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LINKING PROCESS TO PATTERN IN COMMUNITY ASSEMBLY IN DRY EVERGREEN AFROMONTANE FOREST OF HARARGHE HIGHLAND, SOUTHEAST ETHIOPIA

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Abstract.

Many scholars have attempted to identify the role of deterministic and stochastic processes in community assembly, but there is no consensus on which processes dominate and at what spatial scales they occur. To shed light on this issue, we tested two non-exclusive processes, scale-dependent hypotheses: (i) that limiting similarity dominates on small spatial scales; and (ii) that environmental filtering does so on a large scale. To achieve this, we studied the functional patterns of dry evergreen Afromontane forest communities along elevation gradients in southeastern Ethiopia using floristic and functional trait data from fifty-four 0.04 ha plots. We found evidence of functional overdispersion on small spatial scales, and functional clustering on large spatial scales. The observed clustering pattern, consistent with an environmental filtering process, was most evident when environmental differences between a pair of plots were maximized. To strengthen the link between the observed community functioning pattern and the underlying process of environmental filtering, we demonstrated differences in the topographical factors of the most abundant species found at lower and higher elevations and examined whether their abundance varied over time or changed with time along the elevation. We found (i) that the largest functional differences in the community (observed between lower and upper dry evergreen Afromontane forest assemblages) were primarily the result of strong topographical influence; and (ii) that the abundance of such species varied along the elevation gradient. Variation in stand structure and tree species diversity within the DAF plots shows that topography is among the important drivers of local species distribution and hence the maintenance of tree diversity in dry Afromontane forest.

Our results support the conclusion that environmental filtering at large spatial scales is the primary mechanism for community merging, since functional grouping pattern was associated with species similarities in topographic variation, ultimately leading to changes in species abundances along the gradient. There was also evidence of competitive exclusion at more homogeneous and smaller spatial scales, where plant species compete effectively for resources.

Key words: Limiting similarity; environmental filtering; functional traits; spatial scale; non-metric dimensional scaling.

Introduction

Determining the processes behind patterns of species richness and community composition variation is a key challenge in ecology due to the variety of natural systems and mechanisms that can be at play simultaneously (Chave 2008; Kraft et al. 2010). The neutral process and deterministic process are the two main assembly processes proposed to detect the patterns of species diversity and distributions at the community level (Diamond 1975). The neutral process emphasizes the great importance of random genetic drift of species rather than the influence of the environment (Chase 2014). In contrast, the deterministic process (niche-based process) deems that the pattern of which and how many species live in a community is closely related to the abiotic and biotic environment, and may change along the environmental gradients (Cornwell and Ackerly 2010). Previous studies considered that neutral and deterministic processes in conjunction lead to community assembly (Kraft et al. 2008; Swenson and Enquist 2009), while deterministic process is the main process during assembly (Purschke et al. 2013; Yang et al. 2014). Limiting similarity and environmental filtering are two contrary niche-based mechanisms occur simultaneously along various environmental axes during deterministic assembly even within a single community, and influence the community structure (Kraft et al. 2008; Cornwell and Ackerly 2010). In general, limiting similarity means excluding similar species of coexisting species, while environmental filtering should select highly similar species among coexisting species that share similar habitat conditions (Di´az and Cabido 2001; Andersen et al. 2012 and Kraft et al. 2015). Nevertheless, it is still a major challenge for ecologists about understanding what and how environment factors drive balance of these processes (Mayfield and Levine 2010; Luo et al. 2016).

To achieve mechanistic insight into community assembly processes along environmental gradients, functional ecology has emerged as a more powerful and suitable tool than classical taxonomic approaches based on Linnaean binomials, because indices of species composition and

abundances provide little information about the ecological strategies of those species (Fukami et al. 2005, Swenson 2012; Cornwell and Ackerly 2015; Funk et al. 2017). Instead, the functional approach is based on the functional traits of species, which are easily measurable morphological or physiological characteristics of individuals relevant to growth, survival, or reproduction (Lavorel and Garnier 2002; Funk et al. 2017) as proxies of ecological performance and, consequently, capable of explaining how species interact with their abiotic and biotic environment (Wright et al. 2001; McGill et al. 2006; Donovan et al. 2011; Kraft et al. 2015). Some recent studies have shown that abiotic factors such as topographical factors (e.g., elevation, slope, aspect etc.) are important environmental filters of species with similar functional traits ((Sargent and Ackerly 2008; Jiang et al. 2018; Mengistu Teshome et al. 2020). In this regard, functional traits play a major role in understanding plant ecological strategies related to resource acquisition, regeneration potential or shade tolerance (Westoby et al. 2002; Chave et al. 2009; Hulshof et al. 2013) along environmental gradients (Mcgill et al. 2006; Hulshof and Swenson 2010; Hulshof et al. 2013). In functional ecology framework, environmental filtering has been recognized as a primary pressure shaping groups throughout some of biomes, which includes drylands (Le Bagousse-Pinguet et al. 2017), alpine ecosystems (de Bello et al. 2013a; Lopez-Angulo et al. 2018), temperate forests (Cornwell and Ackerly 2010) and tropical forest ecosystems (Swenson and Enquist 2009, Lebrija-Trejos et al. 2010; Baraloto et al. 2012). However, the overwhelming importance of environmental filtering in community assembly has recently been questioned due to a lack of consideration for spatial scale (Chase 2014) and uncertainty as to whether functional traits can reliably indicate mechanisms (Mayfield and Levine 2010).

The consideration of spatial scale is paramount in ecology (Levin 1992; McGill 2010), and its implications for community assembly are undeniable (Snyder and Chesson, 2004; Munkemuller et al. 2013). For example, environmental filtering appears to prevail over other processes at a broad/large spatial scale, and limits similarity (which competitive exclusion) has virtually no effect on individuals many kilometers apart, although it may have an effect on individuals in close proximity at a smaller spatial scale. However, ignoring the implications of spatial scale has often led to disagreements about which processes dominate the community assembly (Chase 2014; Chalmandrier et al. 2017). To address the issue of scale, a hierarchical model has been proposed, according to which assembly mechanisms operate sequentially at different spatial scales (Gotzenberger et al. 2012; HilleRisLambers et al. 2012). This model includes evolutionary and biogeographical processes such as historical patterns of speciation, extinction or large-scale migration; to abiotic and biotic processes such as environmental filtering or similarity limitation (competition exclusion) on smaller or local scales. Earlier processes define a regional pool of potential colonizing species whose latter operate on a local scale, producing a final assembly of local communities. Under this issues, changing the scope of the community and species pool studies allows us to clarify whether the various assembly processes are constrained to operating at specific spatial scales (Colwell and Winkler 1984; Swenson et al. 2007). For example, the environmental filter may occur more frequently when the composition of the species comes from a large area with strong abiotic heterogeneity, e.g. ecologically homogeneous area (de Bello et al. 2013b; Garzon-Lopez et al. 2014; Kraft et al. 2015).

Community patterns based on co-occurring species, diversity and abundance combined with functional diversity are generally considered to reflect different community-assembly processes (Lavorel and Garnier 2002; Funk et al. 2017). However, it is controversial to interpret them as clear signs of actual assembly processes. Traditionally, and according to the community-assembly processes mentioned above, two mutually exclusive scenarios for species co-occurrence have been proposed: (i) Species could diverge in their ecological strategies to achieve co-occurrence, thereby avoiding competitive exclusion, i.e. to consider this functional over-dispersion within the community (Silvertown 2004, Stubbs and Wilson 2004, CavenderBares et al. 2009); or (ii) species might converge in their ecological strategies to allow them to thrive in the same abiotic environment, resulting in functional grouping (Keddy 1992; Cornwell et al. 2006; Ackerly and Cornwell 2007; Kraft et al. 2015).

Our study aims to improve the understanding of community assembly by considering spatial scaling implications and avoiding over-reliance on community patterns. To achieve this, we assessed the diversity and composition of the woody plant community along elevation gradient in dry evergreen Afromontane forest of southeast Ethiopia and estimated the contribution of the different processes leading to its assembly. In this regard, we assume that, at a given spatial scale, only a single mechanism or process will have a stronger effect on the community assembly. On this premise, we posit that while limiting similarity (competitive exclusion) would operate primarily at small spatial scales where the environment is relatively homogeneous, environmental filtering would primarily emerge as a significant force that shapes community assembly on a larger scale where there is a functioning community response. Hence, we hypothesize that (i) if limiting similarity drives community assembly on small spatial scales (e.g., between neighboring individuals within a community), functional patterns would be over-dispersed compared to a null expectation, and (ii) when the environmental filter rules at larger scales (e.g. among plots hundreds of meters apart or at different elevations), functional patterns would be clustered.

Materials and Methods

Study area

The present study took place in the Dindin Dry Evergreen Afromontane Forest (DAF) of Hararghe highlands located in Southeast Ethiopia. The geographical location of the study site lies between 40°10’40” to 40°18’50” E and 8°33’0” to 8°40’40” N. The DAF is approximately 13,000 ha in area with elevation ranges between 2,124 and 3,069 m a.s.l.. Because of the lack of long-term climatic data for the study site, we used the climate estimator software tool, New LocClim to produce long-term monthly precipitation and temperature (FAO 2005; Grieser et al. 2006). The mean annual temperature (MAT) and mean annual precipitation (MAP) at the study site are estimated to be 25.6 °C and 804 mm/year, respectively. Precipitation at the study site has a bimodal distribution pattern with a long rainy season lasting from June to October and a short rainy season from April to May. The soils of the study area developed from a wide range of parent materials, including volcanic and mixed limestone and sandstone over a Precambrian basement. Leptosols are the most abundant soil type which is classified as Haplic and Lithic leptosols. Lithic leptosols covers are most extensive on high in mountainous relief hills and parallel ridges and river, gorges having very steep slopes (30-60%) (Tefera et al. 1996; Elias, 2016). According to Friis et al. (2010), the vegetation type in the study area is categorized as tropical dry evergreen Afromontane forest, which is characterized by a dry climate. Woody species such as *Afrocarpus falcatus, Maesa lanceolata, Allophylus abyssinicus,* and *Vernonia myriantha* are dominant species.

Sample design

The reconnaissance survey was conducted with the preliminary observation of physiographical distinct community composition along elevation gradient. Following the reconnaissance, the vegetation composition was assessed using a transect line approach. This is because, transect approach is considered an efficient approach to investigate the spatial patterns of species’ functional traits and their underlying mechanisms from the sites to the regional scale. It is also suggested that along the environmental gradient, a transect approach offers excellent opportunities for researchers to study the drivers of community structure and ecosystem functioning in response to environmental heterogeneity and global change (Mayor et al. 2017).

In order to obtain adequate sampling relative to the study area, fifty-four 20 m × 20 m plots for the inventory of woody species were established along the elevation gradient from 2,300 m to 2,900 m. This design was used because it is a standard sampling design for assessing the diversity and composition of tree species in tropical forests. Three 5m x 5m subplots were constructed along the diagonals of the main plot to collect shrubs. In order to provide a comprehensive representation of the entire study area, we have established four sites (points) per 200 m elevation range. The location of each site was chosen at random, while topographical factors or species composition had to be different for each plot within a 200 m range to maximize variation in environmental factors and capture variations in functional traits.

A horizontal transect line was systematically established at each sampling point. For each horizontal transect line, two sites were selected along with the tree-canopy cover, which is characterized by a closed (> 40%) and open canopy (10-40%). We visually assessed the canopy coverage (%) of individual trees and counted the number of individuals. This is because, the visual assessment of the canopy cover provides a direct and reliable assessment of the field estimation (Chiarucci et al. 2001). The plots within the same horizontal transect were 200-300 m apart, depending on local conditions (Arellano et al. 2016). We adopted this approach for two major reasons: (i) there is a minimum sampling bias as they represent all woody species of the study forest and to capture the natural variation in functional traits along elevation; (ii) the effect of area (the decrease in the area from bottom to the top of a mountain) minimized, like all forest areas included (Abiyot Berhanu et al. 2016 and Jiang et al. 2018). Therefore, this procedure gives a precise indication of species represented and is used to achieve better documentation of changes in species distribution patterns along an elevation gradient (Ermias Aynekulu et al. 2012; Arellano et al. 2016).

Field data collection

A total of 216 quadrats (162 for shrubs, and 54 for trees and lianas) were laid at sampling sites with the maximum possibility of plant species diversity. In each plot, all woody individuals (trees and shrubs) ≥ 2.5 cm diameter at breast height (DBH) rooted within the plot were identified to species in the field and measured for their diameter and height. Although for this study lianas ≥ 1 cm diameter at breast height (DBH) within the plot was also taken into an account. Stem diameter was measured with caliper and diameter tapes over bark. We measured the diameters of all stems individually for multi-stem tree species that fork below breast height. At least one specimen was collected from each taxon for identification. A total of 2297 individuals were inventoried in the study plots. Elevation and diameter were measured with a Suunto Clinometer and a Caliper, respectively. Geographical coordinates and elevation were recorded at the center of each plot using a Garmin GPS. The inclinations (in degrees) were again measured with a Suunto inclinometer.

Verification of all species names was done at the National Herbarium, Addis Ababa University, and nomenclature followed the flora of Ethiopia and Eritrea (Hedberg et al. 1997; Edwards et al. 2000). The species accumulation curve shows the relationship between the sample size and the number of species found within that plot, therefore it is important to determine the adequacy of the sampling effort (Gotelli and Colwell 2001). For the sample completeness or adequacy of the sampling effort the species-accumulation curves was plotted for the study forest (Fig. S1).

Functional trait data

Selection of traits plays an important role in determining assembly processes in communities of interest. Our selection of traits connected to the leaves, wood, and overall life form of each species covers a range of traits frequently mentioned essential to quantitatively represent several axes of woody plant functional strategy (Westoby et al. 2002). In total, we used three functional traits that are believed to represent fundamental functional trade-offs in leaves, wood, and plant height among tree species (Westoby 1998). The community weighted mean (CWM) values of traits estimated for each plot were used in this study. This is because, traits of interest are known to vary with respect to the local-scale environment, and therefore, assigning species-level means may introduce several biases and reduce the power of functional trait-based community ecology.

The three traits included maximum plant height (Hmax (m)), wood density (g/cm^3), and specific leaf area (cm^2/g). A specific leaf area (SLA) was used to represent the leaf economics spectrum (Wright, 2004). SLA is a fresh leaf area divided by dry leaf mass, and provides a measure of the allocation of biomass to light harvesting. Therefore, SLA is regarded as key traits related to resource allocation strategies (Cornelissen et al., 2003 and Pérez-Harguindeguy et al. 2013). Wood density (WD) was used to represent a wood economics spectrum (Chave et al. 2009). Therefore, SLA is regarded as key traits related to resource allocation strategies (Cornelissen et al. 2003; Chave et al. 2009; Pérez-Harguindeguy et al. 2013). Wood density (WD) was used to represent a wood economics spectrum (Chave et al. 2009). Wood density shows a tradeoff between volumetric growth and mechanical vulnerability on the tissue and organismal scale, and it is often the trait related to hydrological niche and demographic rates (Chave et al. 2009). Maximum plant height (Hmax) was used to represent the adult light niche of the species (Kohyama et al. 2003; Moles et al. 2009).

In each of the plots for all woody plants ≥ 2.5 cm in diameter at breast height (DBH), we measured DBH and height. For trees with buttresses that prevented DBH measurement at the usual height (1.30 m), the diameter was measured outside the bark immediately above the buttresses. Then we calculated maximum plant height by taking average of three tallest values for common species (100+ individuals), the tallest two for less common (50+), and the tallest observation for rare species (< 50 individuals). We followed the same procedure for obtaining the maximum DBH by taking average of largest DBH values. In case of species, which are represented by single individual, we obtained maximum attainable height from published regional flora, and online biodiversity database. Wood density (g/cm^3) data was sourced from the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009). Specific leaf area was extracted from TRY plant database (Kattege et al. 2011).

Diversity and statistical analyses

Cluster analysis

All analyzes were performed in R software (version 3.6.0). An average linkage of agglomerative hierarchical clustering was applied to cluster plots in community types using the *hclust* function. The average linkage method was chosen because of its ability to maximize cophenetic correlation between input dissimilarities and dissimilarities from the resulting dendrogram between pairs of species (Gauch et al. 1981). The optimal number of clusters was determined iteratively whilst looking for the one which best represents the community plots (Fig. S2), and was further verified with a cophenetic correlation (Kassambara 2017). A multi-response permutation procedure (MRPP) was carried out with 999 permutations to test for differences in species composition between the identified community types. Species Indicator analysis (Indval function in R) was used to determine species indicator for each community type (De Cáceres et al. 2010).

Ordination

Before ordination, all data were checked for normality and plant abundance data was Hellinger transformed. Nonmetric Multidimensional Scaling (NMDS) was used to visualize variation in plant community assembly. We used the *dimcheckMDS* function to select the best NMDS axis number ($k = 2$) based on the stress plot. Woody plants species richness, Shannon diversity, and Simpson diversity were then determined for each community type, using standard procedures (Magurran and McGill 2011). Total mean stem density (number of stems/ha) and total mean basal area (m^2/ha) of all individuals with a DBH $\geq$ 2.5 cm were computed for each community type, as the average plot level (400 m^2) of total basal area and total density across all measured plots of that community type, and then scaled up to 1 ha.

We employed the *Envfit* function in the vegan R package to evaluate the relationship between community composition, functional traits, and environmental factors (Oksanen et al. 2020). The function *Envfit* fits environmental factors onto an ordination diagram, and thereby computes the significance of the correlation between the fitted vectors and corresponding environmental variables and functional traits (Oksanen et al. 2020). We employed the *Adonis* function, a permutational multivariate analysis of variance, to test for differences in species composition among the identified communities, and to evaluate the effects of environmental gradients and functional traits on the species composition of the study forest (Oksanen et al. 2020). *Adonis* partitions dissimilarities in multivariate data for the sources of variation and uses permutation tests (999 permutations) for determining significances (Oksanen et al. 2020). The differences in species richness and diversity, functional traits, and environmental factors among the identified community types were assessed with Kruskal-Wallis tests and Dunn's post hoc tests with Bonferroni correction.

In order to evaluate the percentage of variance in community composition explained by topographic factors and functional traits, we performed variance partitioning (VARPART: Legendre 2008; Peres-Neto et al. 2005). VARPART allows identification of "pure effects" of topographic factors and functional traits, how much of the variation explained by environmental gradients is spatially structured, and how much remains unexplained (Legendre et al. 2005). We performed the Hellinger transformation on species abundances to decrease the weight of the most abundant species in the analysis (Legendre and Gallagher 2001).·

We reported adjusted R^2 values (R^2Adj) indicating the proportion of variation explained by each of the predictor matrices (Peres-Neto et al. 2006). The significance of variance fractions explained by each predictor matrix, as well as the individual and joint fractions, was tested with an analysis of variance by permutation test ($p < 0.05$, 999 permutations). Analysis variations partition was performed in in the R (R Development Core Team, 2018) with the vegan package; varpart function (Oksanen et al. 2020).

Testing community-wide trait structure

To clarify how different spatial scales can affect the relative effect of different deterministic mechanisms, observed functional trait distribution patterns and the null model were demonstrated for two hypotheses regarding spatial scale: (i) trait distribution within a subplot versus trait distribution of species between neighboring subplots of the same plot (small spatial scales), and (ii) trait distribution within a plot versus trait distribution between plots along the gradient height (large spatial scales). The deviations of the observed distribution pattern from the null expectation would indicate the existence of different deterministic processes of community formation, such as environmental filtering or competitive exclusion, while a close match between the distributions could be interpreted as evidence for stochastic community formation (Connor and Simberloff 1979).

Mean species trait values were used to calculate trait similarity patterns within the community. For both spatial scales, the scaled observed characteristic range (OTR) (highest minus lowest observed characteristic value of the species divided by the mean trait value) was calculated for each trait within each plot and subplot. In addition, we calculated the observed trait evenness (OTE) for each trait within each plot and subplot. Observed trat evenness (OTE) was defined as 1/(sdT+1) where sdT is the standard deviation of the distances between adjacent trait values. It was therefore, a measure of the evenness of the differences between adjacent co-occurring trait values, with values close to zero indicating very low evenness and a value of one indicating maximum evenness. To test whether the OTR and OTE values in the plots obtained to be higher or lower than expected, i.e. under- or over-expanded(trait range) or under- or over-dispersed (evenness of trait), we used two different null models. To study trait expansion, we performed 10,000 random draws from the species pool without replacement at each observed species richness. The species pool was defined as all species sampled in this study. The probability of drawing a given species from the species pool was proportional to the number of plots or subplots in which it occurred, to avoid false produced by over-representation of rare species with extreme trait values in random communities. From the 10,000 random draws performed at each species richness, we calculated the mean scaled random trait range (SRT). The unscaled trait residual range (ReTR) or trait expansion for each plot was defined as: ReTR = OTR - RTR, where RTR is the random trait range for random draws with the same richness as in the observed plot. Positive ReTR values indicated trait overexpansion (i.e., a higher range of traits within the community than expected by chance), while negative values indicated trait under expansion.

In the second null model, we take 10,000 random community draws under constrained conditions for each plot and subplot. From the species pool (again defined as all species observed during this study (where S is the observed plot species richness), species were selected with trait values that fell within the range of observed traits without scaling. Again, the probability of a species being responsible for the random community selected was proportional to their relative abundance in the species pool. In addition, the species with the highest and lowest trait value in each observed community were also present in the random community. In this way, we constructed new random communities in which species richness and trait range remained the same as in observed communities, while spacing of trait values varied could change within this range. We then calculated the average trait evenness of the 10,000 random draws for each plot (Random Trait Evenness or RTE). For each plot, the unscaled Residual Trait Evenness (ReTE) or traits dispersion was calculated using the formula ReTE = OTE - RTE. Thus, positive values of ReTE indicated overdispersion of the trait (i.e., higher evenness of the trait within the community than expected by chance), while negative values indicated under-dispersion of the trait.

Finally, a Wilcoxon signed-rank test was used to test for overall significance of trait expansion and dispersion across plots and subplots. All calculations and the construction of null models were performed with R software version 3.6.0 (R Development Core Team, 2018).

RESULTS

Community composition

A total of 72 woody plant species representing 42 families were identified (Table S1). Myrsinaceae (34.4%), Podocarpaceae (14.9%), Simaroubaceae (8.2%), Sapindaceae (7.3%), and Cuperessaceae (6.5%) were the most represented families, whereas most of the remaining families were represented by one species. Trees accounted for 69.41%, tree/shrub for 5.97%, shrubs for 12.03%, and lianas for 12.51% of the total forest survey. The overall mean

Table 1 Mean values of species richness, diversity, functional traits, and environmental gradients in the three identified plant communities, DAF of Hararghe highland, Southeast Ethiopia. Community 1, 2, and 3 are represented by 13, 28, and 13 plots, respectively. S, species richness; H', Shannon wiener diversity index; E, Evenness. Letters (a, b) in the superscript indicate the statistical significance of differences among communities following a Kruskal-Wallis pairwise test. '***'$p < 0.001$; '**' $p < 0.01$ '*' $p < 0.05$. S, species richness; H, Shannon wiener diversity; E, Evenness.

Environmental and vegetation gradients	Kruskal Wallis statistics ($\chi2$ and *P*-values)	*A. falcatus-T. nobilis* (1)	*M. melanophloeos-M. lanceolata* (2)	*O. europaea-J. Excelsa* (3)
S	$\chi2$=6.03*	$(11.2\pm3.53)^{a}$	$(9.7\pm2.69)^{ab}$	$(8.4\pm2.10)^{b}$
H'	$\chi2$=7.34*	$(2.003\pm0.36)^{a}$	$(1.856\pm0.34)^{ab}$	$(1.630\pm0.26)^{b}$
E	$\chi2$=5.32	$(0.84\pm0.07)^{a}$	$(0.83\pm0.07)^{ab}$	$(0.77\pm0.09)^{b}$
Elevation (m)	$\chi2$=18.13***	$(2480.8\pm116)^{b}$	$(2686.7\pm88.7)^{a}$	$(2866.9\pm95.4)^{a}$
Slope (%)	$\chi2$=0.61	$(27.2\pm17)^{a}$	$(32.4\pm24.5)^{a}$	$(33.5\pm21.9)^{a}$
Aspect (degrees)	$\chi2$ =8.82*	$(215.3\pm136)^{a}$	$(250.4\pm107.4)^{a}$	$(97.9\pm128)^{b}$

(±se) species richness, Shannon wiener diversity, and evenness per plot were 9.7±2.9, 1.837±0.35, and 0.82±0.08, respectively (Table 1).

Community classification and ordination

NMDS coupled with cluster analysis resulted in three distinct plant communities (Fig. 2, Fig. S3). The goodness of fit between the ordination and the observed dissimilarities at k = 2 was very high (non-metric fit $R^2 = 0.985$; Fig S4) indicating a good representation of the vegetation data by the ordination diagram. Furthermore, the MRPP confirmed a significant difference ($d = 0.227$, $p = 0.001$) in species composition among the three identified community types. The homogeneity within communities was 0.230, which indicates more homogenous communities than would be expected by random. In addition, the multivariate analysis of variance indicated that the community types differed significantly (F = 13.95, $p = 0.001$) in their species composition. Further analysis with Kruskal-Wallis tests showed significant differences in species richness ($\chi2 = 27.78$, $p < 0.001$), Shannon Wiener diversity ($\chi2 = 38.05$, $p < 0.001$), and Evenness ($\chi2 = 31.11$, $p < 0.001$) among the community types. Dunn's post hoc test significantly differentiated species richness and diversity between the three identified plant communities (Table 1).

Afrocarpus falcatus-Teclea nobilis community (1)

Afrocarpus falcatus-Teclea nobilis community (1) found at an average elevation of 2480 m a.s.l. In our dataset, it consisted of 40 woody species with an average plot level species richness of 11.2±3.53, Shannon wiener diversity of 2.003±0.36, and Evenness of 0.84±0.07. A total of 7 indicator species were identified, of which *Afrocarpus falcatus* (indicator value (*indval)*=0.54, $P < 0.05$) and *Teclea nobilis* (*indval*=0.52, $P < 0.01$) were considered community identifiers (Table S2). The most abundant plant species and widespread in the community was *Afrocarpus falcatus* (14.9%) followed by *Brucea antidysenterica* (7%). Trees with the highest average DBH were *Juniperus Excelsa* (28 cm) and *Croton macrostachyus* (26.9 cm). *Afrocarpus falcatus*, *Teclea nobilis*, *Myrsine melanophloeos*, *Brucea antidysenterica* and *Maesa lanceolata* were both abundant and widespread in the community, and about 25% of the occurring species were distinctive to this community. The community showed typical vertical layering, with the emergent canopy layer mainly consisting of *Afrocarpus falcatus*, *Allophylus abyssinicus*, *Bersama abyssinica*, *Canthium oligocarpum*, *Croton macrostachyus*, *Ekebergia capensis*, *Ficus sur Forssk*, *Galiniera saxifraga*, *Hagenia abyssinica*, *Juniperus Excelsa*, *Maesa lanceolata*, *Maytenus arbutifolia*, *Myrsine melanophloeos*, *Olea capensis*, *Olea europaea*, *Prunus Africana*, *Psydrax schimperiana*, *Schefflera abyssinica* and *Schefflera volkensii*. The understory canopy consisted mainly of *Acanthus sennii*, *Allophylus macrobotrys*, *Balanites aegyptiaca*, *Brucea antidysenterica*, *Calpurnia aurea*, *Carissa spinarum*, *Clutia robusta*, *Ozoroa insignis*, *Rytigynia neglecta*, *Solanum marginatum*, *Struthiola thomsonii*, *Teclea nobilis* and *Vernonia myriantha*. The total mean (±se) stem density, basal area, and DBH of the community were 210.5±100 stems /ha, 32.5±21, and 18.8±6 cm**,** respectively (Table 3).

Myrsine melanophloeos-Maesa lanceolata community (2)

Myrsine melanophloeos-Maesa lanceolata community (2) found at an average elevation of 2686 m a.s.l. It consists about 13 plots. It also contained 44 woody species in our dataset, with an average species richness of 9.7±2.69, Shannon diversity of 1.856±0.34 and Evenness of 0.83±0.07per plot. A total of ten indicator species were identified, of which *Myrsine melanophloeos* (*indval*=0.49, $P = 0.001$) and *Maesa lanceolata* (*indval*=0.36, $P = 0.01$) were considered community identifiers (Table S2). The most abundant plant species in the community was *Myrsine melanophloeos* (21%) followed by *Afrocarpus falcatus* (16%) and *Maesa lanceolata* (11.5%). Trees with the highest average diameter were *Olea europaea* (58 cm) and *Juniperus Excelsa* (57 cm). The community showed vertical layering, with the emergent canopy layer mainly consisting of *Afrocarpus falcatus*, *Allophylus abyssinicus*, *Bersama abyssinica*, *Croton macrostachyus*, *Dombeya aethiopica*, *Ficus sur*, *Hagenia abyssinica*, *Juniperus Excelsa*, *Maesa lanceolata*, *Maytenus arbutifolia*, *Millettia ferruginea*, *Myrica salicifolia*, *Myrsine melanophloeos*, *Olea capensis*, *Olea europaea*, *Osyris quadripartite*, *Osyris wightiana*, *Psydrax schimperiana*, *Schefflera abyssinica* and *Schefflera volkensii*. The understorey canopy consisted mainly of *Brucea antidysenterica*, *Buddleja polystachya*, *Carissa spinarum*, *Clutia robusta*, *Euphorbia tirucalli*, *Lippia adoensis*, *Myrsine Africana*, *Olinia rochetiana*, *Ozoroa insignis*, *Premna schimperi*, *Rumex nervosus*, *Solanum marginatum* and *Vernonia myriantha*. The total mean (±se) cover, stem density, basal area, and DBH of the community were 279.9±140 stems/ha, 64.4±51 m^2/ha, and 26.9±12 cm, respectively (Table 3).

Olea europaea-Juniperus Excelsa community (3)

Olea europaea-Juniperus Excelsa community (3) found at an average elevation of 2866 m a.s.l. and it comprises 28 plots. It was composed of 28 woody species with average species richness, Shannon Wiener index, and Evenness of 8.4±2.10, 1.630±0.26, 0.77±0.09 per plot, respectively. A total of ten woody species diagnostic to the community were identified, of which *Olea europaea* (*indval* = 0.34, $p = 0.001$) and *Juniperus Excelsa* (*indval* = 0.23, p=0.005) were considered community identifiers (Table S2). *Dombeya aethiopica* (DBH = 52 cm) and *Juniperus Excelsa* (DBH = 42.5 cm) were the dominant trees with the highest DBH. The community showed vertical layering, with the emergent canopy layer mainly consisting of *Afrocarpus falcatu*, *Allophylus abyssinicus*, *Bersama abyssinica*, *Discopodium penninervium*, *Dombeya aethiopica*, *Galiniera saxifrage*, *Hagenia abyssinica*, *Juniperus Excelsa*, *Maesa lanceolata*, *Maytenus arbutifolia*, *Myrica salicifolia*, *Myrsine melanophloeos*, *Olea capensis*, *Olea europaea* and *Schefflera volkensii*. The understory canopy consisted mainly of *Clutia robusta*, *Euclea divinorum*, *Euphorbia tirucalli*, *Myrsine Africana*, *Ozoroa insignis*, *Rhus vulgaris*, *Rumex nervosus*, *Rytigynia neglecta*, *Struthiola thomsonii* and *Teclea nobilis*. The mean (±se) stem density, basal area, and DBH of the community were 256.1±81 stems/ha, 42.7±27 m^2/ha, and 23.01±7 m**,** respectively (Table 3).

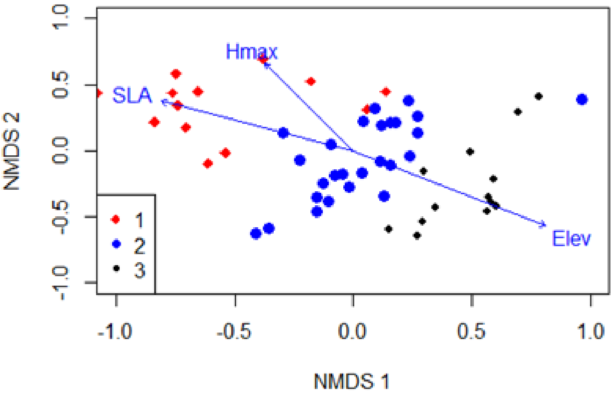


Fig. 1 NMDS ordination of 54 plots based on Bray-Curtis similarities among plots in the Dindin dry evergreen Afromontane forest, Southeast Ethiopia. The three plant communities are visualized; 1: *Afrocarpus falcatus-Teclea nobilis* (Lower elevation), 2: *Myrsine melanophloeos-Maesa lanceolata* community (Intermediate elevation), 3: *Olea europaea-Juniperus Excelsa* community (Upper elevation). *Envfit* of significantly correlated environmental variables (Elev, Elevation ($p < 0.001$); and functional traits (SLA, specific leaf area ($p < 0.01$), (Hmax, maximum plant height ($p < 0.05$).

Functional traits and topographic factors drive community composition

To evaluate the underlying environmental gradient structuring the identified community types, we overlaid the topographic variables and functional traits onto the community NMDS using the *Envfit* function. The analysis showed a significant correlation of topographic factors and functional traits with community type (Fig. 2). For instance, elevation was showed a significant effect on community composition, while slope and aspect had shown a non-significant effect on the community composition. Kruskal-Wallis tests further revealed that both environmental factors (Elev, elevation ($\chi2$= 18.13, $p < 0.001$) and functional traits (specifically, SLA ($\chi2$=23.97, $p < 0.001$), and Hmax ($\chi2$=19.66, $p < 0.001$)) were significantly different among the communities (Table 3.1). Finally, we identified the diagnostic species characterizing the three community types by using *Indval* analysis in R software, and the communities were named after the two species with the highest indicator values (Table S2).

NMDS1 was negatively correlated with SLA (r = -0.91, $p < 0.01$, Table 1) and positively correlated with elevation (r = 0.82, $p < 0.001$). NMDS2 was positively correlated with Hmax (r = 0.87, $p < 0.05$) (Table 2).

Table 2 Correlation coefficients of the two non-metric multidimensional scaling (NMDS1 and NMDS2) with environmental variables and functional traits.

Variables	NMDS1	NMDS2
Maximum plant height (Hmax)	-0.49	0.87*
Wood density (WD)	0.70	-0.72
Specific leaf area (SLA)	-0.91**	0.42
Elevation (Elev)	0.82***	-0.57
Slope	-0.01	-0.99
Aspect	-0.66	0.76

Variation partitioning of community composition by environmental variables

The VARPART (Fig. 2) showed that 20.3% of the variation of the abundance-based community composition of woody species was explained by topographic factors and functional traits. Overall, topographic factors and functional traits explained 15% and 7% of the variation, respectively (Fig. 2). However, “pure” effects of individual predictor matrices, though significant ($p < 0.001$), were smaller, with R^2adj = 0.129 and 0.052, respectively, for topography and functional trait. Shared effects between two variables were 2.2% and it was statistically significant ($p < 0.05$).

Structural attributes of forest communities

We presented the structural attributes of the forest communities in Table 3. The overall total mean (± SE) stem density, basal area, and DBH were 257.49±120.8 stems/ha, 51.50±42.8 m^2 /ha, and 24.01±10.5 cm, respectively (see Table 3). Stem density (≥ 5 cm DBH), over the gradient ranged between 210 and 279 stems/ha and showed humped pattern. We found that the highest mean stem density for community 2 (intermediate elevation) with the highest mean diameter. The highest basal area (64.4 m^2/ha) were combined with high stem densities (279.9 stem/ha) (≥ 5 cm DBH, Table 3).

The basal area of small (5-10 cm DBH) and medium (10-30 cm DBH) trees increased with elevation. A difference between the three communities was that the highest basal area in the medium trees occurred in community 3 (Table 4). However, the most important difference was that large trees with a diameter ≥ 50 cm DBH have been recorded in the community 2. A higher proportion of large trees in terms of the basal area were also found in community 2. Despite the medium proportion of large trees

Fig. 2. Variance partitioning results for predictor matrices of factors explaining variation in the species composition for trees, shrubs, and lianas in 54 plots on the study elevation gradient. Overall, adjusted R^2 was 0.203. Adjusted R^2 values, respectively, for topographic factors and functional traits are shown for each predictor matrix for the overall effect (R^2Adj = 0.15,0.07) and the “pure” effect of each matrix when controlling for the effects of all the others (R^2Adj = 0.129, 0.052).

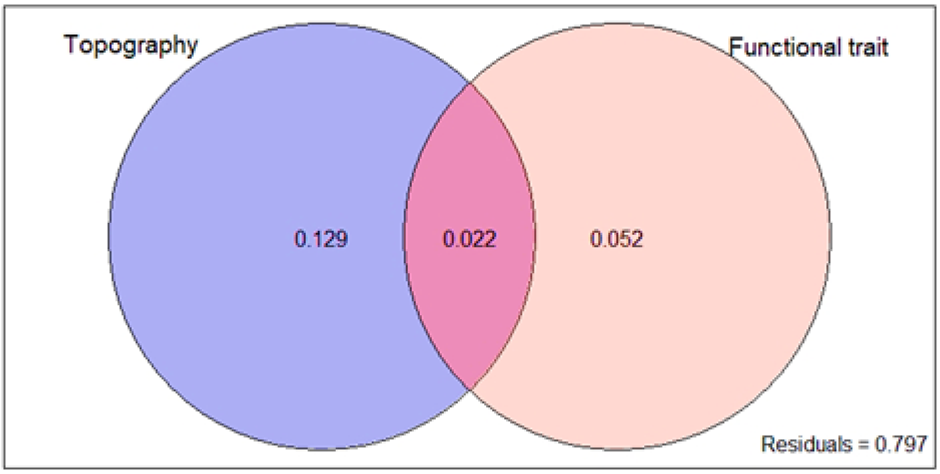


Table 3 Structural attributes of the three identified plant communities in Dindin dry evergreen Afromontane forest of Hararghe highland, southeast Ethiopia. Mean±standard error on per ha basis. n=stem number.

Community type	Stems ≥ 5 cm DBH				
	Stem density (n/ha)	Basal area (m^2/ha)	Mean DBH (cm)	Maximal Height (m)	Maximal DBH (cm)
1	210.5±10	32.5±21	18.8±6	60	152.7
2	279.9±14	64.4±51	26.9±12	60	160
3	256.1±81	42.7±27	23.01±7	45	150
Overall mean	257.49±120.8	51.50±42.8	24.01±10.5		

Table 4 Basal area (BA) of stems by diameter class distribution.

Community type	BA (m^2 /ha) per stem size class			
	> 5 cm DBH	5-10 cm DBH	10-30 cm DBH	≥ 30 cm DBH
1	0.19±0.13	0.54±0.43	7.3±4.6	25.1±20
2	0.12±0.07	0.55±0.34	7.4±3.7	57.5±50.7
3	0.12±0.09	0.64±0.54	8.9±3.94	33.3±28.7

Table 5 Stem density and stand basal area of largest trees (≥ 50 cm DBH)

Community type	Stem number	% of stems	BA (m^2)	% of BA
1	19	14.18	10.91	79.29
2	94	70.15	14.40	104.68
3	21	15.67	13.45	97.78

(14-70% of the total density), they can reach a significant proportion of the stand's basal area (up to 79-104%) (Table 5).

The relationship between stem density and basal area was positive, show the disproportionate contribution of a few long-lived and large trees. The coefficient of determination in the quadratic regression analysis between basal area and elevation showed a low variation percent; only 8.6% of the variation in the basal area is accounted for the elevation (Fig. 3).

Community assembly functional patterns

Across our fifty four sampling plots, observed SLA, Hmax and WD values had significantly higher ranges than communities from the null model. Therefore these traits were over-expanded, or, in local communities, overall greater variable (difference between lowest and highest trait value) than expected from random community assembly (Fig. 5). We found significant over-dispersion across our subplots (Fig. 4) for all trait values, indicating limiting similarity.

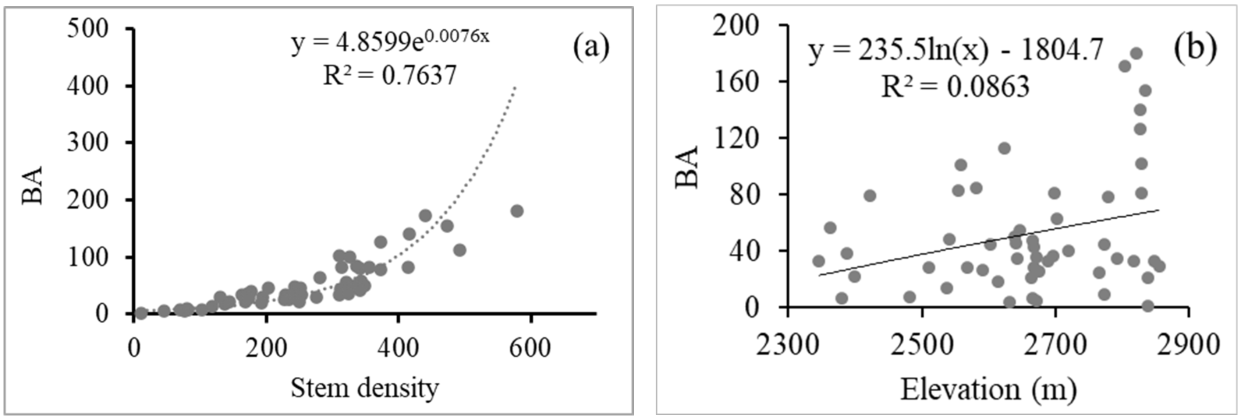


Fig. 3 (a) The relationship between basal area (BA) and stem density; (b) basal area (BA) and elevation (m).

Fig. 4. Hypothesis 1: community functional distances distribution patterns at small spatial scale (within plot). Frequency of distribution of observed (black) and null (gray) values as measured based on three functional traits (specific leaf area [SLA], left; maximum plant height [Hmax], center; wood density [WD], right) after 10,000 randomizations, in all six cases. There were significant differences (α = 0.05) between observed and null for all traits.

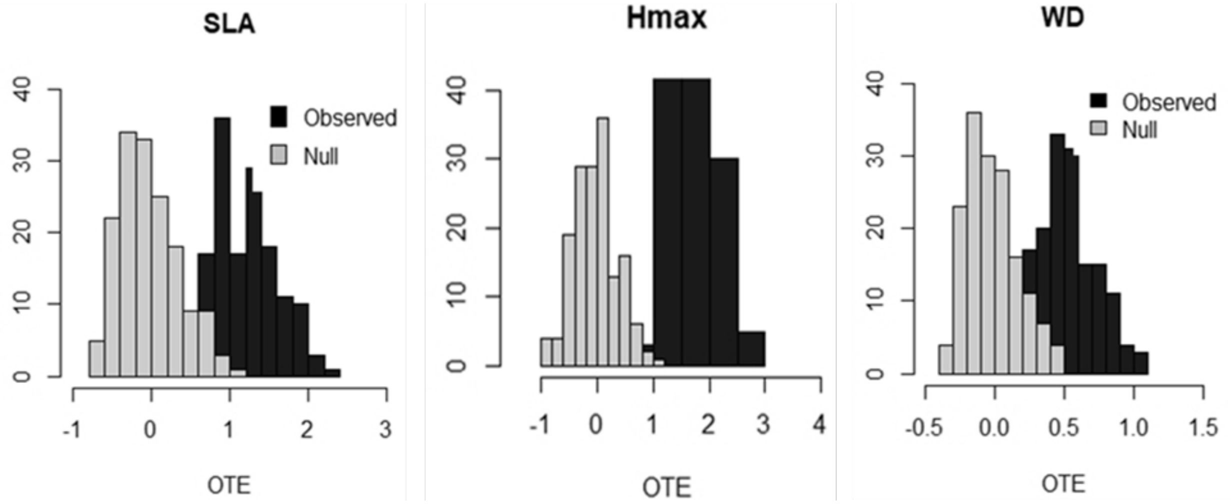
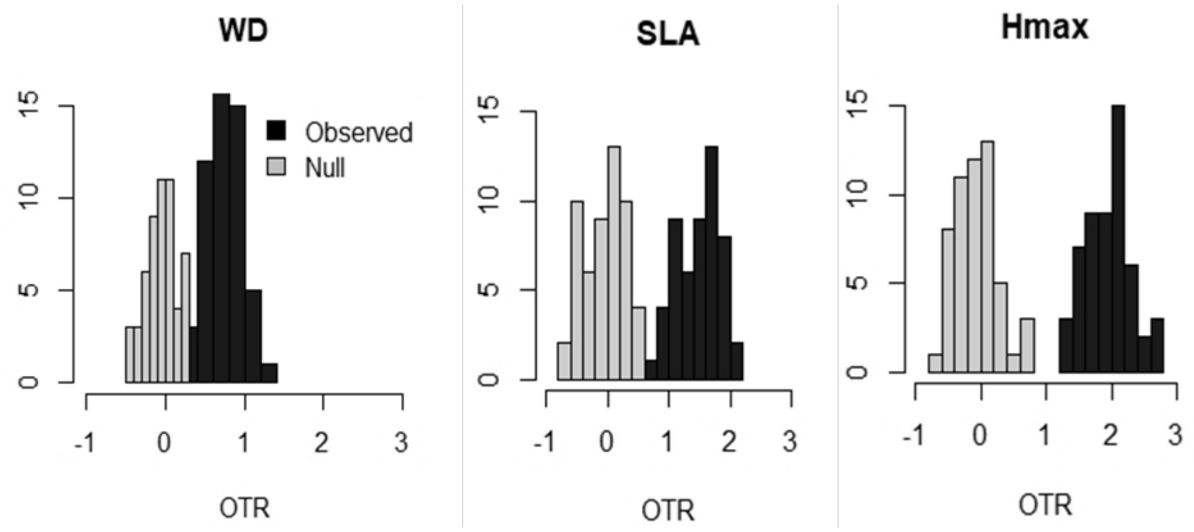


Fig. 5. Hypothesis 2: community functional distances distribution patterns at large spatial scale (among plot). Frequency of distribution of observed (black) and null (gray) values as measured based on three functional traits wood density [WD], left; (specific leaf area [SLA], center; maximum plant height [Hmax], right) after 10,000 randomizations, in all six cases. There were significant differences (α = 0.05) between observed and null for all traits.



Discussion

Our results showed that topography is an important driver for habitat differentiation, thereby determining community composition and structure, also species richness, at the local scale in dry evergreen Afromontane tropical forest ecosystems. More specifically, we found that elevation and slope were the main factors that explained habitat differentiation in the study areas and thus determined the differences in community composition. Our results support the hypothesis that topographical factors determine community composition and structure in tropical forest ecosystems (Guo et al. 2017; Ali et al. 2018; Ali et al. 2019). The observed community pattern along topographic gradients is likely related to the underlying spatial variation in resource availability, which are strongly influenced by topographical factors (Moeslund et al. 2013; Ali et al. 2019). This study shows that environmental filtering is a critical process in shaping the community in tropical forests (Liu et al. 2014), even at the local scale, indicating that species composition changes over time.

Forest structure is assessed using structural attributes such as tree diameter, height, stem density, and basal area (McElhinny et al. 2005), which are used as an alternative approach to measuring the composition of forest communities. Community structural attributes including maximum plant height and basal area differed among woody communities in the studied forest. In our analyses, maximum plant height decreased from lower to upper elevation. The increased plant height observed in lower elevation is a typical feature of the fastest growing of trees with resource acquisitive strategy, whereas the decreased height of trees from upper elevation is characteristic of plants with conservative strategies in resource use (Ackerly and Cornwell 2007; Cavender-Bares et al. 2009). These results are consistent with findings from a previous study that species distribution along topographic gradients can be strongly influenced by habitat filtering that selects attributes such as tree height and relates them to resource use, such as the light niche and colonization strategy (Liu et al. 2014; Ali et al. 2018). While these results suggest that habitat differentiation affects the distribution of many individual species, the impacts of functional strategy variation at the community level have not been extensively studied, which can be analyzed using functional traits and topographical data to examine their relative contributions to diversity and composition (Chiang et al. 2016; Ali et al. 2018).

Relationship between woody species functional strategies and distribution patterns

The definition of the plant communities based on the multivariate analysis provides important information about the species distributions and the underlying gradients that form their distribution (Tadesse Woldemariam Gole et al. 2008). We did find three distinct woody plant communities for the Dindin dry evergreen Afromontane forest on Hararghe highland of southeast Ethiopia, each containing a distinct species composition and characterized by a set of non-overlapping indicators species. Such high dissimilarity in species composition suggests inherent differences in factors that determine their assembly (Valencia et al. 2004). The result indicated that elevation and functional traits explained significant variation of the diversity and species composition of identified plant communities in the dry evergreen Afromontane forest of Hararghe highland. Elevation gradient is identified as the key environmental factor shaping species composition in the plant communities (Ordonez et al. 2009), because elevation exerts a significant influence on the temperature and moisture availability (Dyer 2009). Our result is consistent with the findings reported by (Getaneh Gebeyehu et al. 2019; Mengistu Teshome et al. 2020), reported elevation as an important factor driving the diversity and community composition in dry Afromontane forest ecosystems.

The biotic interactions could also be influential in shaping plant community diversity and composition (Warren and Bradford 2011). However, our findings showed functional traits could be as powerful drivers of diversity and composition in dry evergreen Afromontane forests as in grasslands or mesic forests (Warren and Bradford 2011; White et al. 2014). The use of plant functional traits may allow for more informative comparisons regarding gauging ecosystem integrity (Warren and Bradford 2011). These biotic interactions may covary with gradient of environment, further confounding our understanding of the true strength of the abiotic drivers of diversity and community composition. Previous studies have also pointed out that it is difficult to identify between biotic and abiotic drivers (Hettenbererova et al. 2013). The functional traits of plants mainly reflect the response of plant species diversity to changes in resource. Some studies have also proposed that Hmax, SLA, and species abundance are correlated, which is consistent with the theory of plant resource acquisition (Heino and Tolonen 2017). In our study, plant functional traits explain significant change in plant species diversity, indicates the importance of trait changes of abundant species. This is because these factors would allow for the capture of more resource material, proving beneficial for competition. For example, a species with a larger height can obtain more light resources, thereby becoming a dominant species in the community and increasing its distribution.

Species with acquisitive ecological strategies are generally associated with higher SLA, while species with conservative ones are usually related to the opposite ones (Lalibert and Legendre 2010; Pérez-Harguindeguy et al. 2013). Species with an acquisitive ecological strategy usually have a stronger competitive ability for resources and grow quickly in local resource-rich environments (Pérez-Harguindeguy et al. 2013). Our results showed that species with relatively high SLA in community 3 (upper elevation) and community 1 (lower elevation) had relatively higher local species richness, suggesting that species with a conservative ecological strategy tended to maintain more species in local areas. Other evidence has suggested that some plant ecological strategies involved starting as an acquisitive type and later becoming a conservative type as succession signs of progress (Garnier et al. 2004). In community 3, which is found at the upper elevation, slow-growing shade-tolerant species with conservative ecological strategies are more adaptable than those with acquisitive ones (Mason et al. 2012).

Inferring limiting similarity at small spatial scales

In line with our first hypothesis, we found an evidence of limiting similarity at small spatial scale. It has been hypothesized that competitive exclusion occurs on small spatial scales, where individuals of different species effectively compete for local resources (Weiher and Keddy, 1995; Stoll and Weiner, 2000), thus a pattern of trait divergence as a result of limiting similarity (Watkins and Wilson, 2003; Stubbs and Wilson, 2004). However, as obvious as it may seem, scale dependence has sometimes been ignored. For example, Baraloto et al. (2012) rejected the importance of limiting similarity as an assembly process when comparing functional species distances within 1 ha plots (Dw) and between plots tens of kilometers apart (Da). In our opinion, the results should be interpreted with caution for two reasons. First, it makes little sense to test for competitive exclusion in plant individuals that are spatially very far apart; for example, up to one hundred forty meter apart and thus hardly compete for the same resources (e.g., light, soil nutrients, water availability etc.). In this context, the scale at which interspecies competition takes place is certainly organism-dependent, while sessile organisms such as plants compete for key resources mainly on small spatial scales (up to tens of meters), mobile organisms such as birds or mammals can at much larger ones scales (up to a few tens of kilometers) compete. Consequently, studies should consider the spatial scales at which community assembly processes are most likely to occur relative to the group of organisms under study; For example, if the organisms were plants, a widely observed checkerboard pattern (Diamond 1975) could be misinterpreted as an effect of limiting similarity. Second, even if there were competitive exclusion between individuals within such a large plot, their trait overdispersion signal would be masked by the effect on functional distance of environmental differences between plots.

To avoid spatial-scale bias, we looked for evidence of limiting similarity at small spatial scales (i.e., within 5 x 5 m adjacent plots). At this scale, competing individuals can be assumed to compete directly for the same resources, and the effect of filtering on functional distance can be ruled out since environmental conditions within a subplot are essentially the same (de Bello et al. 2013b). In line with our hypothesis, we did find evidence of a pattern of functional overdispersion resulting from the limiting similarity (competitive exclusion) of the traits we measured. Instead, our results suggest random assembly of the community at this small scale (Gallien 2017).

Contrary to our result, some studies have found no evidence of functional overdispersion between concurrent species at small spatial scales (Schamp et al. 2008; Thompson et al. 2010), while others have. However, the studies that found functional overdispersion did not generally find it for all traits analyzed, and it sometimes happened that both functional overdispersion and clustering were reported simultaneously within the same study system (CavenderBares et al. 2004; Kraft et al. 2008; Cornwell and Ackerly 2009; Swenson and Enquist, 2009; Kraft and Ackerly 2010; de Bello et al. 2013b; Luo et al. 2016). In agreement with with our findings, previous studies systematically reported the existence of limitation of similarity (Wilson, 2007; Kraft et al 2015) was based on the evidence found in relatively low-diversity communities, such as the sand dunes (Stubbs and Wilson, 2004), lawn (Mason and Wilson, Wilson, 2006) or salt marshes (Wilson and Stubbs, 2012).

Environmental filtering linked to environmental heterogeneity at large spatial scale

In this study, we found strong evidence for environmental filtering at a large spatial scale. Given the more restrictive and homogeneous abiotic environment that exists on small spatial scales, the potentially successful functional strategies that allow community members to survive are reduced, thereby diminishing the role of environmental filtering for the community assembly. But on large spatial scales spanning different habitat conditions, such as topography or edaphic variables or expanding environmental gradients, there is consensus on the importance of environmental filtering. In this scenario, selecting the right traits that allow species to thrive in specific environmental conditions would result in a functional clustering pattern. However, the reliability of grouping patterns, which are themselves widely recognized as indicators of habitat filtering, have recently been questioned as some biotic processes can also produce grouping patterns (Sargent and Ackerly 2008). We agree with Kraft et al. (2015) on their claim that experimental manipulations aimed at assessing species' failure to become established and persist in the absence of biotic interactions are the strongest evidence for environmental filtering. However, we argue that not only is this impractical in field studies, particularly in logistically challenging tropical montane forests, but it also doesn't necessarily make sense from an ecological perspective. Instead, according to Cadotte and Tucker (2017), we rely on the existence of an environmental filtering, independent of co-occurring biotic phenomena.

Conclusion

Our results demonstrate a clear link between the pattern and the mechanism by showing that the pattern is only revealed when environmental differences exist, and by demonstrating how those differences correlate with species' ecological strategies, maintained across their entire distribution range in the dry evergreen Afromontane forest, and abundances, along elevation. This study thus helps to emphasize the importance of considering the implications of spatial scale in order to discern the extent to which assembly mechanisms are at work. Furthermore, it highlights the undeniable role of environmental filtering in community assembly and the usefulness of such a concept, showing that neither the exclusion of potentially confounding biotic processes nor the identification of abiotic tolerance ranges are strictly necessary to validate its effect_Future studies are encouraged to advance the discussion and shed light on the remaining details, e.g. whether the environmental filter effect equally influences low- and high-diversity communities. Furthermore, we suggest that future researchers could study trait-mediated community assembly processes to understand the relationship between plant traits and the realized niches of species and hence, provide a way for predicting potential changes in community composition with global and regional environmental change.

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Supplementary Materials

Table S1 Lists of woody species collected from Dindin dry evergreen Afromontane forest of Hararghe highland, south-east Ethiopia

Scientific name	Local name (Afan Oromo)	Family name	Habit
Acacia decurrence	Uttee	Fabaceae	Liana
Acanthus sennii Chiov.	Sokorruu	Acanthaceae	Shrub
Afrocarpus falcatus(Thunb.)R.B.ex Mir.	Birbirsa	Podocarpaceae	Tree
Allophylus abyssinicus (Hochst.) Radlk.	Hirqammuu	Sapindaceae	Tree
Allophylus macrobotrys Gilg.	Haadha Jiloo (Sarara)	Sapindaceae	Shrub
Apodytes dimidiata	Oda-baddaa		
Balanites aegyptiaca (L.) Del.	Baddannoo	Balanitaceae	Tree
Bersama abyssinica Fresen.	Lonchiisaa (Qillisaa or Waraqqaa)	Melianthaceae	Tree
Brucea antidysenterica J.F. Mill.	Haxaawwii (Ciroontaa or Buna Jinnii)	Simaroubaceae	Shrub
Buddleja polystachya Fresen.	Adaaddii	Loganiaceae	Tree
Calpurnia aurea (Ait.) Benth.	Ceekataa	Fabaceae	Tree
Carissa spinarum L.	Agamsa	Apocynaceae	Shrub
Cassipourea malosana Alston	Xiilloo	Rubiaceae	shrub
Celtis africana Burm.f.	Mata qomaa (Cayii)	Ulmaceae	Tree
Clerodendrum myricoides (Hochst.) vatke	Xortoo	Lamiaceae	Shrub
Clutia robusta Pax	Muka uroo	Euphorbiaceae	Shrub
Coffee Arabica	Buna	Rubiaceae	Shrub
Conzyza hypoleusa A.Rich	Balaad	Asteraceae	Shrub
Croton macrostachyus Del.	Bakkanniisaa	Euphorbiaceae	Tree
Discopodium penninervium Hochst.	Garrii (Bosoqqee or Tamboo jaldeessaa)	Solanaceae	Tree
Dombeya aethiopica Gilli	Daannisa	Sterculiaceae	Tree
Dovyalis verrucosa (A.Rich) Warburg	Wanta fullaas	Flacourtiaceae	Shrub
Dregea schimperi (Decne.) Bullock	Hidda gaalee	Dracaenaceae	Liana
Echinops allenbeckii O.Hoffin	Sokorruu	Asteraceae	Shrub
Ekebergia capensis Sparrm.	Somboo	Meliaceae	Tree
Embelia schimperi Vatke	Haanquu	Myrsinaceae	Liana
Erica arborea L.	Saatoo	Ericaceae	Shrub
Euclea divinorum Hiern.	Mi'eessaa	Ebenaceae	Tree/shrub
Euphorbia tirucalli L.	Aannannoo	Euphorbiaceae	Tree
Ficus sur Forssk.	Harbuu	Moraceae	Tree
Galiniera saxifraga (Hochst.) Bridson	Hirqammuu gurraattii (Adamoo)	Rubiaceae	Tree
Grewia furreginea Hochst.ex A.Rich	Not identified a	Tiliaceae	
Hagenia abyssinica (Bruce) J. F. Gmel.	Heexoo	Rosaceae	Tree
Hypericum revolutum (H. lanceolatum)	Muka foonii	Hypericaceae	
Jasminum abyysinicum Hochst. Ex De	Biluu	Oleaceae	Liana
Juniperus Excelsa Endle	Gaattiraa biyyaa	Cuperessaceae	Tree

Landolphia buchananii (Hall.f.) Stapf	Balcha	Apocynaceae	Liana
Lippia adoensis Hochst. ex Walp.	Kusaayee	Verbenaceae	Shrub
Lobella giberroa Hemsl.	Not identified b	Lobeliaceae	
Maesa lanceolata Forssk.	Abbayyii	Myrsinaceae	Tree
Maytenus addat (Loes.) Sebsebe	Kombolcha	Celastraceae	Tree
Maytenus arbutifolia (A.Rich.) Wilczek	Qarxammee	Celastraceae	Shrub
Maytenus senegalensis	Wanta fullaas	Celastraceae	Liana
Maytenus undata (Thunb.) Blakeloock	Gaalee	Celastraceae	T/S
Mikaniopsis clematoides (Sch. Bip. ex A. Rich.) Milne-Redh.	Sariitii	Asteraceae	Liana
Millettia ferruginea (Hochst.) Bak.	Shakammee (Dhadhaatuu)	Fabaceae	Tree
Myrica salicifolia	Tona	Myricaceae	
Myrica salicifolia A.Rich.	Tonaa	Myrsinaceae	Tree
Myrsine africana L.	Riqata leencaa (qacama)	Myricaceae	Shrub
Myrsine melanophloeos (L.) R. Br.	Tullaa/Odaa badda	Myrsinaceae	Tree
Olea capensis L.	Ejersa dhalaa (Sagada or Gagamaa)	Oleaceae	Tree
Olea europaea L.subsp.cuspidata(Wall.exG. Don).CF.	Ejersa (Ejersa kormaa)	Oleaceae	Tree
Olinia rochetiana A. Juss.	Gunaa	Oliniaceae	Tree
Osyris quadripartita Decn.	Watoo	Santalaceae	Liana
Paullina pinnata L.	Xaroo	Sapindaceae	Liana
Premna schimperi Engl.	Urgeessaa	Lamiaceae	Shrub
Prunus africana (Hook.f.) Kalkm	Sukkee	Rosaceae	Tree
Psydrax schimperiana (A. Rich.) Bridson	Gaallee	Rubiaceae	Liana
Rhoicissus tridentata	Haarrii jaawwii	Vitaceae	Liana
Rhus vulgaris Meikle	Xaaxessaa	Anacardiaceae	Tree
Rubus apetalus Poir.	Haniyaa (Injoorrii)	Rosaceae	Shrub
Rubus steudneri Schweinf.	Goraa	Rosaceae	shrub
Rumex nervosus Vahl	Dhangaggoo (Koshommii)	Polygonaceae	Shrub
Rytigynia neglecta (Hiern) Robyns	Mixxoo	Rubiaceae	Shrub
Schefflera abyssinica (Hochst.ex.A.Rich.)	Gatamee	Araliaceae	Tree
Schefflera volkensii (Harms) Harms	Hanshaa	Araliaceae	Tree
Solanum marginatum Linn. f.	Hiddii	Solanaceae	Shrub
Stephania abyssinica (Dillon & A.Rich.)	Kalaalaa	Menispermaceae	Liana
Struthiola thomsonii Oliv.	Mixi gurree	Thymelaeaceae	Shrub
Teclea nobilis Del.	Hadheessaa	Rutaceae	Shrub
Urera hypselodendron (A. Rich.) Wedd.	Haliillaa/Laanqisaa	Urticaceae	Liana
Vernonia myriantha Hook.f.	Reejjii	Asteraceae	Shrub

Table S2 Species Indicator of the three identified communities in the Dindin dry evergreen Afromontane forest, South-east Ethiopia, as determined by indicator species analysis.

Significance levels: **p*=0.05; ***p*=0. 01; ****p*=0.001.

Species Indicator	Plant communities	Indval
Afrocarpus falcatus	*Afrocarpus falcatus-Teclea nobilis*	0.54*
Ozoroa insignis	*Afrocarpus falcatus-Teclea nobilis*	0.18*
Teclea nobilis	*Afrocarpus falcatus-Teclea nobilis*	0.52**
Bersama abyssinica	*Afrocarpus falcatus-Teclea nobilis*	0.49***
Croton macrostachyus	*Afrocarpus falcatus-Teclea nobilis*	0.48***
Struthiola thomsonii	*Afrocarpus falcatus-Teclea nobilis*	0.45***
Vernonia myriantha	*Afrocarpus falcatus-Teclea nobilis*	0.24***
Acanthus sennii	*Afrocarpus falcatus-Teclea nobilis*	0.23*
Maesa lanceolata	*Myrsine melanophloeos-Maesa lanceolata*	0.36*
Dombeya aethiopica	*Myrsine melanophloeos-Maesa lanceolata*	0.18*
Schefflera abyssinica	*Myrsine melanophloeos-Maesa lanceolata*	0.05*
Schefflera volkensii	*Myrsine melanophloeos-Maesa lanceolata*	0.24*
Myrsine melanophloeos	*Myrsine melanophloeos-Maesa lanceolata*	0.49***
Euphorbia tirucalli	*Olea europaea-Juniperus Excelsa*	0.17*
Olea europaea	*Olea europaea-Juniperus Excelsa*	0.34***
Juniperus Excelsa	*Olea europaea-Juniperus Excelsa*	0.23*
Olea capensis	*Olea europaea-Juniperus Excelsa*	0.15*
Rubus steudneri	*Olea europaea-Juniperus Excelsa*	0.17*
Hagenia abyssinica	*Olea europaea-Juniperus Excelsa*	0.12*
Myrsine africana	*Olea europaea-Juniperus Excelsa*	0.15*

Figure S1 Species-accumulation curve

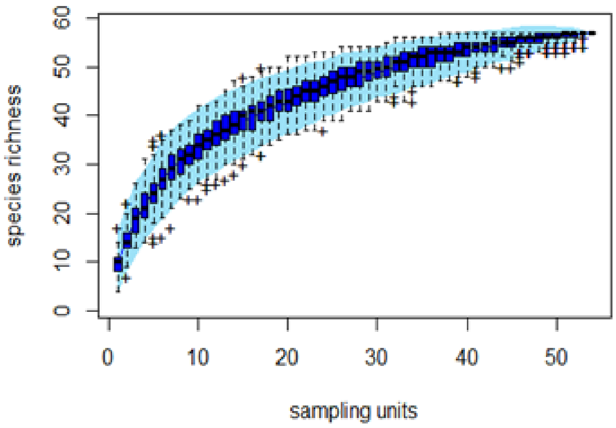

Figure S2 Optimum number of clusters which represented by broken line.

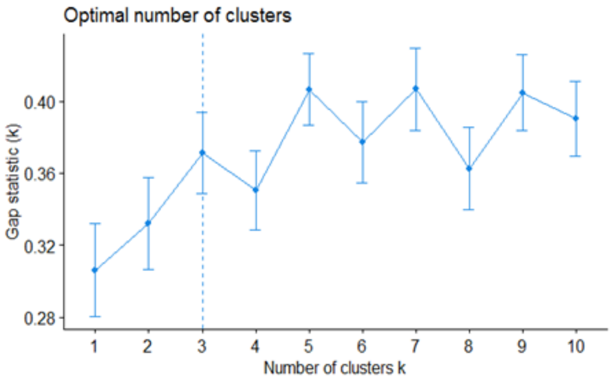

Figure S3 Dendrogram or tree diagram showing three plant communities as identified by the agglomerative hierarchical cluster analysis using similarity ratio.

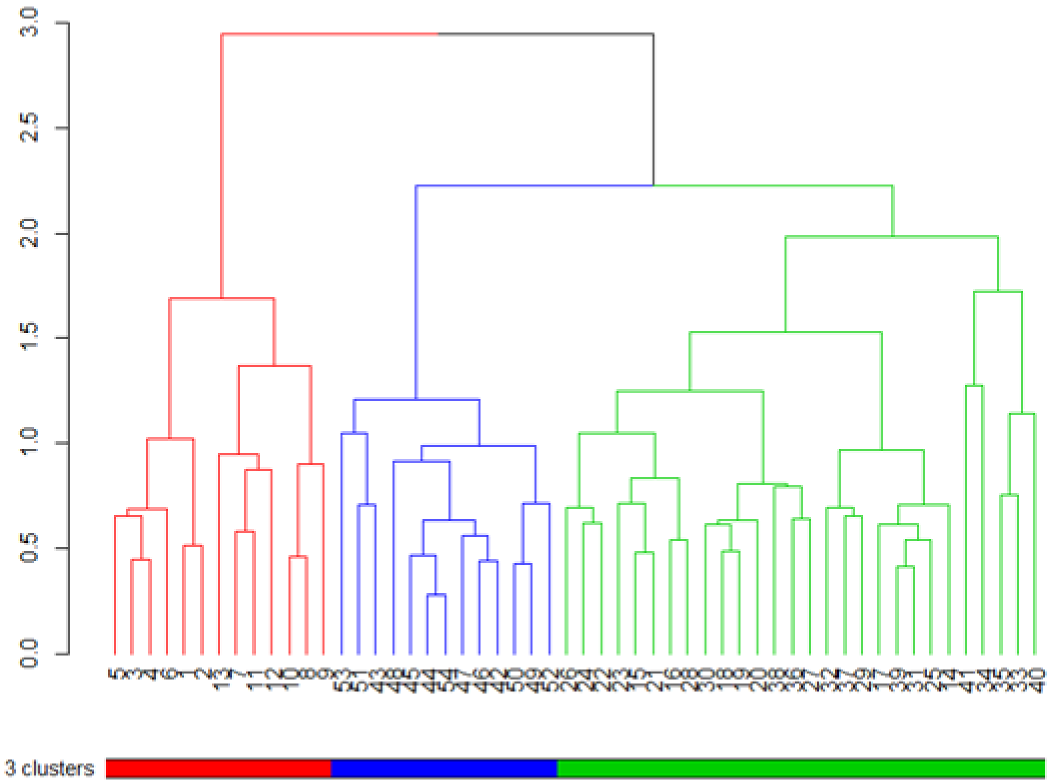

Figure S4 Goodness of fit between the ordination and the observed dissimilarities