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Environment differentially affects the functional and phylogenetic structures of plant communities in a dry evergreen Afromontane tropical forest

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Abstract

Testing how local environmental conditions influence plant community assembly is important to understand the underlying mechanisms that promote and/or maintain biodiversity. Functional traits are used to find the broad spectrum of resource use strategies that plants use to respond to environmental variation. The patterns and drivers of plant community assembly through the lens of traits and phylogeny; however, remain to be studied in a uniquely biodiversity rich but poorly known fragmented dry Afromontane forest of Ethiopia. Here, we combined trait and community phylogenetic data from thirty sampling plots of 20 × 20 m size to determine the functional and phylogenetic structures and their drivers in a fragmented, human-dominated dry evergreen Afromontane forest. We found phylogenetic and functional clustering of plants in which the effect of environment was found to be trait specific. A weak phylogenetic signal for traits was detected suggesting that species resource use strategies may not be inferred using species phylogenetic distance. Additionally, we found functional traits to be weak in predicting species abundance distribution. Overall, while this study shows a non-random community assembly pattern, it also highlights the importance of deterministic processes being trait specific.

Abstract in Amharic is available with online material.

KEYWORDS
community assembly, ecological drivers, Ethiopia, functional traits, phylogenetic diversity, species abundance, trait diversity

1 | INTRODUCTION

Globally, tropical forests are centers of high species diversity (Giam et al., 2011). However, anthropogenically driven environmental change has mainly been responsible for the decline of tropical forests (Corlett, 2016). The East African Afromontane and Horn of Africa region where Ethiopia is at the center, have been identified as global biodiversity hotspots due to their high endemism and growing biodiversity threats (CEPF, 2016; Mittermeier et al., 2004). Economically driven anthropogenic activities such as agriculture, grazing, and firewood extraction, have largely threatened the forest biodiversity of the region. The climate and topography of the region have driven the establishment of diverse vegetation types ranging from tropical Afroalpine vegetation in the mountains to arid and semi-arid vegetation in the lowlands (Asefa et al., 2020). The dry evergreen Afromontane forest in which this study was conducted is one of the vegetation types that are heavily disturbed resulting in small patches of fragmented forests. Habitat fragmentation can change plant community composition and diversity through edge effects thereby affecting the soil physical and chemical properties (Ruwanza, 2019). Disturbance was found to greatly influence the soil physical and chemical properties of Ethiopian fragmented forests (Cardelús et al., 2020) suggesting that the fragmentation history of our study region in this regard has left heterogeneous soil nutrient availability that could influence the functional and phylogenetic distribution of plants. It is, therefore, crucial to test whether soil nutrient-based species selection has consequences for the functional, phylogenetic and abundance distribution patterns of plants in the fragmented forest.

Trait-based approach have been widely used to explain species co-occurrence patterns, as traits are used to capture the response of plants to environmental change (Valladares et al., 2007). Therefore, trait distributions may be used to determine the relative importance of ecological drivers for plant distribution. In this regard, it is not known how the ecological drivers shape trait distributions in a fragmented dry Afromontane forest of Ethiopia. Particularly, whether soil nutrient-based habitat requirements of plants as environmental filtering provides insight into the effect of forest fragmentation on plant trait distributions has not been investigated. The environment can select some species with similar trait values causing trait clustering or species with contrasting trait values leading to trait overdispersion. Some of the trait distributions could also be phylogenetically conserved leading to a non-random accumulation of closely related species (phylogenetic clustering). Mixed results have been reported in this regard depending on environmental conditions. Functional and phylogenetic clustering was indicated in tropical forests reflecting the co-occurrence of species with similar trait values and evolutionarily related species (Viana & Dalling, 2022; Yang et al., 2014). Overdispersion of traits such as specific leaf area, under fertile soil conditions has also been reported, suggesting functional divergence (Libalah et al., 2017). Spasojevic and Suding (2012) also indicated trait overdispersion both at low and high soil nutrients. This discrepancy could be associated with multiple factors. Differences in spatial scale, species identity, study systems, climate types, and environmental conditions among studies might be accounted for the observed inconsistent results (Swenson et al., 2012). This suggests the importance of conducting further studies on various forest and climate types, particularly in disturbed fragmented Afromontane forests, to find the general patterns and underlying mechanisms. Of course, it is important to note that accurately quantifying and inferring ecological drivers from ecological patterns has been challenging (Mayfield & Levine, 2010).

Testing how species evolutionary history contributes to species co-existence is also essential to understand how evolution shapes plant resource use strategies. While this has been tested in undisturbed and/or less disturbed forest ecosystems worldwide (Kraft & Ackerly, 2010; Swenson et al., 2012), the role of species evolutionary history in structuring local communities in a highly disturbed and fragmented forest remains to be studied. Prinzing et al. (2021) reported that species resource requirements have not been contingent on their phylogenetic relationships in highly disturbed habitats suggesting that disturbance may cause phylogeny to play no and/or less role for local species co-occurrence. While traits have been used to determine plant response to environmental factors, phylogenetically closed species may have similar trait values leading to trait-phylogeny correlation. As a result, phylogenetic relatedness has been used as a proxy for the ecological strategies of species (de Bello et al., 2015). Although phylogenetic niche conservatism has been proposed to make inferences about the proxy of phylogeny for the resource requirement of species (Cooper et al., 2010), it has been rarely tested in a fragmented dry Afromontane forest. Closely related species are expected to be similar in their ecological requirements compared to phylogenetically distantly related species (Swenson et al., 2007; Webb et al., 2002). Previous studies have shown that there might be contrasting patterns between phylogenetic and functional dispersion even under significant phylogenetic signal (Swenson & Enquist, 2009). This suggests that functional convergence and divergence of the species may not necessarily be inferred using only phylogenetic distance as a proxy (Swenson, 2013). While phylogenetic information is important in understanding the role of species evolutionary histories for species co-occurrence under variable environments, combining it with multiple functional traits provides crucial evidence on trait-environment relationships through the lens of species phylogeny.

While functional traits are used to predict plant responses to environmental change (Visakorpi et al., 2023), to what extent changes in plant abundance are predicted by functional traits is less known, particularly in the context of forest disturbance. Hence, understanding. trait–abundance relationships in the context of forest disturbance is crucial to predict the effect of environmental change on plant abundance. The evidence generated on trait–abundance relationships has primarily come from either relatively stable forest ecosystems (Yan et al., 2013) or other disturbed/undisturbed non-forest systems (Cingolani et al., 2007; Mouillot et al., 2007). A better understanding of how disturbance influence the ability of traits in determining species abundance distribution in fragmented forests is, therefore, required. Since functional traits can be linked to species fitness (Violle et al., 2007), the abundance of a species in a given environment is determined by its adaptive capacity and resource use strategy. Species abilities to adapt to variable environmental conditions coupled with their abilities to co-occur with others through niche-differentiation determine their distribution in a given environment (Weiher et al., 1998). That means species with certain traits are more favored by the environment than other species with less favored traits causing plants to vary in their abundance distribution. Therefore, testing whether plant functional strategies can predict plant abundance distributions is crucial to understand how environmental change influences species performance by changing plant resource use strategies.

In this study, we combined trait, phylogenetic, and abundance data to investigate the patterns and drivers of plant communities at the local scale by asking the following questions: (i). How are plant communities functionally and phylogenetically structured in this human-dominated fragmented forest? (ii) Are functional traits phylogenetically conserved showing similar ecological strategies between closely related species? (iii) Do soil nutrients act as an environmental filter to shape trait and phylogenetic structures? (iv) Are trait distributions related to species abundances? We hypothesized that soil nutrient-based environmental filtering would play a key role in the non-random trait and phylogenetic distribution patterns of plants with the trait-mediated response of species abundance distributions to a disturbance in this fragmented forest.

2 | METHODS

2.1 | Study area

We carried out this study in Kulkual Ber Forest, Central Gondar Administrative Zone, Amhara National Regional State, northwest Ethiopia located between 12°18′29″–12°18′35″ N and 37°36′01″–37°36′02″ E (Figure S1). The altitude of the study site ranges from 2000 to 2300 m above sea level. It is one of the remnants of the dry evergreen Afromontane vegetations of the country that are largely characterized by a human-dominated landscape (Cardelús et al., 2017). The study area is climatically characterized by unimodal rainfall pattern with a high amount of rainfall in the rainy season and a low amount of rainfall in the dry season. The meteorological data taken from 2009 to 2018 showed that the study area has a mean annual rainfall and temperature of, respectively, 876 mm and 21°C with a mean minimum of 12°C to a mean maximum of 31°C (National Meteorological Service Agency, 2018). The soil of the study area is mostly shallow and sand-dominated with low organic matter content.

The study area is characterized by the dry evergreen Afromontane forest which covers most of the Ethiopian highlands with mountainous topography. *Juniperus procera*, *Podocarpus falcatus*, *Olea europaea* subsp. *cuspidata*, and Eucalyptus species dominate this forest type (Friis et al., 2010). While this forest type is biologically the richest ecosystem following the Acacia-Commiphora woodland, it is located within the human-dominated landscape. Agriculture, overgrazing, and plantations have been the historical drivers resulting in the small and isolated forest fragments in the northern and northwestern parts of the country (Asefa et al., 2020). This suggests that the structure and function of plant communities in this forest is primarily the result of human-led fragmentation effects. In 1994, the Amhara Regional Government designated these fragmented forests as state forests and priority forest areas to prevent them from further fragmentation (Abere et al., 2017).

2.2 | Sampling method

We collected vegetation, functional traits, and environmental data using systematic sampling. Eight parallel transect lines were systematically laid down along the slope gradient. Sampling plots of 20 × 20 m size were established along these transect lines to collect the data. While the distance interval between transects was 100 m, the distance interval between consecutive plots was also 100 m. A total of thirty 20 × 20 m plots were used in which all standing woody plant species with a diameter at breast height (DBH) ≥2 cm was recorded, measured, and identified. The abundance of each species in each sampling plot was also counted.

2.3 | Functional traits measurement

We measured four functional traits that are expected to reflect plant growth and resource use strategies: leaf area (LA, cm^2), specific leaf area (SLA, $cm^2\,g^{-1}$), leaf dry matter content (LDMC, $g\,g^{-1}$), and leaf thickness (LT, mm). These traits are part of the leaf economics spectrum that can reflect species ecological trade-offs (Wright et al., 2004). Differences in leaf area reflect an ecological trade-off between energy capture and leaf temperature (Swenson & Enquist, 2009). SLA reflects a trade-off between the life span and construction costs of the leaf (Wright et al., 2004). LDMC is related to mechanical damage, herbivory, and leaf decomposition and leaf lifespan. Leaf thickness is related to the defense ability and physical strength of the leaf (Mendes et al., 2001).

We measured these functional traits based on the protocol of Pérez-Harguindeguy et al. (2013). We selected five healthy adult individuals for each species. Three to five intact fully expanded fresh leaves were collected from each individual. All the collected leaves were sun exposed and free from any obvious herbivore and pathogen attacks and physical damage. Leaves were collected from the top of the plants for understory plant species. For rare species, we collected trait data outside the plots. To analyze interspecific differences among species, species mean trait values were obtained by taking the average trait values of individuals of each species. LA was measured using Area Meter (AM 300 ADC Bioscientific Ltd.). SLA was calculated as leaf area divided by the dry mass. Leaf dry matter content was calculated as leaf fresh mass divided by leaf dry mass. Leaf thickness was measured at the center of the leaf lamina by avoiding major leaf veins using a stainless caliper. We dried leaves in an oven at 60°C for 72 h.

2.4 | Soil nutrients measurement

We used soil nutrients for our analyses as environmental factors. A standardized protocol for soil nutrient analyses was used. Soil samples were collected at the center and corner of each sampling plot and become composited. After removing humus and litter, we took a 500 g topsoil at a depth of 20 cm from each sampling plot. We collected soil from the center and corners of a plot and mixed them in the plastic bag. We replicated this three time within each plot. A total of 90 soil samples were taken from the 30 plots for nutrient analyses. We put the fresh soil samples in the pre-labeled plastic bags and transported to the Soil Chemistry Laboratory of Amhara Design and Supervision Works Enterprise. We used the oven drying method to estimate soil moisture content. Immediately after collection, soil sub-samples were dried at 60°C in the oven to constant weight. We then estimated the soil moisture content by subtracting the weight of oven dry soil from the fresh weight of moist soil and dividing this by the weight of oven dry soil. We used a soil pH meter to measure the soil pH (Shanghai Precision and Scientific Instrument Corporation).

We used the Kjeldahl digestion method to estimate total nitrogen, total phosphorus, and total potassium. The soil samples were digested, distilled, and titrated with different chemicals and catalysts, depending on the estimated nutrient type, to effectively quantify the amount of nutrients in the soil samples. In general, to estimate total nitrogen, phosphorus, and potassium, we used the standard Kjeldahl digestion method with the 2.5 g of catalyst/salt mixture of sodium sulphate copper sulphate in 5 mL sulfuric acid (Amin & Flowers, 2004).

2.5 | Community phylogeny construction

We used the newly updated megatree with calibrated branch lengths to construct our own community phylogenetic tree for the 42 species we found (Jin & Qian, 2022). We checked and standardized species names for accuracy based on The Plant List (TPL, http://www.theplantlist.org). We used the package "V. PhyloMaker2" with scenario 3 to produce a phylogenetic tree of our species. The V. PhyloMaker2 takes the species in our list to match with the most resolved position in the megatree. The generated tree was calibrated using BLADJ thereby the branch lengths corresponded to the phylogenetic distance between species.

2.6 | Functional and phylogenetic community structures

We used a null model to determine whether the observed functional and phylogenetic structures of plants are different from expected by chance. This model randomly shuffles species names across the tips of phylogeny and trait dendrogram 999 times to randomize species phylogenetic and functional relationships. The 999 values are null distributions from which standardized effect sizes are calculated. We computed the observed and null phylogenetic and functional dispersion patterns of plant communities. For the ease of direct comparison with phylogenetic dispersion, we constructed a trait dendrogram for each functional trait separately and for all traits together. We estimated the functional dispersion of multiple traits using a trait dendrogram which was constructed from the Euclidean distance matrix of the four functional traits and hierarchical clustering (Swenson, 2014). We then calculated the abundance weighted functional and phylogenetic dispersion patterns of each plot community from, respectively, the trait dendrogram and phylogenetic tree using two widely used metrices: the mean pairwise distance index (MPD) and the mean nearest taxon distance index (MNTD). While these two measures are used to evaluate whether the functional and phylogenetic communities are non-randomly structured, they are different in their sensitivity to phylogenetic depth. The MPD and MNTD indices are, respectively, the basal and terminal metrices that are sensitive to the deep phylogenetic structures and structures near the tips of the phylogenetic tree (Webb, 2000). While the MPD is a standardized effect size (S.E.S.) of the observed mean pairwise phylogenetic/functional distance (MPD) of all species in a community, MNTD is a S.E.S of the observed mean nearest neighbor phylogenetic/functional distance between species in a community. We measured phylogenetic and functional dispersions using these two metrics and termed SES PW for pairwise phylogenetic/functional dispersion and SES NN for nearest neighbor phylogenetic/functional dispersion using the following formula:

$$\text{SES PW} = \frac{\text{MPD}_{\text{obs}} - \text{mean}\left(\text{MPD}_{\text{null}}\right)}{\text{SD}\left(\text{MPD}_{\text{null}}\right)}$$

$$\text{SES. NN} = \frac{\text{MNTD}_{\text{obs}} - \text{mean}\left(\text{MNTD}_{\text{null}}\right)}{\text{SD}\left(\text{MNTD}_{\text{null}}\right)}$$

where, MPD is the mean pairwise functional distance between all species in a community, whereas MNTD is the mean nearest neighbor functional distance between species in a community. The mean(MPD_{null}) and mean($\text{MNTD}_{\text{null}}$) represent the mean values from a null distribution of the communities. The SD(MPD_{null}) and SD($\text{MNTD}_{\text{null}}$) represent the standard deviations of the null distribution. We used one sample *t*-tests to determine whether the observed SES PW and SES. NN are significantly deviated from random expectations (zero).

2.7 | Phylogenetic signal of functional traits

We quantified the phylogenetic signal in the four functional traits to determine whether phylogenetic distance can be used as a proxy for species functional distance. We used Blomberg *K* to test the phylogenetic signal in traits (Blomberg et al., 2003). We randomized the trait data on the tips of the phylogeny 999 times to generate random *K* values to which the observed data was compared whether it significantly deviated. Under a Brownian motion model of trait evolution, *K* values <1 indicate less phylogenetic signal of trait evolution on the phylogeny, whereas *K* values >1 indicate that related species show higher trait similarity than that expected from Brownian motion. We used the function and package "phyloSignal" in R.4.1.3.

2.8 | Data analysis

Soil moisture, soil pH, soil total nitrogen, soil total phosphorus, soil potassium, and topographic slope were used as environmental predictors. To reduce environmental dimensionality, we applied principal component analysis using "dudi.pca" function in ade4 package on these environmental variables and retained two axes that explained 59.8% of the variation. The first axis was associated with soil pH, total phosphorus, and total potassium, whereas the second axis was associated with soil moisture, total nitrogen, total phosphorus, and slope (Table S2). We used these two axes for our analyses.

The first and second aims of this paper were to examine how the local plant communities are functionally and phylogenetically structured and whether soil characteristics drive the change in functional and phylogenetic community structures across environmental gradients. We used a linear model to regress mean pairwise and nearest neighbor phylogenetic and functional dispersion patterns (SES-MPD and SES-MNTD for both traits and phylogeny) against environmental axes. The model was fitted separately for each functional trait. The third aim was to test whether functional traits were able to predict species abundance distribution. We first calculated abundance weighted community trait values for each study plot using the function "functcomp" in FD package. We then used a linear model with species abundance as a response variable while community weighted traits as predictors. Also, we analyzed how environmental factors influence species abundance distribution by regressing species abundance against environmental factors. Before analyses, all traits and environmental data were log-transformed and Z-scaled for data normality and ease of comparison. All the analyses were carried out using R 4.1.3 (R Core Team, 2022).

3 | RESULTS

3.1 | Functional and phylogenetic structures

A total of 42 species that represent 26 plant families and 40 genera were recorded (Table S1). Fabaceae (eight species), Oleaceae (three species), and Asteraceae (three species) were the plant families with the highest number of species. Most of the remaining plant families were represented by a single species. The species abundance curve showed *Dodonaea angustifolia*, *Rhus vulgaris*, *Calpurnia aurea*, *Olea europea* subsp. *cuspidata*, and *Maytenus arbutifolia* as the most common species in the study plots (Figure 1). The number of species observed in each plot ranges from 5 to 19 with a mean of 10.6.

We used pairwise and nearest neighbor metrics to compute functional and phylogenetic dispersion patterns. In general, we found non-random functional and phylogenetic structures in our study plot. Phylogenetic clustering was detected for mean pairwise phylogenetic distance (Figure 2), whereas the mean nearest neighbor phylogenetic dispersion was not significantly different from a null random distribution under the Brownian motion of trait evolution (Figure S2).

While most traits showed significant mean pairwise functional clustering except leaf thickness which was not different from random distribution, leaf area however was found to be overdispersed. The analysis of all traits together also showed significant mean pairwise functional clustering (Figure 2). Similarly, we found trait clustering of the mean nearest neighbor species for all traits together and for other most individual traits, except for leaf area and leaf thickness which were not different from null expectations (Figure S2).

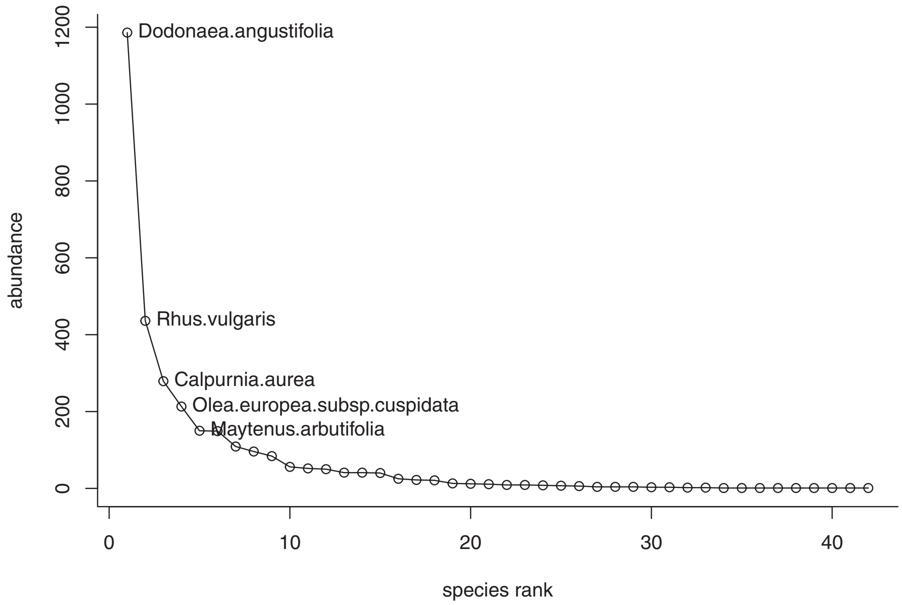

FIGURE 1 Abundance-based species rank in the study area. Few species are common while many of them are rare.

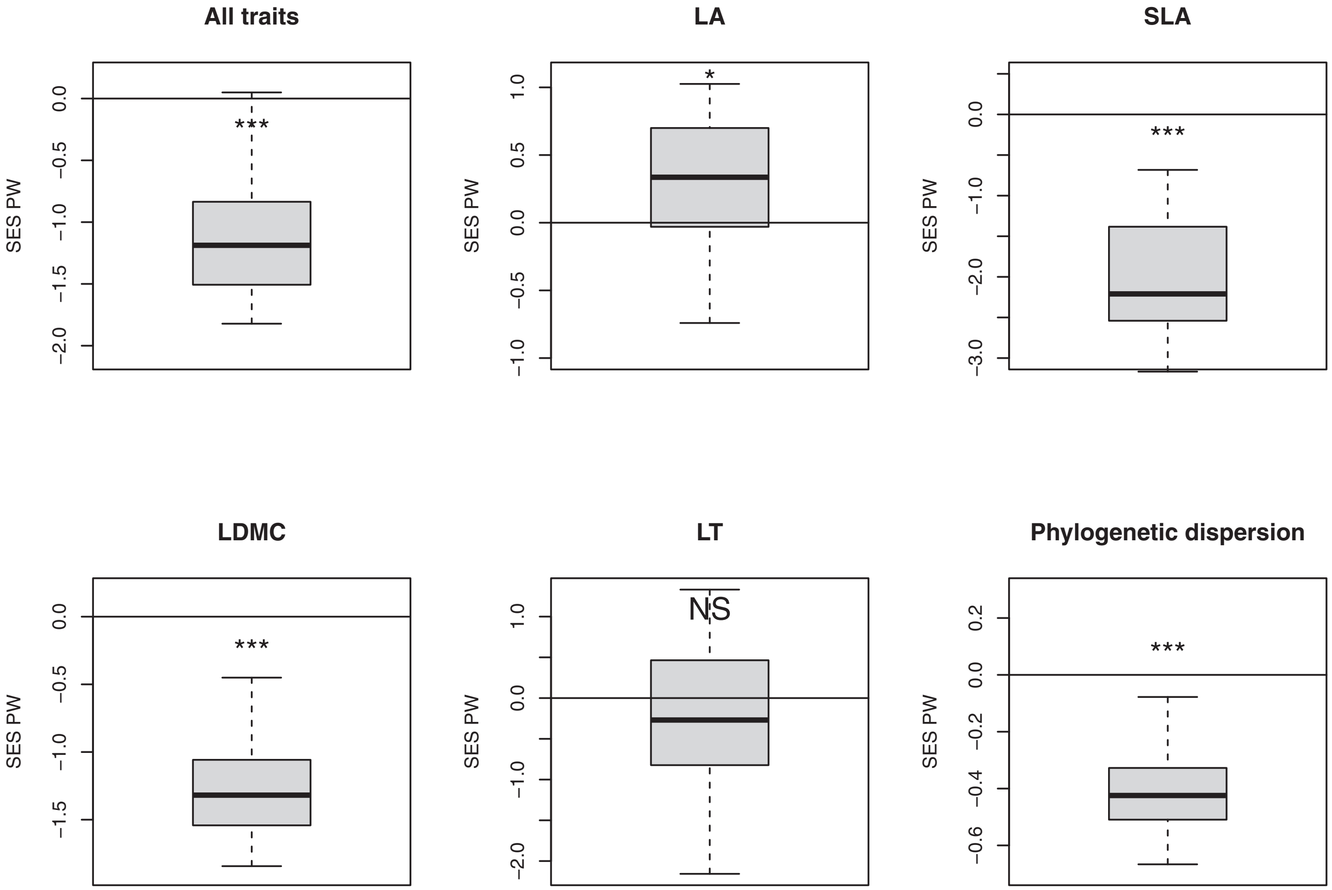

FIGURE 2 Mean pairwise trait and phylogenetic dispersion patterns (standardized effect sizes, SES). Error bars indicate a 95% confidence interval. Asterisks indicate significant deviation from zero based on a one-sample *t*-test. Error bars below zero line show trait and phylogenetic convergence (clustering) while above the zero line show trait and phylogenetic divergence (overdispersion). NS, not significant. ***$p < .001$; **$p < .01$; *$p < .05$.

TABLE 1 Summary of environmental factors measured in the study area.

Environmental factors	Minimum	Maximum	Mean	Standard deviation
TN ($g\,kg^{-1}$)	0.23	0.5	0.353	0.083
TP ($g\,kg^{-1}$)	0.00088	0.00454	0.0019	0.00098
TK ($g\,kg^{-1}$)	0.0163	0.0698	0.03954	0.014
pH	5.84	6.48	6.17	0.163
Soil moisture (%)	31.92	59.74	42.62	7.2
Slope (degree)	2	20	8	6.08
Elevation (m)	2034	2728	2258.8	100.22

3.2 | Effects of environmental factors on functional and phylogenetic structures

We expected soil nutrients to be highly variable across sampling plots given the disturbance history of the study area. However, given this study being conducted at the local scale, we found the sampling plots less heterogeneous in their soil nutrient properties (Table 1). We mapped the distribution of soil nutrients across sampling plots (Figure S3).

We tested the effects of environmental factors on the functional and phylogenetic structures of woody species. The effects of environmental factors on the mean pairwise functional dispersion of plants varied among traits. The functional dispersion of SLA and LDMC was significantly associated with the first environmental axis (Axis 1). Other functional traits, however, individually or in combination, did not show significant relations with environmental factors (Figure 3). Similarly, we found a non-significant association of mean pairwise phylogenetic dispersion with environmental factors.

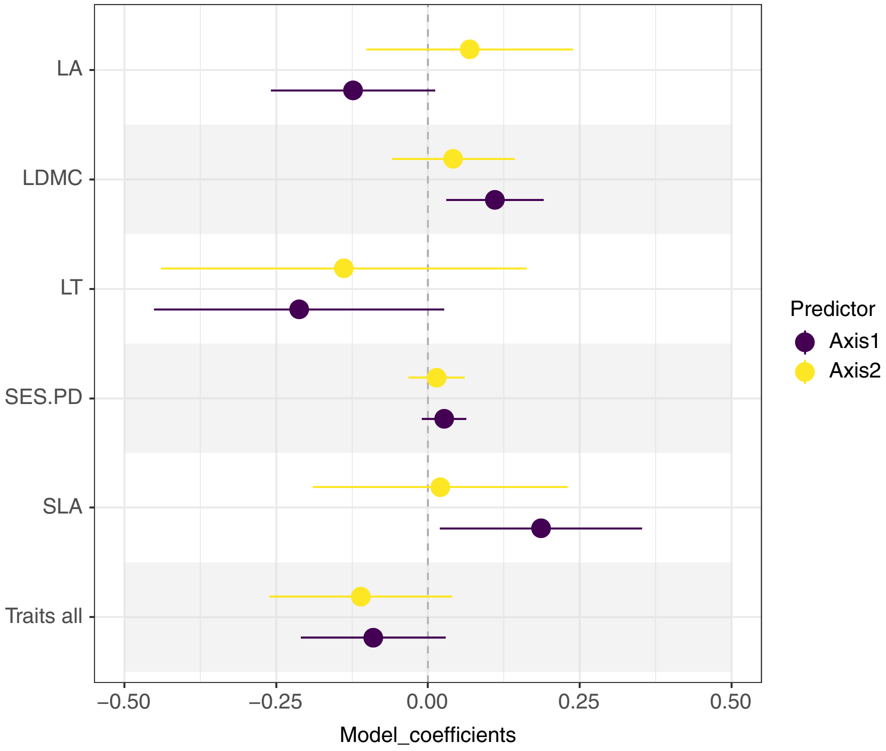

FIGURE 3 Standardized regression coefficients modeling effects of environmental factors on the mean pairwise trait and phylogenetic dispersion patterns. Circles indicate medians for each studied parameter and lines indicate 95% confidence intervals derived from the linear models.

TABLE 2 Phylogenetic signal of functional traits tested using Blomberg *K* for the 42 plant species.

Traits	Number of species	*K*
LA	42	0.405^{ns}
SLA	42	0.314^{ns}
LDMC	42	0.320^{ns}
LT	42	0.286^{ns}

Abbreviations: LA, leaf area; SLA, specific leaf area; LDMC, leaf dry matter content; LT, leaf thickness; ns, not significant.

Also, we analyzed the relationships of mean nearest neighbor functional and phylogenetic dispersion with environmental factors. Except for the significant negative association of LT with the first environmental axis (Axis 1), all traits and phylogenetic dispersion did not significantly relate to environmental factors (Figure S4).

3.3 | Phylogenetic signal of functional traits

We have tested whether phylogenetic relatedness among species predicts trait similarity in our plots. All traits showed weak phylogenetic signal with *K* values ranging from 0.286 for LT to 0.405 for LA (Table 2). *K* values are <1 for all functional traits showing that trait values were more dissimilar among closely related species than expected by chance under the Brownian motion of trait evolution.

3.4 | Effects of traits on species abundance

We quantified whether functional traits can predict species abundance distribution in our plot. Traits were found to be weak in predicting plant abundance. All traits showed non-significant negative relationships with species abundance (Figure 4). Also, environmental factors were found to non-significantly affect species abundance (Table S3).

4 | DISCUSSION

Plants change their ecological strategies in response to environmental change. Although this study was conducted at the local scale, we still found differences in the soil physical and chemical characteristics in the study plots. How this environmental variation influences the functional strategies and evolutionary relationships of plants in a poorly studied dry Afromontane forest is, therefore, essential to understanding the effect of disturbance on plant community assembly patterns. This study in general investigated plant community patterns and drivers through the lens of phylogeny and traits in a tropical dry evergreen Afromontane forest. We specifically tested how the phylogenetic and functional structures of plants are assembled and what drives the assemblages in one of the fragmented forests of northern Ethiopia. We found phylogenetically and functionally clustered plant communities suggesting co-occurrence of functionally and phylogenetically similar species. The role of environmental factors for plant functional structures was found to be trait specific. We discuss this in detail below.

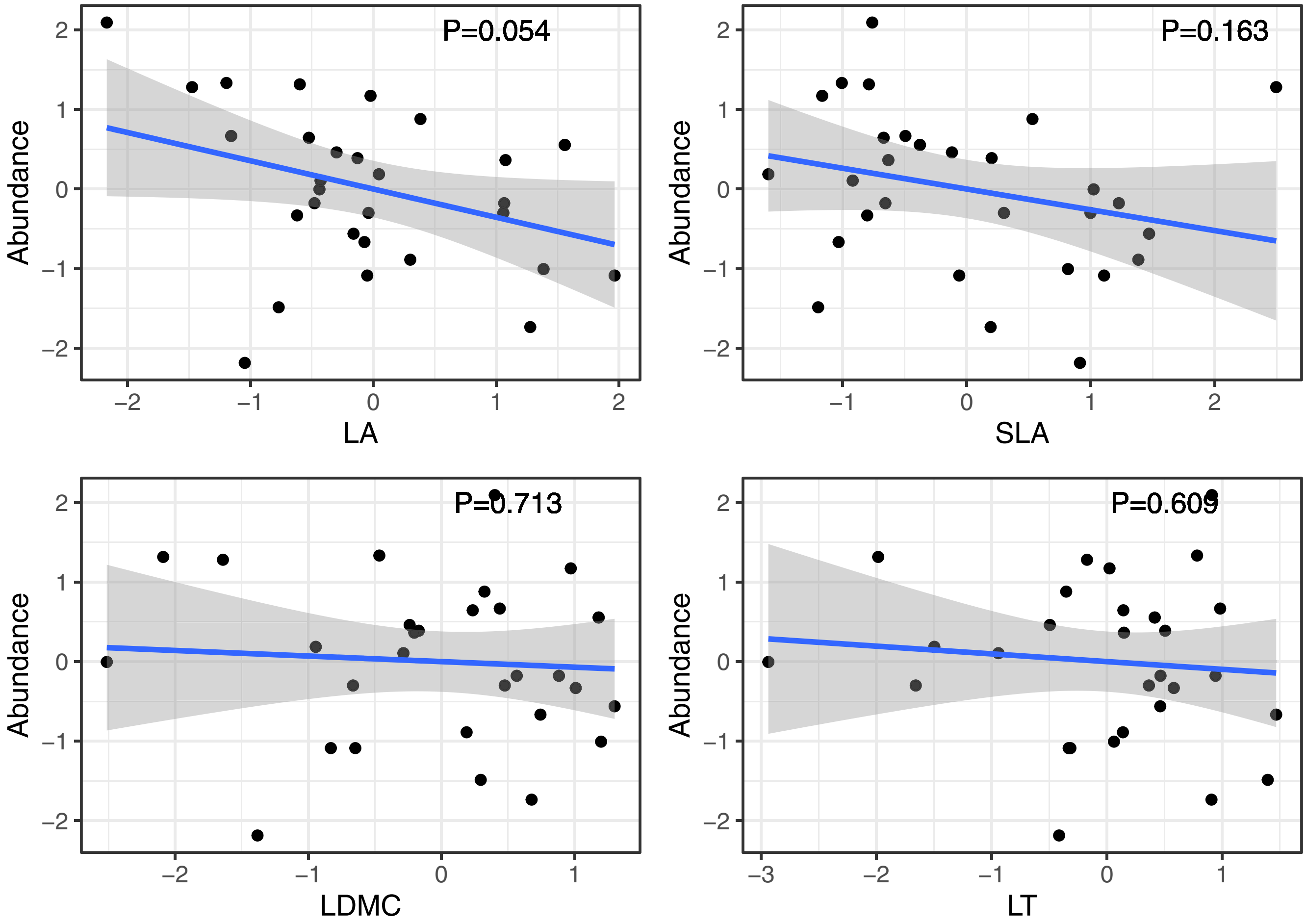

FIGURE 4 Results of linear models showing the effects of functional traits on species abundance. The shaded regions show a 95% confidence interval of the models.

4.1 | Functional and phylogenetic structures

We tested how phylogenetic and functional structures of plant communities are distributed in a dry Afromontane forest. The results demonstrated that plant assemblages are both functionally and phylogenetically clustered suggesting co-occurrence of functionally and closely related species, that is, species with similar resource use strategies and phylogenetically closely related species could co-exist in a local environment, as Zhang et al. (2020) also reported functional and phylogenetic clustering in a Chinese subtropical forest. Our study area is one of the remnants of fragmented dry evergreen Afromontane forests in which environmental conditions are being heavily influenced (Cardelús et al., 2020). The northern highlands of Ethiopia are uniquely known for heavy forest fragmentation that left many small forest patches in which biodiversity loss is widely common (Aerts et al., 2016; Muluneh et al., 2021). Consistent with our prediction, this disturbance history of the region has therefore selected species with certain traits that can adapt to the changing environmental conditions leading to co-occurrence of plants with similar trait values. *Juniperus procera*, *Podocarpus falcatus*, *Olea europaea subsp. Cuspidata*, *Croton macrostachyus*, and Eucalyptus have been identified as the most common plant species that are adapted to this disturbed forest ecosystem (Friis et al., 2010). Similarly, in other study systems, disturbance history played a significant role for the functional and phylogenetic structures of plants, as it was found to cause communities to support plants with more similar traits and closely related species compared to the undisturbed environment (Cavender-Bares & Reich, 2012; Ding et al., 2012; Yang et al., 2014). The results highlighted that disturbance may filter out plant communities to be functionally more similar in the environment.

We also found phylogenetic clustering indicating similar ecological requirements of closely related species. This result confirmed the phylogenetic niche conservatism hypothesis that closely related species could have similar resource use strategies (Losos, 2008). To complement our result, we tested the phylogenetic signal of traits to reveal whether phylogenetic distance can be used as a proxy for functional distance. Although it was not strong, the result of phylogenetic signal analysis further showed a phylogenetic signal of traits indicating clustered trait distribution among closely related species. Similarly, phylogenetic distance among species was used to predict the functional strategies of species in a tropical forest (Yang et al., 2014). Prolonged dry environments with limited water availability can considerably affect plant hydraulic functions, and some lineages that are not able to adapt to such environments might be filtered out. Other species that are able to tolerate and adapt to this environment may dominate the area causing an assemblage of closely related species. Consistently, phylogenetic clustering was found in environmentally stressful conditions (Fine & Kembel, 2011; González-Caro et al., 2014). Degraded environmental conditions, particularly soil moisture limitation, characterize our study area that can greatly filter species that are not able to tolerate and adapt to the conditions. Our study in general showed the detection of non-random phylogenetic and functional patterns in a tropical dry evergreen Afromontane forest, and perhaps the phylogenetical and functional clustering of plant assemblages in our plot suggests that disturbance history may not leave plant communities to randomly assemble in a fragmented environment.

We have also examined whether soil nutrients and soil moisture were act as an environmental filter to shape the phylogenetic and functional structures of plants. While modern coexistence theories were proposed to explain community assembly patterns, successfully identifying the underlying mechanisms for the observed non-random community assembly patterns; however, is challenging (Mayfield & Levine, 2010), as multiple biotic and abiotic drivers are involved in shaping the patterns. The development of sophisticated statistical methods, however, has been found to be crucial in quantifying the patterns and estimating the relative contribution of ecological drivers. We related the observed trait and phylogenetic dispersion patterns with soil properties to assess whether soil nutrients as an environmental filter contribute to the observed non-random dispersion pattern, as other previous studies did (Asefa et al., 2017; Yang et al., 2014). Therefore, partially consistent with Zhang et al. (2020), we found evidence for the soil nutrient-based deterministic process that drives the functional but not the phylogenetic structure of plant communities in our plot. While the effect of the abiotic environment on phylogenetic dispersion was not significant, functional traits were specific in their response to environmental factors. Environmental factors accounted for the functional clustering of SLA and LDMC, whereas the responses of other functional traits were not significant suggesting trait specific effect of abiotic conditions. The detection of plants with high SLA and LDMC may reflect multiple resource use strategies. According to the leaf economics spectrum, a given environment is expected to favor plants to have either resource acquisitive traits or resource conservative traits but not both (Wright et al., 2004). However, plants may have a range of functional strategies that cannot be captured using a single resource use axis (Kramer-Walter et al., 2016). Multiple physiological and anatomical functional traits are required at the whole plant level to better understand plant functional responses to environmental change. Trait-specific response to environmental change has also previously been reported that many functional traits may not show similar responses to environmental conditions (Morel-Journel et al., 2020; Weemstra et al., 2021). Being similar in functional clustering does not necessarily mean that all traits should respond similarly to an environmental driver, as each trait has the potential to capture the various plant life history strategies. A single environmental factor may not be responsible for the clustering of multiple functional traits that have multiple ecological functions in the ecosystem. The absence of a significant effect of environment on the functional clustering of all traits together may explain this discrepancy. The various ecological strategies of plants could be captured by different functional traits showing the absence of a similar response of multiple traits to a single ecological driver (Kramer-Walter et al., 2016). Therefore, our result highlights that a single ecological driving mechanism may not be responsible for the variation of multiple traits suggesting the presence of multiple sources of trait variation.

4.2 | Phylogenetic signal of functional traits

We quantified the phylogenetic signal of four functional traits for 42 plant species in a fragmented dry evergreen Afromontane forest in Ethiopia. All functional traits showed weak phylogenetic signal indicating that functional similarity among species may not be inferred using species evolutionary relationships (Figure S5 shows phylogenetic relationships among species). This result in combination with the result of our functional clustering signifies that the trait clustering we observed was not strongly associated with species phylogenetic distance. Instead, regardless of phylogenetic relatedness, the clustering was mainly based on similar ecological requirements. Disturbed environments often select species with certain traits that can tolerate the harsh environmental conditions causing trait convergence among co-occurring species highlighting that closely related lineages may not be favored under disturbed environments. Prinzing et al. (2021) also found low phylogenetic signal of traits in more disturbed habitats highlighting that habitat disturbance may reduce the role of phylogeny for local species co-occurrence. More similar results were also reported that trait similarity was not strongly associated with species phylogenetic distance (Zhang et al., 2020). Our finding, however, is in contrast with other previous studies that showed the proxy of species phylogenetic distance for similar resource use strategies (Cadotte et al., 2013; Swenson et al., 2007). This inconsistency could be related to studying forest types, species identity, location, and other factors. In summary, unlike other previous studies (Swenson et al., 2007; Yang et al., 2014), our result, therefore, revealed that evolutionary relationships among species may not be used to make robust inferences about the ecological requirement of plants in a fragmented dry Afromontane forest.

4.3 | Effects of traits on species abundance

Linking plant ecological strategies with plant abundance is important to understand how the environment determines plant performance by favoring plants with certain traits to be abundantly distributed. Plant functional strategies were indicated to greatly influence plant performance, especially at the local scale (Lisner et al., 2021). We examined the consequence of trait distributions on species abundance distribution at a local scale in a fragmented forest. We predicted that since the disturbance history of the forest would greatly alter the microenvironmental conditions of the study area, the most abundant species are expected to be conservative in their resource use (have low SLA and LA but high LDMC and leaf thickness).

In general, we found functional traits to play a limited role in determining the abundance distribution of plants. As expected, LA (marginally significant) and SLA have shown negative relationships with species abundance in our plot which is consistent with Lisner et al. (2021) report of the negative association between SLA and species abundance. The negative relationship of species abundance with SLA could suggest that high plant abundance might be linked to the predominance of species with low resource acquisition strategy thereby plants with better adaptive capacity and low resource turnover might be common in fragmented forests. While some previous studies have shown similar results to our finding (Yan et al., 2013), others also showed contrasting results on trait-abundance relationships (Janečková et al., 2017). Differences in species identity, vegetation types, biotic and abiotic filters are potentially the sources for the mixing results we observed among studies. It was indicated that traits measured in different vegetation types were not found to respond similarly showing that the environmental conditions coupled with the species identity may differentially operate species abundance and their functional strategies (Thakur et al., 2023). Additionally, a spatial scale can also determine the role of functional traits to influence species abundance, as different traits were found to be important in predicting species abundance at different spatial scales (Mokany & Roxburgh, 2010). While our result showed that traits were found to be weak in predicting species abundance distribution, further study is required perhaps at the intraspecific level of trait–abundance relations with more physiological traits included, as the present study is at the species level, whether this is the general pattern and/or to identify the ecological mechanisms behind the relationships.

Our study investigated how local environmental change shapes plant community assembly in this uniquely fragmented but poorly studied dry Afromontane forest.

This local study generally revealed the soil nutrient-mediated effect of disturbance on plant community assembly through the lens of traits and phylogeny in a fragmented dry evergreen Afromontane forest. It enhances our understanding of how plants are functionally adapted to a fragmented forest patch and help predict future plant responses to environmental change.

Gathering evidence at the local scale, especially in a poorly studied region that uniquely supports high biodiversity, may contribute to the global effort to understand how forest biodiversity responds to environmental change. In this regard, we highlighted how the region with unique biogeographic history may influence plant responses to changing environmental conditions, as previous studies at different biogeographic regions with their histories similarly showed the impact of environmental change on the observed biodiversity patterns (Page & Shanker, 2018; Silva-Souza & Souza, 2020). Given the little understanding of global environmental change on forest biodiversity especially through the lens of forest fragmentation, maximizing the global collections of studies from regions with different biogeographic histories is, therefore, important to generate biogeographic-based evidence to broadly understand biodiversity maintaining mechanisms in the context of global change.

AUTHOR CONTRIBUTIONS

Eshete Kassaw and Mengesha Asefa conceived the idea and designed the study; Eshete Kassaw collected the data; Eshete Kassaw and Mengesha Asefa analyzed the data; Eshete Kassaw and Mengesha Asefa wrote the manuscript. All authors substantially contributed to the manuscript and provided final approval for the publication.

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CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.djh9w0w5r (Kassaw et al., 2023).

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SUPPORTING INFORMATION

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