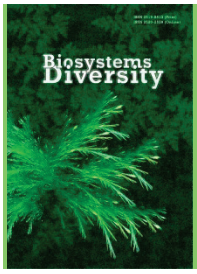

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Functional diversity along disturbance and environmental gradients in Ethiopian moist Afromontane forest

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Considering multiple measures to fully capture functional diversity is important. However, the effects of disturbance gradients on diversity have been controversial, as species diversity alone may not fully capture these effects. This study aimed to evaluate trait-based diversity across disturbance gradients in the moist Afromontane forest of Ethiopia, Yayu Coffee Forest Biosphere Reserve (YCFBR). Vegetation data and relevant traits related to plant-life strategies, competition, and responses to disturbances were collected. A multiple regression model was used to test the response of functional diversity to disturbances and environmental gradients. The results revealed functional diversity in plant communities, including dendrogram-based functional diversity for plot-based (FDp), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersions (FDis), and community-weighted mean of maximum tree height (CWM.Hmax), showed decreasing patterns with increasing disturbance intensity in the YCFBR. Additionally, the findings highlighted that FDis and Hmax are the most vulnerable functional traits to anthropogenic factors and are less tolerant in disturbed ecosystem environments. Therefore, reducing disturbances is crucial to maintaining higher levels of these functional diversities. For example, the results showed that the CWM.Hmax declined from 27.25 m to 15 m, indicating a shift towards shorter plant species. In contrast, the community-weighted mean of woody density (CWM.WD), the community-weighted mean of specific leaf area (CWM.SLA), and the community-weighted mean of seed mass (CWM.SM) increased significantly with an increase in disturbance intensity. For instance, CWM.SM and CWM.SLA changed from 5 to 14.25 (g) and 90 to 130 (cm^2/g), respectively. These indices may serve as indicators of ecosystem resilience at disturbed forest ecosystem sites. Furthermore, the regression results indicated that FDp, FRic, FEve, FDiv, FDis, CWM.WD, and CWM.Hmax showed increasing patterns with increasing species richness, which suggests that protecting and promoting species diversity can contribute to maintaining high levels of functional diversity. The mixed effects model revealed that anthropogenic disturbance and elevational gradients had significant effects on functional diversity in the YCFBR. Therefore, when managing and conserving biodiversity in heterogeneous environments, both anthropogenic factors and environmental variables need to be considered. Species with low SLA and SM are recommended for the restoration of disturbed ecosystems. Overall, this study demonstrates that trait-based functional diversity is useful for predicting the adaptation potentials of species in heterogeneous environments and disturbance gradients.

Keywords: heterogeneous environments; ecosystem resilience; low specific leaf area; patterns of functional diversity; species richness.

Introduction

The total area under forests across the globe is estimated to be 4.06 billion hectares (ha), which is 31 percent of the total land area and equivalent to 0.52 ha per person (FAO and UNEP, 2020). Forests provide a plethora of ecosystem services that include biodiversity conservation, sociocultural benefits, nature experiences and climate regulation. Unfortunately, these pristine natural resources are under tremendous threat both from natural and anthropogenic stresses (Sasidharan & Kavileveettil, 2023). Many of the world's most biodiverse regions are found in Africa; a continent facing exceptional challenges due to increasingly severe climate change and environmental conflict, all of which will ravage biodiversity (Chapman et al., 2022). Forty-five percent of the world's forested areas are in the tropics, and they are among the most important regulators of regional and global climate, natural carbon sinks and the most significant repositories of terrestrial biomass (Griggs, 2023). This implies that they are of immeasurable value to biodiversity, ecosystem services, social and cultural identities, livelihoods, and climate change adaptation and mitigation. Tropical forests are also the most biodiverse ecosystems in the world, yet their ecosystem functions, such as carbon sequestration for climate change mitigation and the provisionary services, are threatened by anthropogenic disturbances and climate change (Aguirre-Gutiérrez et al., 2022; Smit et al., 2023).

Human activities, principally through emissions of greenhouse gases, have unequivocally caused global warming, with global surface temperature reaching 1.1 °C above 1850–1900 in 2011–2020 (IPCC, 2023). Furthermore,over 420 million ha of forest were lost to deforestation from 1990 to 2020; more than 90% of that loss took place in tropical areas, threatening biodiversity, environmental services, the livelihoods of forest communities, and resilience to climate shocks (Griggs, 2023). For example, the Global Forest Resources Assessment (GFRA) revealed that Africa had the largest annual rate of net forest loss in 2010–2020, at 3.9 million ha, followed by South America, at 2.6 million ha (Lee & Ha, 2022). Deforestation, climate change, and land use change are the major factors posing threats to forest sustainability (Akram et al., 2023). Following this, much attention has been paid in recent years to the massive loss of ecosystem services and biodiversity worldwide due to forest clearance. Similarly, these rapid environmental changes are putting species at risk, and such changes in species composition can have strong effects on ecosystem processes and functions (Singh, 2021). Forest loss and degradation have been the main causes of tropical biodiversity loss and this continues rapidly at regional or global scales due to increasing intensity of disturbances such as overexploitation of species, destruction of habitats and climate change (Griggs, 2023). Therefore, protecting tropical forests has become increasingly important given the recognition that the loss of these forests accounts for between 6% and 17% of global carbon dioxide emissions (Baccini et al., 2017).

Ethiopia has a diverse climate of various ecological regions, and novel habitats with different topography have driven the establishment of diverse vegetation types, which range from afroalpine vegetation to semi-arid and arid vegetation types (Lemessa & Teka, 2017; Zerihun et al., 2023). Among these, the moist Afromontane forest of Ethiopia is mainly found in the Southwest escarpment of Ethiopia (Mengesha et al., 2020), where most of the country's Biosphere reserves (Yayu, Kafa, Sheka and Majang) are located and known as "Ethiopia's green lungs" (Semegnew et al., 2021). The moist Afromontane forests of Southwestern Ethiopia are the most biodiversity- and carbon-rich biomes in Ethiopia, playing an important role in climate change mitigation (DeVries et al., 2015). However, this forest is under threat from expansion of the coffee cultivation, agriculture expansion, overgrazing, firewood collection, and charcoal production (DeVries & Kooistra, 2016). Similarly, in the case of YCFBR, commercial coffee (*Coffea arabica*) farming is an important economic activity but can contribute to forest degradation, leading to a decline in species diversity and ecosystem services (Hundera et al., 2013). Therefore, the biosphere reserve management needs to be strengthened by continuous and focused research for sustainable development and support for mitigation and adaptation to climate change and other global environmental changes (Špulerová et al., 2023).

Ecological investigations are increasingly using functional diversity in order to understand different patterns, such as species occurrence, species competitive abilities, and the influence of biological communities on ecosystem functioning (Laureto et al., 2015). Generating trait-based functional information at local as well as global scales is vital to implementing effective restoration of forest ecosystems (Singh, 2021). Functional diversity holds the ability to understand ecosystems in ways unattainable by taxonomic diversity studies (Malaterre et al., 2019) because plants have certain characteristics that allow them to respond to various environmental conditions, like changes in climate, water scarcity in the soil, a lack of minerals, and others (Laureto et al., 2015; Malaterre et al., 2019). These quantifiable properties of individual species are known as plant functional traits (Kattge et al., 2020) and a specific functional trait can reflect the adaptive strategy of plants (Li et al., 2019). These traits can be further divided into response traits and effect traits. Response traits describe a plant's response to environmental change, while effect traits describe the effect of a plant on ecosystem functioning (Li et al., 2019). Functional diversity refers to the value, range, and distribution of functional traits in a specific ecosystem or to the components of biodiversity that have an impact on how an ecosystem operates or performs and are determined disproportionately by the specific traits (Yi et al., 2020). These traits mediate species' responses to environmental changes (Jesse et al., 2016); moreover, these changes point to mechanism alterations in ecosystem functioning and services (Nicola et al., 2021). In addition, functional traits play a crucial role in how species respond to their surroundings and influence ecological processes because functional diversity can improve predictions of the resiliency and resistance of plant communities to varying levels of disturbance (Tinoco-Ojanguren et al., 2018).

Most of the time, assessments to understand changes in plant diversity and ecosystem functioning focus on the analysis of taxonomic diversity. However, the resilience of ecosystems depends not only on species richness but also on the functions of species within communities and ecosystems (Peña-Lara et al., 2022). Studies focused on functional diversity are an important component of biodiversity information about species vulnerability in the context of disturbance and climate change. This provides a solid base for planning conservation decisions, restoration programs, and the maintenance of ecosystem services (Tinoco-Ojanguren et al., 2018). In addition, linking species richness and functional diversity is potentially valuable for planning, conservation, and restoration strategies by identifying areas that maximize ecosystem service and biodiversity conservation (Peña-Lara et al., 2022). Despite the significance of forests for preserving ecosystem function, there is surprisingly little empirical data demonstrating how functional diversity varies across disturbances and environmental gradients in forests.

The selection of functional trait(s) critically determines functional diversity, with large consequences for studies relating biodiversity to ecosystem functioning (Lilia et al., 2022). Therefore, careful consideration of the traits required to capture the ecosystem process of interest is essential (Paula et al., 2023). Functional diversity is expected to scale positively with species diversity because each new species added to the ecosystem will not only contribute to species diversity but will also contribute to functional diversity. Species diversity is a good proxy for functional diversity in tree communities (Whitfeld et al., 2014).Therefore, an integrated taxonomic and functional diversity approach can be used to support environmental assessment, restoration, and conservation planning of biological resources (De et al., 2023). Furthermore, functional traits capture essential aspects of species' ecological tradeoffs and roles within an ecosystem, making them useful in determining the ecological consequences of environmental change, however, they have not been used as commonly as more traditional metrics of species diversity (Lueder et al., 2022).

In many previous studies, the conclusions about the effects of disturbance and environmental gradients on diversity remain controversial (Jesse et al., 2016). This is because,the traditional way of measuring diversity does not give clear conclusions due to the exclusion of trait-based diversity measurements. Also, the effects of disturbance and environmental factors on biodiversity have been investigated mostly with a focus on taxonomic diversity; however, this presents relevant shortcomings that may result in misleading conclusions for forest conservation (Brockerhoff et al., 2017). To account for these shortcomings, functional approaches have recently been proposed as an alternative way to assess biodiversity conservation-related factors (Lelli et al., 2019). Therefore, trait-based diversity measurements are a useful method of measuring diversity metrics concerning disturbance and environmental gradients to come up with a clear policy for biodiversity conservation, but they are a poorly understood aspect of conservation strategy. Therefore, we hypothesized that increased species richness leads to higher functional diversity. Also, increased heterogeneity of environmental conditions will lead to higher functional diversity, which is another expectation from this study's findings. Here, the researchers' proposition was that disturbance variation and environmental factors can influence functional diversity, and functional diversity indices are responding differently against these factor gradients. Based on these hypothetical claims, this study was initiated to: 1) examine how the functional diversity metrics respond to anthropogenic disturbance and environmental factors in YCFBR; and 2) examine the relationships of functional diversity indices with species richness.

Materials and methods

Study area descriptions. This study was conducted at Yayu Coffee Forest Biosphere Reserve, Southwest Ethiopia, which is located 582 km Southwest of Addis Ababa. This biosphere is one of the largest remaining patches of the Afromontane Rainforest in the Southwestern part of Ethiopia. The YCFBR was registered in 2010, and it is one of the five UNESCO-registered biosphere reserves in Ethiopia with the primary objective of maintaining biodiversity and supporting sustainable development (Gole et al., 2009). The biosphere covers five districts: namely Yayu, Hurumu, Bilo-Nopa, Dorani, Alge-Sachi and Chora. Geographically, it lies between latitudes 8° 0′ 42″ to 8° 44′ 23″ N and longitudes 35°20′31″ to 36°18′20″ E (Gole et al., 2009). The total area of YCFBR is about 167,021 ha and its core, buffer and transition zones cover 27,733, 21,552, and 117,736 ha, respectively, with altitudes ranging between 1240 and 2400 m above sea level (Beyene et al., 2020). The area receives bimodal rainfall, with a mean annual rainfall of, 1798 mm per year. The long rainy season for the area is from March to October, and the short rainy season is from December to January. The mean annual temperature of the study area is 18.7 °C, and the mean maximum and minimum temperatures are 27.7 °C and 11.1 °C, respectively (Fig. 1).

Sampling design. In this study, multistage sampling techniques were employed. At the first stage, stratification of the biosphere reserve into core, buffer, and transitional zones was done to ensure the representation of the three zones in the sampling (Jemal et al., 2018). In the second stage, Yayu and Hurumu districts were purposefully selected because the two districts contain three zones. In the third stage, Wabo and Gaba kebeles were purposefully selected from Yayu and Hurumu districts, respectively, using the same criteria used for district selection (Fig. 2). At the final stage, anthropogenic disturbance and environmental variables such as slope, aspect and elevation were selected to study the relative patterns of woody diversity along anthropogenic disturbance and environmental gradients.

Data were collected using stratified systematic sampling with a random start (Michalcová et al., 2011) and this sampling approach was also used for this study. Representative plots and transect lines were systematically distributed for the core, buffer and transitional zones. All transect lines were oriented northwards as a rule of thumb (North-South compass direction). A plot size of 20 × 20 m (400 m^2) was used to collect vegetation data from the core and buffer zone, while a 30 x 30 m (900 m^2) plot size was used for the transitional zone based on the expected density of woody species in each zonation. To minimize the influence of edge effects, all plots were laid at least 150 m away from the nearest roads, and the coordinates for the location of plots were recorded (Djomo et al., 2016). Transect lines and sample plots were laid 300 m from each other. Then, a total of 90 plots were systematically distributed for the core, buffer, and transitional zones.

Vegetation data collection and environmental factors. In each plot, the diameter at breast height (DBH) of trees and shrubs was measured for DBH > 2.5 cm. In two perpendicular directions, the DBH was measured in two perpendicular directions, and its average value was recorded. When the branching of multi-stemmed individuals occurred below the DBH, each stem was measured separately. Furthermore, all woody lianas with a DBH > 1 cm at 1.30 m from the rooting point were recorded, since this provides a detailed assessment of diversity (Snowdon et al., 2002). Here, liana is defined as any long-stemmed, woody vine that uses trees or other means for vertical support, whereas a shrub is a woody plant that is multi-stemmed at the base of the plant (Groover, 2020). Whereas for the coffee plants, the diameter at stump height of all coffee shrubs (height of 40 cm) was measured in two perpendicular directions, and the average value was taken. In the case of multi-stemmed coffee plants, all stems in a single plant were measured independently and the equivalent diameter (40 cm) of the plant was calculated. Plant identification was carried out both in the field (vernacular names) and in the herbarium. For species that were difficult to identify in the field, plant specimens were sampled, labeled, pressed, and transported to the National Herbarium (ETH), Addis Ababa University, for further identification and nomenclature of plant taxa following the flora of Ethiopia and Eritrea (Edwards et al., 2000).

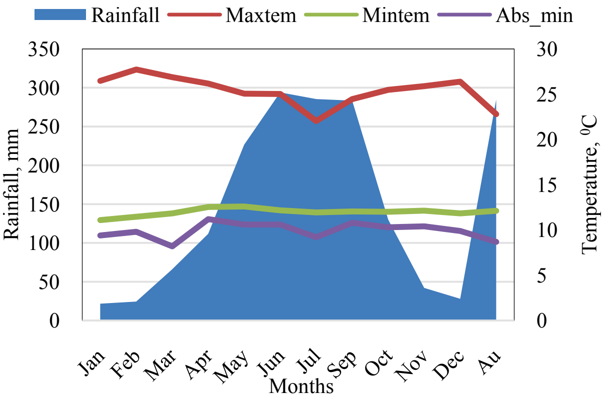

Fig. 1. Climate diagram results for the study area for rainfall (mm) and temperature (°C) (1981–2021): maxtem – maximum temperature; mintem – minimum temperature; Abs_min – minimum absolute temperature

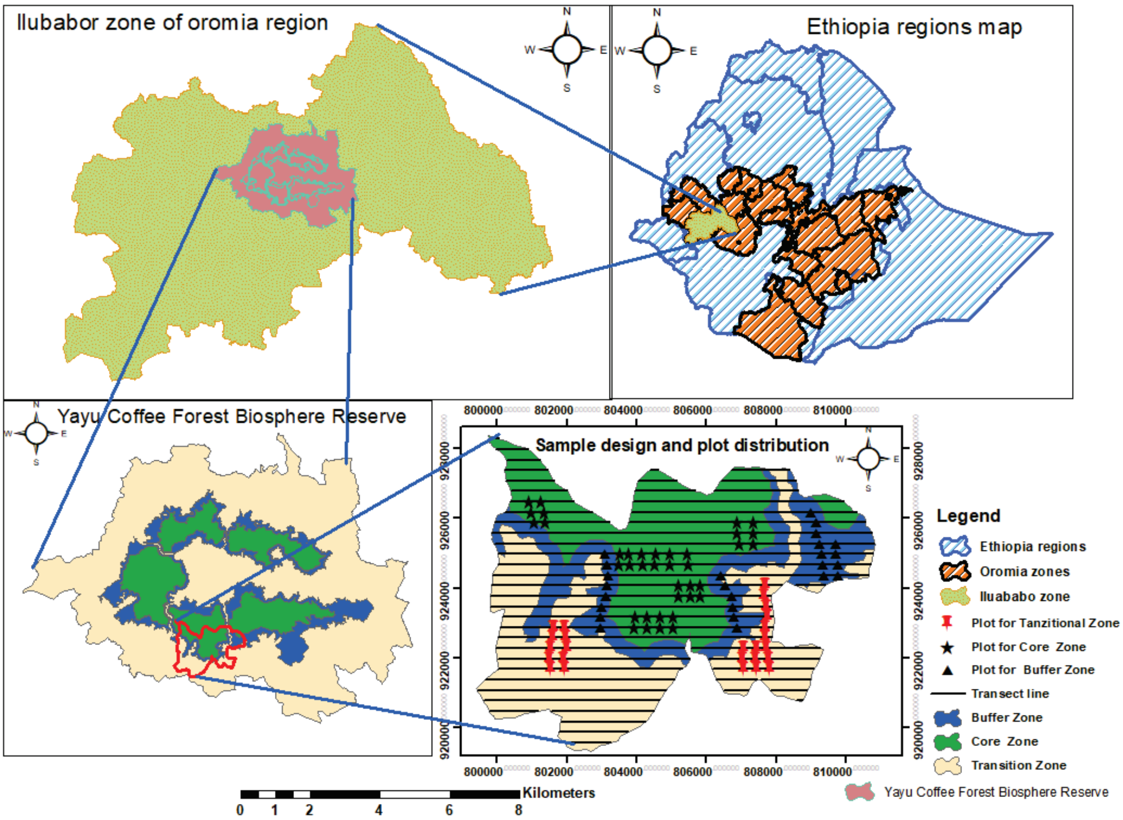

Fig. 2. Map of the study area (Yayu Coffee Forest Biosphere Reserve), sample design and plot distributions within zones and transect lines

The disturbance intensity evels were derived from the relative measurement of major disturbance indicators for each plot following the modified methods (Yuan et al., 2018; Woldu et al., 2019). Each disturbance was collected for each plot based on visible signs and measured as: grazing intensities (if the damage observed is > 50%, it is described as high grazing intensity; if the damage observed is 10–50%, it is described as medium; and if the damage observed is <10%, it is described as low grazing intensity) (Wekesa et al., 2016); number of tree stumps (ratio of total stumps to total stems per plot in percentages (%) (Yuan et al., 2018); and coffee dominance was measured as a ratio of coffee plants to the total number of woody plants in each plot in % (Girma et al., 2018, 2021). Stumps in this study are defined as the remains of the stems of woody plants measuring a diameter at stump height 30 cm above-ground level (DSH = 30 cm) of ≥ 2 cm after cutting (Melese et al., 2021). Then, plots were categorized into four disturbance intensity levels (DIL) based on the percent of each disturbance scored as: relatively undisturbed (<5%), slightly disturbed (5–25%), moderately disturbed (25–50%), and disturbed forest (>50%) (Yuan et al., 2018).

The elevation, aspects, slope and geographical location of each plot were recorded. The elevation and aspects were measured using an altimeter, whereas a Sunto clinometer was used to measure slope and indexed it to five levels. Then, slope classification was performed based on: flat (0–3%), gentle (3–8%), moderate (8–25%), hilly (25–40%), and steep (> 40%). The aspect was also classified into 8 sub-directions: North (N) for direction readings between (0.0–22.5) and (337.5–3600), Northwest (NW) if it reads from 22.5 to 67.5, East (E) if it reads between 67.5 and 112.5, Southeast (SE) if it reads between112.5 and 157.5, South (S) if the reads are between 157.5 and 202.5, Southwest (SW) if it is between 202.5 and 247.5–292.5, and Northwest (NW) if it is located between 292.5 and 337.5 (Lujin et al., 2015).

Quantification of functional diversity and taxonomic diversity indices. Traits relevant to plant-life strategy, competition ability, response to disturbances and climate change were selected for functional diversity estimation (McGill et al., 2006; Zhu et al., 2017; Ali et al., 2018). These were wood density (WD), seed mass (SM), specific leaf area (SLA), and tree maximum height (Hmax). Data on species WD was obtained from Ethiopia's Forest Reference Level Submission to the UNFCCC and the average value was used when multiple values were available for a single species. When the WD value was missing for a given species, the average genus WD was used. Similarly, mean WD at the family level was used in the cases where genus data for WD was missed. Also, when a family WD was missing, a plot-level average WD was used (Mensah et al., 2018). SLA, SM and Hmax were extracted from the TRY database (www.try-db.org) (Kattge et al., 2020) and for analyses, average trait values were used per species. Two functional diversity indices were calculated for the nine functional diversity indices, one was based on the species trait values present in the plots, and the other was based on the traits weighted by the species richness. These are functional diversity based on dendrogram for plot-based (FDp), functional evenness (FEve), functional richness (FRic), functional diversions (FDiv), functional dispersion (FDis), community-weighted mean of woody density (CWM.WD), community-weighted mean of specific leaf area (CWM.SLA), community-weighted mean of maximum heights (CWM.Hmax), and the community-weighted mean of seed mass (CWM.SM). Furthermore, species diversity values for the three taxonomic diversity indices, species richness (S), species Shannon-Wiener index (H'), and species evenness index (E), were calculated (Pielou, 1975; Magurran, 1988).

Statistical analysis. For the analysis of functional traits, we constructed a species-trait matrix and a species-abundance matrix. By linking these two matrices, we developed a trait-abundance matrix used to calculate functional diversity indices. All the selected functional diversity indices were calculated by the F Diversity software (Casanoves et al., 2011). Standardization was performed for multi-trait functional diversity indices because the trait variables of this study showed a difference in orders of magnitude and scales of measurement, whereas a single functional trait index was calculated without standardization (Casanoves et al., 2011). Pearson correlation was used to test the association between functional diversity and species diversity, disturbance level, slope, aspect, and elevational gradients. The best-fitting model was selected based on the highest R^2 and 5%, the minimum difference needed to be significant. Based on this significance, a regression model was used to test the varying patterns of functional diversity along disturbance intensity and environmental factors. Furthermore, the effects of disturbance and environmental variables (fixed factors) on functional diversity (response variables) were tested using mixed effects models. By using the package "lme4", the mixed effects model was run, and the selection of variables was done by "backward selection" using the "cAIC4" package (Bates et al., 2015). The significant effect of fixed factors was determined using the "lmerTest" package (Kuznetsova et al., 2017). All statistical analyses were performed using R statistical software (v4.1.2; R Core Team, 2021).

Results

Variation of plant functional diversity along disturbance gradients. Among the calculated functional diversity indices are FDp, FRic, FEve, FDiv, FDis, and CWM.Hmax showed a decreasing pattern with disturbance intensity level, i.e., functional diversity decreased significantly with disturbance intensity increase (Table 1, Fig. 3). The greater the disturbance intensity, the less functional diversity was obtained. According to this, it is imperative to reduce disturbances to maintain higher levels of functional diversity. In contrast, three functional diversity indices for CWM.WD, CWM.SM and CWM.SLA showed an increasing pattern with disturbance intensity levels (Table 1, Fig. 3) because they were positively correlated with each other. These findings reflected that CWM.WD, CWM.SM, and CWM.SLA are less affected in disturbed forest sites (Fig. 3), whereas FDp, FRic, FEve, FDiv, FDis, and CWM.Hmax are affected in the disturbed forest sites of YCFBR (Fig. 3).

Relationships between functional diversity and environmental factors of YCFBR. The coefficients of the regression model showed that functional diversity indices were impacted by the disturbance, slope, aspect and elevation gradients of the YCFBR (Table 1). The disturbance has a significant effect on all functional diversity indices except for CWM.WD. No significant effects were found due to slope on functional diversity indices, except for FDis. Except for CWM.WD, functional diversity indices were significantly influenced by elevational gradients in the YCFBR. Surprisingly, no significant effects were found due to aspects of all functional diversity (Table 1). Furthermore, results revealed functional diversity indices for FRic, FEve, FDiv, FDis, and CWM.Hmax had a negative association with disturbance and elevational gradients. This indicated that higher disturbance and elevational gradients corresponded to lower functional diversity. In contrast, CWM.SLA and CWM.SM showed positive associations with disturbance and elevation.

A mixed effects model revealed that slope, elevation, aspect, and disturbance had a significant effect on functional diversity (Table 1). These suggest that both anthropogenic factors and environmental variables need to be considered when managing and conserving biodiversity in heterogeneous environments. Furthermore, the mixed effects model showed that disturbance had a significant positive effect on all functional diversity indices, except for CWM.WD and CWM.SM, which are negatively affected by disturbance (Table 2), whereas aspect had a significant positive effect on FDp, FEve and FDiv (Table 2). The results show that slope and aspect affect species composition and community structure independently of elevation.

Table 1
Pearson correlation coefficients between functional diversity indices and environmental factors of Yayu Coffee Forest Biosphere Reserve, Southwest Ethiopia

	FDp	FRic	FEve	FDiv	FDis	CWM WD	CWM SLA	CWM Hmax	CWM SM
Disturbance	–0.46***	–0.54***	–0.51***	–0.44***	–0.70***	0.11	0.61***	–0.75***	0.81***
Slope	0.19	0.20	0.03	0.15	0.25*	0.10	–0.00	0.11	–0.12
Aspect	0.00	–0.02	0.02	0.09	–0.02	0.13	0.01	–0.03	–0.02
Elevation	–0.44***	–0.49***	–0.34**	–0.43***	–0.52***	–0.016	0.39***	–0.44***	0.52***

Note: *** – significant at 0.001; ** – significant at 0.01; * – significant at 0.05; FDp – functional diversity plot based dendrogram; FRic – functional richness; FEve – functional evenness; FDiv – functional divergence; FDis – functional dispersion; CWM WD – community-weighted mean of wood density (g/cm^3); CWM SLA – community-weighted mean of specific leaf area (cm^2/g); CWM Hmax – community-weighted mean of maximum heights (m); CWM SM – community-weighted mean of seed mass (g).

Functional diversity indices and species diversity relationships. The nine functional diversity indices were all closely associated with species richness (S), Shannon Weiner diversity (H'), and evenness index (E) in the YCFBR (Table 3). As per the given table, S, and H' show positive and significant correlations with all functional diversity components except for the three indices, i.e., CWM.SLA, CWM.WD, and CWM.SM (Table 3). The strongest positive correlations with S were observed for FDp, and FRic, while FDis shows the strongest positive correlation with H' and E. CWM.Hmax also has strong positive correlations with both S and H'. The evenness index, on the other hand, has significantly positive correlations with most of the components except for CWM.SLA and CWM.SM, indicating that higher values of SLA and SM are associated with lower species diversity (Table 3). These findings demonstrate that there is a substantial correlation between functional diversity and species diversity.

This indicates that protecting and promoting species diversity can also contribute to maintaining high levels of functional diversity. These findings suggested that species diversity and functional diversity are highly correlated to each other, and both positive and negative correlations were found between species and functional diversity indices.

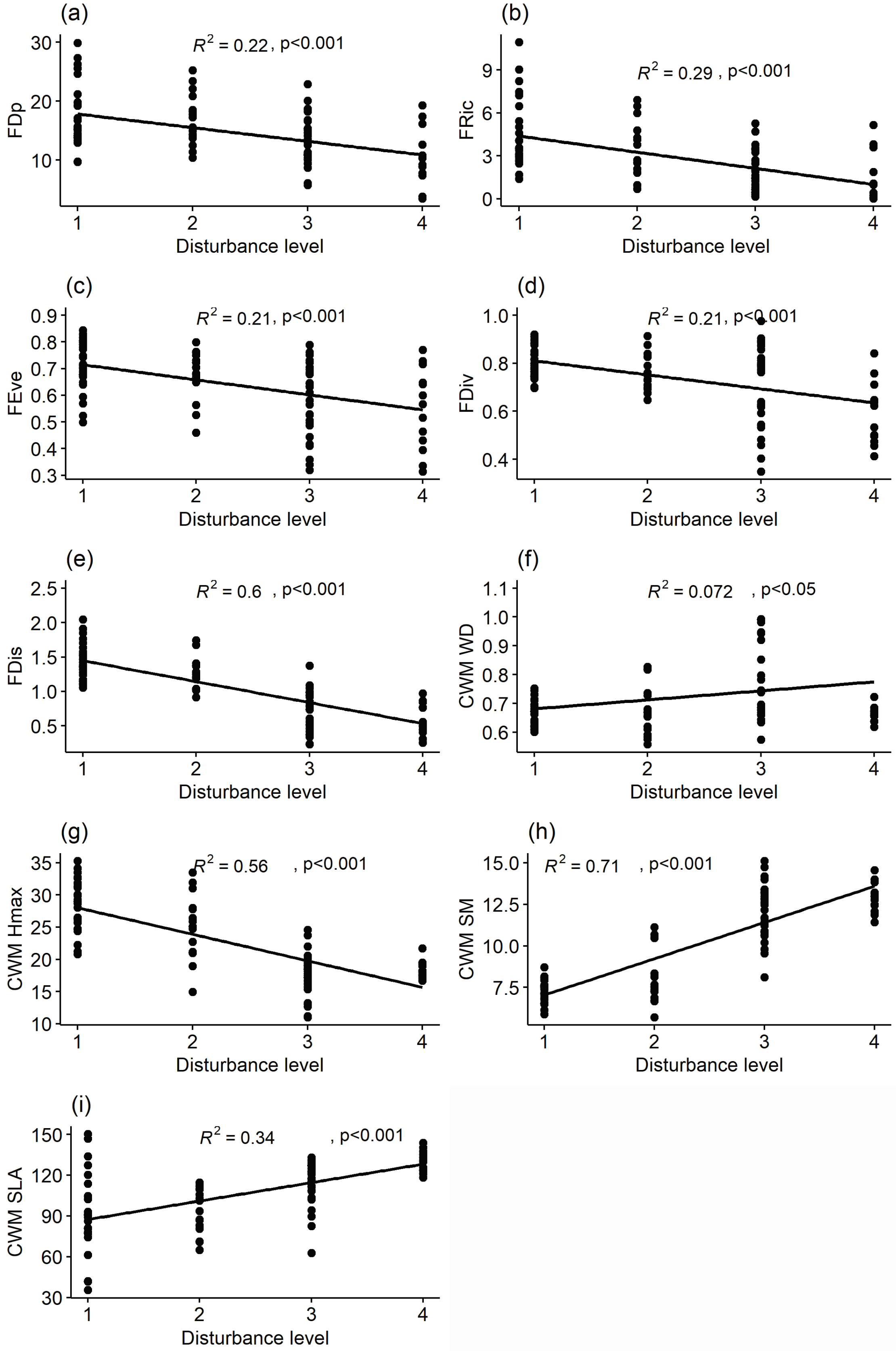

Fig. 3. Changes of functional diversity indices of YCFBR along disturbance gradients: X-axis: 1 – undisturbed forest sites, 2 – slightly disturbed forest sites, 3 – moderately disturbed forest sites, 4 – disturbed forest sites; Y-axis: FDp – functional diversity plot-based dendrogram; FEve – functional evenness; FRic – functional richness; FDiv – functional divergence; FDis – functional dispersion; CWM WD – community-weighted mean of wood density (g/cm^3); CWM SLA – community-weighted mean of specific leaf area (cm^2/g); CWM Hmax – community-weighted mean of maximum heights (m); CWM SM – community-weighted mean of seed mass (g)

Table 2
Mixed effects model representing the effects of aspects and disturbance gradients on functional diversity components with 'type III' analysis of variance and Satterthwaite's methods

Functional diversity component	Effect	Estimate	d.f.	SE	*P* value
FDp	aspect	0.015	81, 615	0.007	0.029
	disturbance	2.311	83, 147	0.565	$9.84*10^{-5}$
FRic	disturbance	1.400	83, 104	0.520	0.009
FEve	aspect	0.001	82, 947	0.001	0.027
	disturbance	0.069	16, 181	0.029	0.031
FDiv	aspect	0.002	82, 960	0.001	0.047
FDis	disturbance	0.277	83, 50	0.032	$2.38*10^{-13}$
CWM WD	disturbance	–0.079	83, 928	0.030	0.011
CWM Hmax	disturbance	1.541	74, 251	0.758	0.046
CWM SM	disturbance	–2.196	83, 33	0.144	$2.02*10^{-16}$

Notes: d.f. – degrees of freedom; SE – standard error; estimate – refers to the estimated values of the fixed effects; FDp – functional diversity plot-based dendrogram; FRic – functional richness; FEve – functional evenness; FDiv – functional divergence; FDis – functional dispersion; CWM WD – community-weighted mean of wood density (g/cm^3); CWM Hmax – community-weighted mean of maximum heights (m); CWM SM – community-weighted mean of seed mass (g).

Table 3
Pearson correlation coefficients between species diversity and functional diversity indices of Yayu Coffee Forest Biosphere Reserve, Southwest Ethiopia

Functional diversity components	Species richness (S)	Shannon Weiner diversity (H')	Evenness index (E)
FDp	0.70***	0.48***	0.40***
FRic	0.64***	0.51***	0.52***
FEve	0.41***	0.50***	0.37***
FDiv	0.33**	0.39***	0.33**
FDis	0.46***	0.63****	0.72***
CWM SLA	–0.36***	–0.56***	–0.51***
CWM WD	–0.04	–0.30**	0.03
CWM Hmax	0.42***	0.71***	0.59***
CWM SM	–0.55***	–0.86***	–0.57***

Notes: *** – significant at 0.001; ** – significant at 0.01; * – significant at 0.05; FDp – functional diversity plot-based dendrogram; FRic – functional richness; FEve – functional evenness; FDiv – functional divergence; FDis – functional dispersion; CWM SLA – community-weighted mean of specific leaf area (cm^2/g); CWM WD – community-weighted mean of wood density (g/cm^3); CWM Hmax – community-weighted mean of maximum heights (m); CWM SM – community-weighted mean of seed mass (g).

Among the nine functional diversity indices, seven of them (FDp, FRic, FEve, FDiv, FDis, CWM.WD, & CWM.Hmax) revealed increasing patterns with increasing species richness (Fig. 4). Functional diversity for the CWM.SM, and CWM.SLA showed a decreasing pattern as species richness increased (Fig. 4). The greater the species richness, the less functional diversity was obtained. This is because the functional diversity of CWM.SM, and CWM.SLA is negatively correlated with species richness (Table 3).

Discussion

Variations of plant functional diversity along disturbance gradients. Most of the functional diversity indices tested in this study showed decreasing values with disturbance intensity level, in accordance with Biswas et al. (2011), who quantified the variation of FRich, FDiv, and FEve along anthropogenic disturbance gradients. In contrast, three functional diversity indices were analyzed for CWM.WD, CWM.SLA, and CWM.SM along disturbance gradients and showed an increasing pattern in agreement with the findings of Levine et al. (2016). This showed that the relationships between CWM.WD, CWM.SLA, and CWM.SM with disturbance gradients can vary depending on the type and intensity of the disturbance, which has similarities with Zhang et al. (2017). Low disturbance intensity promotes the growth of high wood density species, and species with low SLA can allocate more resources to structural tissues and less to leaf production, which provides them with greater drought tolerance and protection against herbivory, consistent with the previous studies. For example, a study by Lasky et al. (2014) found that in low-disturbance forests, tree species with high wood density were more abundant compared to high-disturbance forests. This suggests that low-disturbance intensity can be selected for species with higher wood density traits. A study by Laughlin et al. (2010), Cornell et al. (2014), and Brockerhoff et al. (2017) demonstrated that low SLA was associated with higher leaf dry matter content and higher leaf tissue density, which are traits linked to drought resistance. This implies that species with low SLA may have greater drought tolerance capabilities due to their allocation of resources towards structural tissues instead of leaf production. Moles et al. (2011) found that species with low SLA had higher levels of physical and chemical defenses against herbivory. This suggests that species with low SLA may be better equipped to protect against herbivores, potentially due to their investment in structural tissues rather than leaves.

In addition, low-disturbances can create more heterogeneous environments, allowing for the coexistence of a wider range of species with different trait values, which can lead to functional diversity being increased (Bertrand et al., 2015). The main groups of species that contribute to functional diversity can vary depending on the ecosystem type because their traits and roles differ based on their specific functions within the ecosystem (Wilkinson, 1999; Laureto et al., 2015). For example, plants may differ in their growth rates, nutrient requirements, and tolerance to environmental stressors (Kong et al., 2023). As the heterogeneity of environmental conditions increases, it is expected that functional diversity will increase, consistent with Whitfeld et al. (2014).

Patterns of functional diversity increased for SM with disturbance severity levels for several possible reseasons. These are facilitation, stress tolerance and evolutionary trade-offs of SM against disturbance (Adler et al., 2013). In contrast, but consistent with Singh (2021), species with smaller seeds are more likely to establish themselves in disturbed areas as they require fewer resources for germination and early growth. Along disturbance gradients, such as those created by natural or human-induced disturbances (e.g., fire, logging, and grazing), plant species with larger seeds may have advantages in terms of seedling survival and growth because larger seeds typically have more nutrient reserves, higher germination rates, and better seedling vigor (Maron et al., 2020). Also, larger seed sizes may be more likely to be successfully established due to larger seeds that are better equipped to germinate and establish in environments with high levels of stress (Adler et al., 2013). Furthermore, large seed size may confer advantages in terms of seedling survival and growth;however, there are trade-offs associated with large seed size,such as reduced seed production or dispersal ability (Maron et al., 2020; Honour & Rowan, 2022). Plants with larger seeds tend to allocate more resources to seed production, which can result in reduced seed quantity. Where establishment success is more uncertain, smaller-seeded species may compensate for their reduced ability to compete with larger-seeded species by producing more seeds (Zhang et al., 2017). Additionally, larger seeds may be less efficient for dispersal as they are heavier and have a limited dispersal range compared to smaller seeds (Honour & Rowan, 2022). This can restrict their ability to colonize new habitats or exploit resource-rich patches within unevenly disturbed ecosystems. Therefore, the relationship between disturbance and functional diversity in SM and in general is likely to be complex and context-dependent due to a range of factors.

Functional diversity can be measured by the suite of ecological functions that different species perform in an ecosystem in response to varying levels of disturbance (Levine et al., 2016; Zhang et al., 2017). Aligned with this, patterns of functional diversity along disturbance gradients are typically decreasing because disturbances often favor species that are adapted to the disturbed conditions, such as fast-growing species or opportunistic colonizers, at the cost of other species that are less adapted, as already indicated (Bertrand et al., 2015). This tells us that species diversity with a low tolerance for changes in environmental conditions is likely to be negatively affected by disturbance or other environmental stress. For example, when disturbance occurs, some species may increase or decline depending on their ecological traits, such as their life history, morphology, or physiology, as already pointed out (Zhang et al., 2017; Kong et al., 2023). These contrasted results were obtained due to ecological differences because the study area is characterized as moist Afromontane forests and receives bimodal rainfall, which facilitates photosynthesis and growth rate (Fig. 1). Similar to these findings, a previous study confirmed that functional diversity and environmental variations combined explained 90.4% of the total variation in forest ecosystem functioning in tropical forests (Ying et al., 2022). The reality on the ground showed that maximum plant height reflected in larger trees is highly threatened by human activities for logging, coffee management and conversion to agricultural lands. Farmers are managing their coffee farm land by removing larger trees to minimize shade effects, which affect their coffee seed production. Therefore, the influence of disturbance on functional diversity has an influence on community composition and function in the YCFBR.

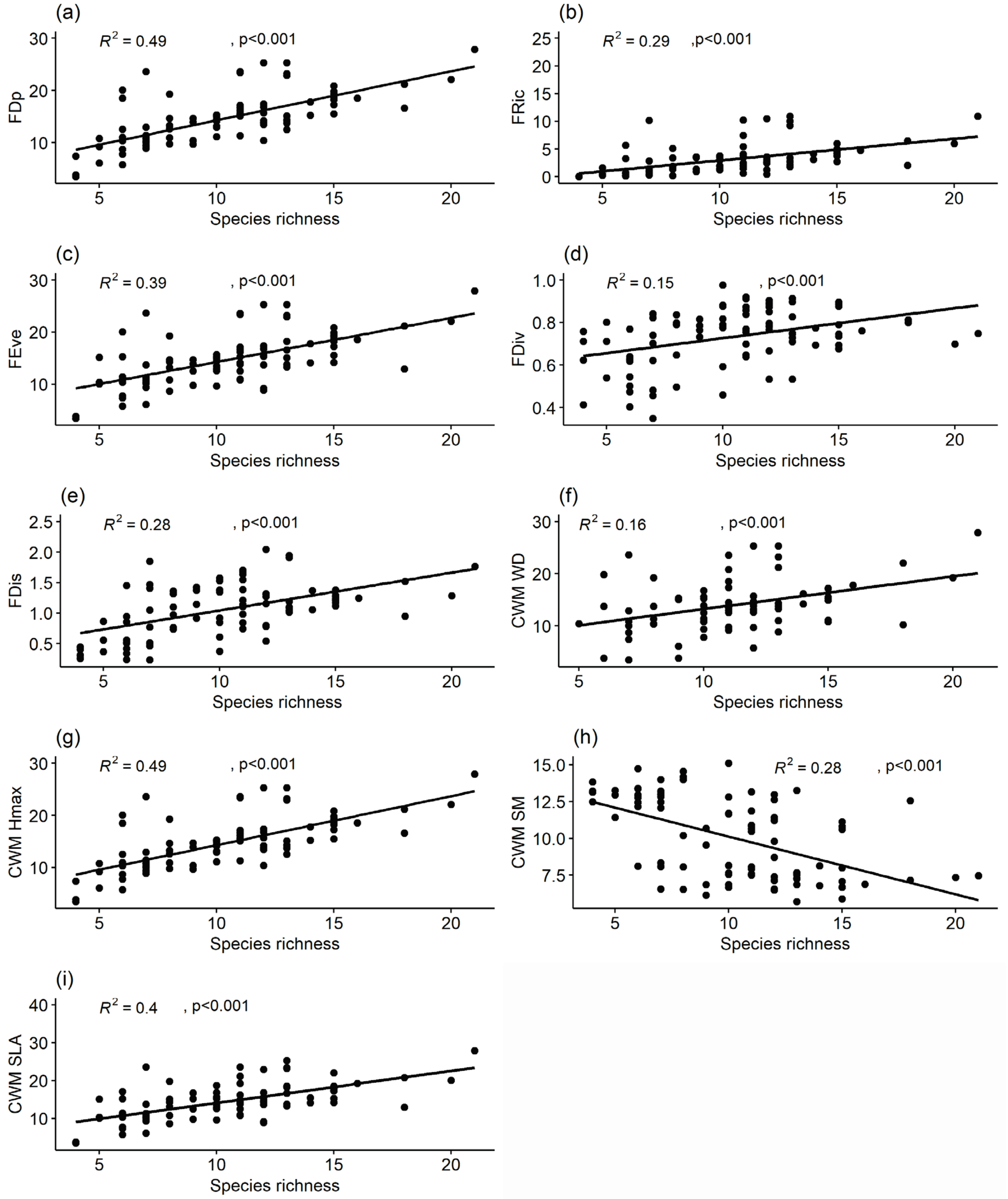

Fig. 4. Relationships of functional diversity and functional dominance indices with species richness in the YCFBR, Southwest Ethiopia: FDp – functional diversity plot-based dendrogram; FEve – functional evenness; FRic – functional richness; FDiv – functional divergence; FDis – functional dispersion; CWM WD – community-weighted mean of wood density (g/cm^3); CWM SLA – community-weighted mean of specific leaf area (cm^2/g); CWM Hmax – community-weighted mean of maximum heights (m); CWM SM – community-weighted mean of seed mass (g); species richness (number of individual tree species per hectare)

Effects of environmental factors on functional diversity. Hmax, SLA, WD and SM are particularly sensitive to anthropogenic disturbance and the whole plant functional ecosystem process (Singh, 2021). In line with this, results indicated that SM has an increasing pattern as disturbance levels increase because large seeds often developed in nutrient-poor environments and survive stressful environmental conditions and the same was true for SLA, Hmax and WD traits. Since specific leaf area is a measure of leaf thickness and can be related to factors such as resource acquisition and light absorption, an increase in CWM.SLA could indicate a shift towards species with thinner leaves, which may have implications for nutrient and water use efficiency (Moles et al., 2011) because, tropical forests experience significant disturbances, as described by Behera et al. (2023). Functional diversity can increase with elevation due to the presence of unique or specialized species adapted to the particular environmental conditions found, which is in agreement with the previous study (Zhang et al., 2015).

Results from the mixed effects model demonstrated that aspect and disturbance had significant effects on all functional diversity indices. Also, as illustrated by Mensaha et al. (2020), functional diversity is closely related to environmental variables such as aspect and elevation, which is consistent with the current findings. Therefore, disturbance and aspect were important factors influencing functional diversity indices in the YCFBR. This implies that those functional diversity indices that have positive relationships with environmental factors can enhance species diversity, whereas those indices that have negative relationships with environmental factors can negatively influence species diversity. Therefore, it is crucial to choose tree species that survive, and adapt in disturbed ecosystems for conservation, and rehabilitation of degraded environments, such as the transitional zone of YCFBR. Also, a recent study showed decreasing patterns of functional diversity, which are driven by the combined effects of local environmental factors (Paula et al., 2023). As already highlighted in the previous findings, monitoring functional diversity is important to gauge the severity of disturbances, and the state of a community (Kong et al., 2023). This implied that different components of functional diversity have different effects on different ecosystem characteristics, and minimizing anthropogenic disturbance to maintain a healthy ecosystem is important in the area. This is because high functional diversity is important for ecological resiliency in the face of global change, which is in agreement with Whitfeld et al. (2014). Overall, the study highlights the importance of considering both anthropogenic factors and environmental variables in understanding biodiversity and ecosystem functioning in heterogeneous environments. Therefore, anthropogenic disturbance and elevation gradients were found to be the major factors influencing functional diversity in the YCFBR because they were correlated with each other.

Functional diversity and species diversity relationships. All the functional diversity indices increased as species richness and diversity increased, which indicated that their relationship is direct but non-linear, which is consistent with the previous studies (Biswas et al., 2011; Mengistu et al., 2020). The non-linear relations between functional diversity and species diversity proved that functional diversity can provide special information that is different from species diversity. Supporting the interpretation of these results, we found that higher species richness, Shannon Weiner diversity and evenness indexes were also associated with higher functional diversity indices for FDp, FRic, Feve, FDiv, FDis and CWM.Hmax, which is in agreement with the previous findings (Arruda et al., 2018; Guy et al., 2021). The consistent pattern was also reported in several previous findings (Bongers, 2012; Lelli et al., 2019). The variation in species abundance and distribution can be mainly explained through species diversity, whereas functional diversity can be explained more through species morphology, physiology, reproduction, ecology, and phenology (Lueder et al., 2022). Previous findings pointed out (Mensaha et al., 2020) that different functions will likely be maximized by functionally different species, and consequently, diverse mixtures would provide combinations that maximize multiple functions. Functional diversity and species richness are interrelated, which is consistent with the previous findings (Zhang et al., 2017; Zhang et al., 2021). Therefore, functional diversity and species diversity can be used as indicators of forest composition, structure, functioning, forest ecosystem process and inner environment, which is supported by the previous findings (Laliberte et al., 2010; Kong et al., 2023).

In contrast, there are possible explanations why functional diversity for CWM.SLA and CWM.SM may decrease with species richness; these are due to biogeographic filtering and complementarity effects (Mayfield et al., 2010; Ruksan & Munoz, 2018). As more species are added to a community, the available niche space may become increasingly filled, leading to greater competition among species for resources. This can result in a shift towards species with similar functional traits that are better adapted to the available environmental conditions, and a decrease in functional diversity overall. Similarly, while functional diversity may initially increase with species richness as new functional traits are added to the community, there may be a point where additional species are redundant in terms of their functional contribution. This would lead to diminishing returns in terms of functional diversity and a leveling off or decrease in functional diversity as species richness increases (Mensah et al., 2018). These results suggest that taxonomic diversity patterns are not easily identifiable at a local scale and are less responsive to topographical variation than functional and structural diversity measures; thus, this study used trait-based diversity measurement. The functional diversity approach can be used to support environmental assessment, restoration, and conservation planning of forest ecosystem services (Kritish et al., 2023), because species diversity alone cannot foresee the risk of losing functional traits needed to monitor ecosystem health (Biswas et al., 2023). Overall, this study suggests that different functional diversity components capture different aspects of community diversity and multiple measures are necessary to fully quantify functional diversity.

Conclusions

Plant characteristics related to competitive ability, resource exploitation, regeneration capacity, and stress resistance are suggested to be excellent indicators of the impact of disturbance and environmental factors on species and functional diversity. Species and functional diversity vary due to disturbances and environmental heterogeneity. According to these findings, CWM.WD, CWM.SM, and CWM.SLA are less affected in disturbed forest sites, which suggests that these indices may serve as indicators of ecosystem resilience in disturbed forest sites. In contrast, FDis and Hmax are the functional traits most vulnerable to anthropogenic factors and have less tolerance in disturbed ecosystem environments.

In summary, our study showed that the functional diversity of plant communities in the YCFBR is significantly influenced by human disturbance, with some functional traits being more vulnerable than others. The results highlight the importance of conservation measures to maintain functional diversity in the face of increasing anthropogenic pressure. Only by protecting intact ecosystems and restoring degraded areas can we ensure the provision of ecosystem services that are critical for human well-being and the sustainability of the planet. Further research is encouraged in the area to apply zonation-based livelihoodsassessments to suit the unique needs of each forest zone and promote sustainable forest management practices.

Ferede Abuye Jeldu, Motuma Tolera and Teshale Woldeamanuel conceived the presented idea and developed the theory and analytical methodologies. Ferede Abuye Jeldu also planned and carried out the data collection and analysis. All authors substantially contributed to a discussion of methodologies and results. Ferede Abuye Jeldu wrote the first draft and received substantial contributions from other authors. The authors read and approved the final manuscript.

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