

Mensah, S., Veldtman, R., Assogbadjo, A.E., Glèlè Kakaï, R., Seifert, T., 2016. Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. Ecol. Evol. 6 (20), 7546–7557. https://doi.org/10.1002/ece3.2525.

Mesa-Sierra, N., Laborde, J., Chaplin-Kramer, R., Escobar, F., 2022. Carbon stocks in a highly fragmented landscape with seasonally dry tropical forest in the Neotropics. For. Ecosyst. 9, 100016 https://doi.org/10.1016/j.fecs.2022.100016.

Mouchet, M.A., Villéger, S., Mason, N.W., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24 (4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Mulder, C.P., Bazeley-White, E., Dimitrakopoulos, P.G., Hector, A., Scherer-Lorenzen, M., Schmid, B., 2004. Species evenness and productivity in experimental plant communities. Oikos 107 (1), 50–63. https://doi.org/10.1111/j.0030-1299.2004.13110.x.

Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. Annu. Rev. Ecol. Syst. 1, 67–88. https://www.jstor.org/stable/2096989.

Nelder, J.A., Wedderburn, R.W., 1972. Generalized linear models. J. R. Stat. Soc. Series A (General) 135, 370–384. https://doi.org/10.2307/2344614.

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., Simpson, G., Wagner, H., 2019. Vegan: community ecology package. R Package Version 2.0–7.

Osuri, A.M., Machado, S., Ratnam, J., Sankaran, M., Ayyappan, N., Muthuramkumar, S., Parthasarathy, N., Pélissier, R., Ramesh, B.R., DeFries, R., Naeem, S., 2020. Tree diversity and carbon storage cobenefits in tropical human-dominated landscapes. Conserv. Lett. 13 (2), e12699 https://doi.org/10.1111/conl.12699.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333 (6045), 988–993. https://doi.org/10.1126/science.1201609.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. https://doi.org/10.1071/BT12225.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.

Petchey, O.L., Hector, A., Gaston, K.J., 2004. How do different measures of functional diversity perform? Ecology 85, 847–857. https://doi.org/10.1890/03-0226.

Piotto, D., 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecol. Manag. 255, 781–786. https://doi.org/10.1016/j.foreco.2007.09.065.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J. M., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512.

Poorter, L., Rozendaal, D.M., Bongers, F., Almeida, D.J., Álvarez, F.S., Andrade, J.L., Arreola Villa, L.F., Becknell, J.M., Bhaskar, R., Boukili, V., Brancalion, P.H., 2021. Functional recovery of secondary tropical forests. Proc. Natl. Acad. Sci. 118 (49), e2003405118 https://doi.org/10.1073/pnas.2003405118.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., 2015. Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24 (11), 1314–1328. https://doi.org/10.1111/geb.12364.

Portillo-Quintero, C., Sanchez-Azofeifa, A., Calvo-Alvarado, J., Quesada, M., do Espirito Santo, M.M., 2015. The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for its sustainable management. Reg. Environ. Chang. 15, 1039–1049. https://doi.org/10.1007/s10113-014-0689-6.

RamõÂrez-Marciala, N., GonzaÂlez-Espinosab, M., Williams-Linerac, G., 2001. Anthropogenic disturbance and tree diversity in montane rain forests in Chiapas, Mexico. For. Ecol. Manag. 154, 311–326. https://doi.org/10.1016/S0378-1127(00)00639-3.

Rödig, E., Cuntz, M., Rammig, A., Fischer, R., Taubert, F., Huth, A., 2018. The importance of Forest structure for carbon fluxes of the Amazon rainforest. Environ. Res. Lett. 13, 054013 https://doi.org/10.1088/1748-9326/aabc61.

Rosseel, Y., 2012. Lavaan: an R package for structural equation modeling. J. Stat. Softw. 48, 1–36. https://doi.org/10.18637/jss.v048.i02.

Ruiz-Jaen, M.C., Potvin, C., 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytol. 189, 978–987. https://doi.org/10.1111/j.1469-8137.2010.03501.x.

Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80 (3), 469–484. https://doi.org/10.1890/08-2225.1.

Schmitt, S., Maréchaux, I., Chave, J., Fischer, F.J., Piponiot, C., Traissac, S., Hérault, B., 2020. Functional diversity improves tropical forest resilience: insights from a long-term virtual experiment. J. Ecol. 108 (3), 831–843.

Simpson, G.L., 2019. Ggvegan: 'ggplot2' plots for the 'vegan' package. R package version 0.1–0.

Singh, R., Pandey, R., 2024. Underlying Plant Trait Strategies for Understanding the Carbon Sequestration in Banj Oak Forest of Himalaya. Tot. Environ, Sci. https://doi.org/10.1016/j.scitotenv.2024.170681.

Song, Y., Wang, P., Li, G., Zhou, D., 2014. Relationships between functional diversity and ecosystem functioning: a review. Acta Ecol. Sin. 34 (2), 85–91. https://doi.org/10.1016/j.chnaes.2014.01.001.

Stovall, A.E.L., Shugart, H., Yang, X., 2019. Tree height explains mortality risk during an intense drought. Nat. Commun. 10, 4385. https://doi.org/10.1038/s41467-019-12380-6.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.-L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Glob. Chang. Biol. 14, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x.

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Ewango, C.E.N., 2017. Diversity and carbon storage across the tropical forest biome. Sci. Rep. 7, 1–12. https://doi.org/10.1038/srep39102.

Tanentzap, F.M., Stempel, A., Ryser, P., 2015. Reliability of leaf relative water content (RWC) measurements after storage: consequences for in situ measurements. Botany 93, 535–541. https://doi.org/10.1139/cjb-2015-0065.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277 (5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300.

Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. 45, 471–493. https://doi.org/10.1146/annurev-ecolsys120213-091917.

Wardle, D.A., 2016. Do experiments exploring plant diversity–ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? J. Veg. Sci. 27, 646–653. https://doi.org/10.1111/jvs.12399.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat. Ecol. Evol. 1, 0063. https://doi.org/10.1038/s41559-016-0063.

Williams-Linera, G., Lorea, F., 2009. Tree species diversity driven by environmental and anthropogenic factors in tropical dry forest fragments of Central Veracruz. Mexico. Biodivers. Conserv. 18, 3269–3293. https://doi.org/10.1007/s10531-009-9641-3.

Wood, A., Stedman-Edwards, P., Mang, J., 2000. The Root Causes of Biodiversity Loss, Illustrate. Earthscan, Washington DC.

Wright, A.J., Wardle, D.A., Callaway, R., Gaxiola, A., 2017. The overlooked role of facilitation in biodiversity experiments. Trends Ecol. Evol. 32 (5), 383–390. https://doi.org/10.1016/j.tree.2017.02.011.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., et al., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403.

Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M., 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91 (12), 3664–3674. https://doi.org/10.1890/09-2335.1.

Yachi, S., Loreau, M., 2007. Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. Ecol. Lett. 10, 54–62. https://doi.org/10.1111/j.1461-0248.2006.00994.x.

Zhang, Y., Chen, H.Y.H., 2015. Individual size inequality links forest diversity and above-ground biomass. J. Ecol. 103, 1245–1252. https://doi.org/10.1111/1365-2745.12425.

Ziter, C., Bennett, E.M., Gonzalez, A., 2013. Functional diversity and management mediate aboveground carbon stocks in small forest fragments. Ecosphere 4, 1–21. https://doi.org/10.1890/ES13-00135.1.