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Differential Responses of Taxonomic, Structural, and Functional Diversity to Local-Scale Environmental Variation in Afromontane Forests in South Africa

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Abstract

Exploring taxonomic, functional, and structural diversity can provide additional insights into our understanding of diversity responses to environment. Using altitude, slope, and relative radiation index as well as floristic and functional data from a South Africa Afromontane forest, we examined how taxonomic, structural, and functional diversity varied with local environmental variation. Taxonomic and structural diversity were quantified through species richness- and diameter class-based Shannon index and evenness, respectively. Skewness and coefficient of variation of diameter distribution were additionally computed for structural diversity. As for functional diversity, we used functional richness, evenness, divergence, and dispersion based on functional traits. Data were analyzed using multimodel inference and subset regression. We found little evidence of environmental effects on local-scale taxonomic diversity patterns. In contrast, structural and functional diversity metrics varied significantly along environmental gradients. Accordingly, diameter class-based Shannon evenness declined with increasing slope while skewness and coefficient of variation of diameter distribution increased with increasing slope. Functional evenness and divergence decreased with increasing altitude and radiation, respectively, while functional richness and dispersion increased with increasing slope. The results showed that taxonomic diversity patterns were less responsive to local-scale topographical variation than structural and functional diversity. Lower functional diversity on lower slope sites suggests weak environmental filtering effect promoting competitive exclusion and dominance of species with acquisitive traits. On higher slope sites, environmental filtering associated with slope gradient seems to favor coexistence of species with conservative traits and adapted to harsh conditions.

Keywords

diversity patterns, environmental filtering, radiation index, species coexistence, slope

Introduction

The structures of natural forest ecosystems are not only outcomes of natural processes (tree growth, mortality, recruitment, and disturbances such as fire and wind damage) and human disturbance (clear-felling, afforestation, etc.) but are also codetermined by environmental constraints (Assogbadjo, Mensah, & Glèlè Kakai, 2017; Foley et al., 2007; Seydack, Durrheim, & Louw, 2012). Environmental effects may vary according to the scale of interest. Regional and global scales diversity and structural patterns are regulated by species tolerance ranges which are well related to climate and environmental

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factors (Woodward & Williams, 1987). At local scale, spatial variations in precipitation and temperature might not be apparent, and environmental variation would most likely be induced by other factors—edaphic or topographic (elevation, aspect, slope, etc.)—which can potentially influence species distribution, structure, and dominance patterns (Baldeck et al., 2013; Laurance et al., 2010; Sharma, Baduni, Gairola, Ghildiyal, & Suyal, 2010; Zhang et al., 2016). In addition, local-scale topography may be an influencing factor for soil nutrients availability and soil moisture (Engelbrecht et al., 2007; John et al., 2007) and thus may act as a key component of environment filtering facilitating or preventing species establishment and growth (Kraft et al., 2015).

There are insights that forest structure and community assembly relate with local environmental variables such as altitude and slope (Gallardo-Cruz, Pérez-García, & Meave, 2009). For instance, basal area and forest biomass are typically reported to be highest at lower slope sites (Sefidi, Esfandiary Darabad, & Azarian, 2016; Takyu, Aiba, & Kitayama, 2003; Vilà et al., 2007). The influence of slope or topographical variables can be mediated by light radiation, temperature, moisture, runoff, infiltration, soil properties, and resources availability (Tsui, Chen, & Hsieh, 2004; Yirdaw, Starr, Negash, & Yimer, 2015). As a result, one might expect tree size variability (structural diversity) to relate with slope or altitude, even at a local scale.

In South Africa, Afromontane Mistbelt forests are one of the few natural forests that, due to the modification of fire regime, have developed in areas that were not covered by forests historically (Geldenhuys, 2000; Geldenhuys & Venter 2002). These forests persisted in fire-prone environment, and then expanded into potentially suitable areas with protection of the larger landscape against fire, for timber plantations and intensive agriculture. One of the most striking characteristics in these Afromontane forests is the tall moist evergreen vegetation occurring at higher altitudes and varying slope aspect. Lower water availability on slopes and hilltops as compared to valleys, as a result of topography effects (Gallardo-Cruz et al., 2009; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010), may govern the structure and functional organization of these forest communities. Most studies in Afromontane Mistbelt forests in South Africa lack information on how diversity relates to local-scale environmental variation, and only few studies paid attention to variability in species functional traits (Mensah, Glèlè Kakaï, & Seifert, 2016; Mensah, Veldtman, Assogbadjo, Glèlè Kakaï, & Seifert, 2016). In the current ecological research context where functional diversity—the value and range of functional traits of the organisms present in a given ecosystem (Díaz & Cabido, 2001)—is being seen as complementary and promising component to assess diversity effects on

ecosystem functioning, it is important to quantify changes in functional diversity as response to environmental filtering (Dyderski, Czapiewska, Zajdler, Tyborski, & Jagodzinski, 2016; Lohbeck et al., 2012). New species—with different functional traits—added to an ecosystem would likely contribute differently to the physiological processes (Mensah, Veldtman, et al., 2016), as response to environmental conditions and available resources. Therefore, functional diversity can also be used as an additional diversity component in assessing biological diversity responses to environmental variation. In addition to insights from structural diversity measures, a functional traits-based analysis of diversity can further our understanding of forest structure and diversity responses to environmental variation.

Combined information on taxonomic, functional, and structural diversity could shed light on our understanding of processes and mechanisms behind community assembly. However, it is unclear how each specific diversity component would respond to local environmental variation. Therefore, in this study, we used taxonomy-, structure-, and functional trait-based diversity to explore how environmental filtering imposed by local environmental factors such as altitude, slope, and radiation influence community assembly. We scrutinized species diversity, separating taxonomic diversity from functional traits-based (wood density, leaf area, and maximum height) diversity and structural diversity (tree size variability), and determined how they would respond individually to local-scale environmental variation. We asked the following questions: (a) How do taxonomic diversity and structural diversity (tree size variability) vary with radiation, slope, and altitudinal gradient? (b) How do different functional diversity metrics respond to local variation in radiation, slope, and altitude? Because species distributions are governed by climatic and edaphic tolerance range and adaptations to physical conditions of the environment, we expect taxonomic diversity patterns to be less responsive to local-scale topographical variation. Conversely, we assumed that functional and structural diversity would relate with slope or altitude, even at a local scale due to gravity-driven processes, mechanical stability constraints and growth challenges faced by trees growing on steeper slopes.

Methods

Study Area and Data

The study was carried out in the Woodbush—De Hoek natural forest (Figure 1), near Magoebaskloof in the Limpopo province, South Africa. The Woodbush—De Hoek natural forest is part of the Limpopo Mistbelt forests (Mucina & Rutherford, 2006), which belong to the Northern Mistbelt Forests group, considered as part

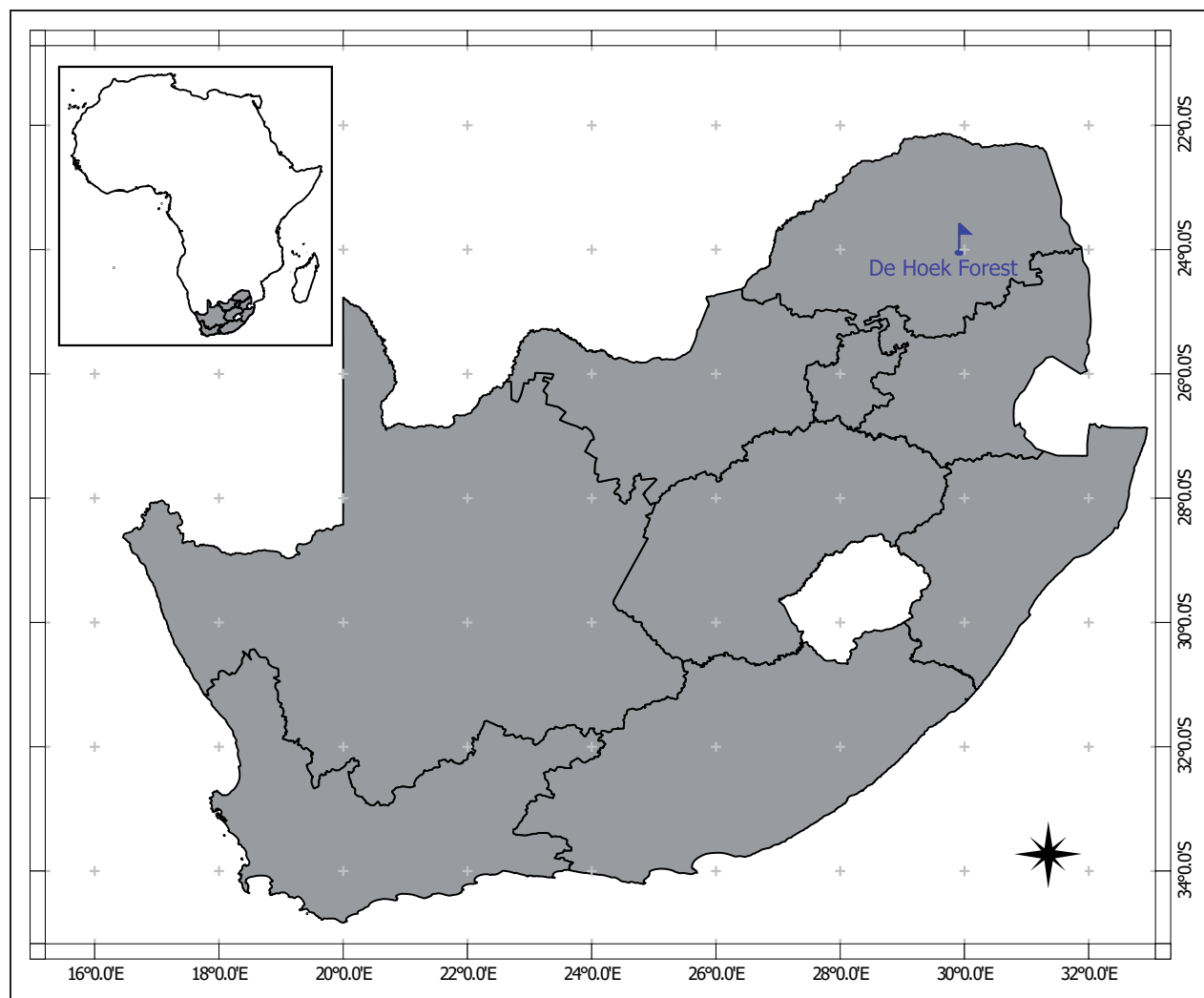


Figure 1. Location of South Africa map in Africa and of the Woodbush-De Hoek natural forest in South Africa.

of the Afromontane Archipelago in Africa (White, 1983). These forests are composed of tall moist evergreen vegetation occurring at higher altitudes and varying slope aspect (Geldenhuys, 2000; Geldenhuys & Venter, 2002; Mensah, Veldtman, & Seifert, 2017). The data were collected in Summer 2015 and consisted of floristic and structural data and additional wood density data for selected species (Mensah et al., 2017). The floristic and structural data were collected by means of forest inventories in a 709 ha forest block in the Woodbush—De Hoek forest. Thirty circular plots of 500 m² were randomly laid out in stratified compartments obtained from subdivision of the research area on the basis of (a) three classes of slope: flat, gentle, and steep; (b) three classes of elevation: low, medium, and high; and (c) four classes of aspect which were North, South, West, and East. Diameter at breast height (dbh) and species name were recorded for all trees with dbh = 5 cm. Additional data on leaf and wood traits (specific wood

density, specific leaf area, and maximum plant height; Mensah et al., 2016) were obtained from publicly available sources. Additional data on species wood density were obtained from the Global Wood Density Database (Zanne et al., 2009). Specific leaf area and maximum plant height data were extracted from TRY database (<https://www.try-db.org/>; Kattge et al., 2011).

Diversity Metrics

We used plot-level taxonomic diversity metrics (species richness, Shannon–Wiener diversity index, and Shannon evenness), structural diversity (tree size variability), and functional diversity (functional traits-based diversity) metrics. Structural diversity was assessed at plot level by calculating four metrics: (a) Shannon diversity Index; (b) Shannon evenness based on the relative proportion of trees in dbh classes of 5 cm width, with 19 classes in total; (c) skewness of dbh distribution, and

(d) coefficient of variation of dbh (Dănescu, Albrecht, & Bauhus, 2016). Functional diversity was quantified using specific leaf area, specific wood density, and maximum plant height. We estimated functional richness, functional evenness, functional divergence, functional dispersion (Fdis), and Rao quadratic entropy (RaoQ) at plot level (Villéger, Mason, & Mouillot, 2008) using the values of the functional traits (specific wood density, specific leaf area, and maximum plant height) with the “FD” package in R (Laliberté, Legendre, & Shipley, 2014). These functional diversity indices are multitrait metrics that combine both the relative weight of each species and the pairwise functional difference between species (Mensah, Veldtman, et al., 2016). Because RaoQ and Fdis are strongly related indices (Laliberté & Legendre, 2010), we considered retaining only Fdis.

Environmental Variables

Slope, aspect, and altitude values were obtained from digital elevation model available for the site, using recorded coordinates and QGIS version 2.2.0. A convenient way to explore the effect of such environmental factors on the diversity metrics would be a three-way analysis of variance (ANOVA), as this would allow for evaluation of interactions effects among factors besides individual effects. However, given the low number of plots, combinations of elevation–slope–aspect in multiple-way ANOVA is impracticable and may produce unreliable results. In addition, aspect as simple variable may not be biologically relevant as compared to radiation index which combines aspect, slope, and latitude degrees (Austin, Cunningham, & Fleming, 1984). Therefore, in addition to slope and altitude which were used as independent variables, we also calculated relative radiation index (RRI), which is a relative measure of the slope exposure to radiation at noon at specific location (Vetaas, 1992). RRI was estimated from the following formula: $RRI = \cos(180^\circ - \Omega) \times \sin(\beta) \times \sin(\Phi) + \cos(\beta) \times \cos(\Phi)$, where Ω = aspect (slope azimuth), Φ = latitude, and β = slope inclination (see Paudel & Vetaas, 2014).

Statistical Analysis

Statistical analyses were done in the R statistical software package, version 3.3.2 (R Core Team, 2016). We first explored the relationships between environmental variables and diversity metrics using Pearson correlations. Correlation matrix heatmaps were built for each diversity component using package “ggplot2” (Wickham, 2009). We next tested for effects of slope, altitude, and radiation on taxonomic, functional, and structural diversity using multiple linear models. The linear models were fitted to assess (a) combined effects of environmental variables

on taxonomic diversity metrics, (b) combined effects of environmental variables on functional diversity metrics, and (c) combined effects of environmental variables on structural diversity metrics. Models were fitted using multimodel inference and subset regression analysis of the package “MuMIn” (Barton, 2017). Multimodal inference is a powerful method to determine which model best fits the data. The optimal models were selected based on the AICc (Akaike Information Criterion, adjusted for small sample sizes). Small difference (<2) in AICc between two subset models indicates that these models are equally supported. To avoid autocorrelation and independence in case two or more models were equally supported, the most parsimonious model was selected by considering the lowest number of uncorrelated predictors. Significance fits were additionally used to determine environmental variables that are relevant for each diversity metric. For interpretation of the results, bivariate relationships between response variables and predictors were plotted using package “ggplot2.” Prior to fitting the models, response variables were checked for normality using the Shapiro–Wilk normality test.

Results

Overall Diversity Patterns and Correlations Between Variables

Fifty tree species and 33 botanical families were enumerated. Overall Shannon–Wiener diversity was 2.84. Most diversified families were Rutaceae and Rubiaceae, with five and four species, respectively. Results of Pearson correlations showed that slope, altitude, and radiation index were more strongly related with functional and structural diversity metrics than taxonomic diversity metrics (Figure 2). Pearson correlations between environmental variables and diversity metrics ranged from $r = -.35$ to $r = .40$ for taxonomic diversity metrics (Figure 2(a)); from $r = -.72$ to $r = .85$ for structural diversity metrics (Figure 2(b)); and from $r = -.58$ to $r = .69$ for functional diversity metrics (Figure 2(c)).

Diversity Responses to Local-Scale Environmental Variation

Results from the model selection process as summarized in Tables 1 to 3 indicate differential responses of taxonomic diversity, structural diversity, and functional diversity metrics, respectively, to local-scale environmental variation.

Among taxonomic diversity metrics, only Shannon evenness responded significantly to local environmental variations (Table 1); and the effects were shown by significantly higher values of Shannon evenness on steeper sites ($R^2 = 13\%$; $p = .031$; Table 1; Figure 3). As for

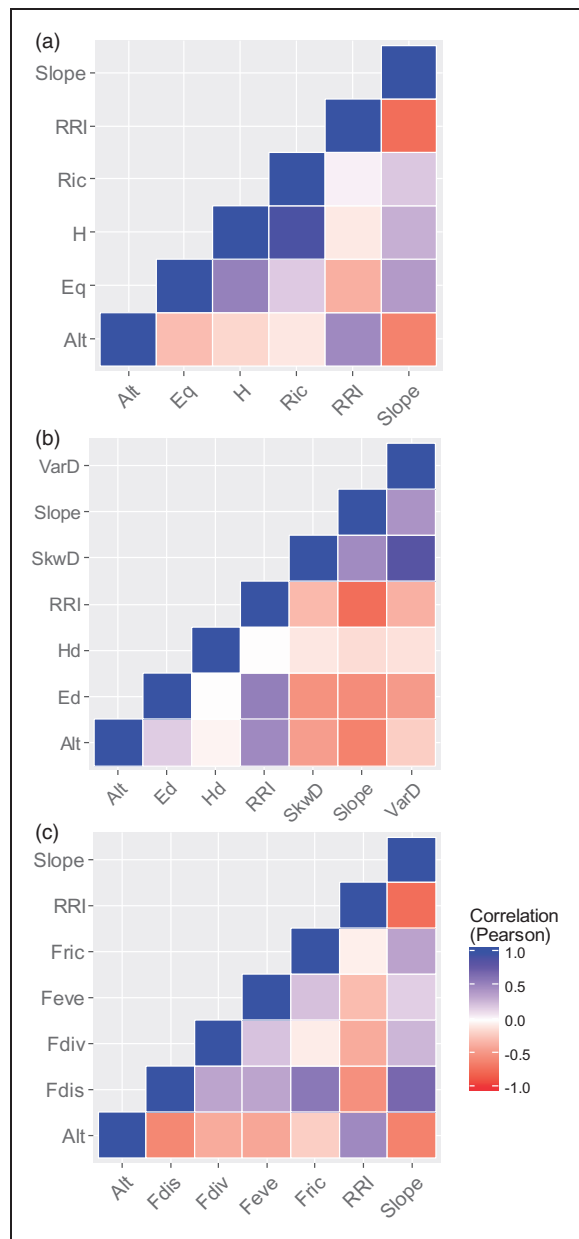


Figure 2. Pearson correlations between environmental variables and (a) taxonomic diversity, (b) structural diversity, and (c) functional diversity. RRI = relative radiation index; Alt = altitude; Ric = species richness; H = Shannon diversity index; Eq = Pielou evenness; VarD = coefficient of variation of diameter; SkwD = skewness of diameter distribution; Hd = size class-based Shannon index; Ed = size class-based Shannon evenness; Fric = functional richness; Feve = functional evenness; Fdiv = functional divergence; Fdis = functional dispersion; blue cells indicate positive relationships while red cells are negative relationships; white cells indicate no established correlation.

species richness and Shannon diversity, there was no statistical influence of local-scale environmental factors, probability values being .301 and .112, respectively.

We found no significant environmental effects on diameter class-based Shannon index, with all environmental factors being left out in the finally selected model (Table 2). However, diameter class-based Shannon evenness declined significantly with increasing slope ($R^2 = 26\%$; $p = .002$; Table 2; Figure 4) while skewness and coefficient of variation of diameter distribution increased (21% and 17% of variance explained, respectively) with increasing slope (Table 2; Figure 4). On the other hand, skewness of diameter distribution also decreased with higher altitude ($R^2 = 16\%$; $p = .016$; Figure 4).

When assessing fitted models for functional diversity metrics, slope was retained as potentially influencing predictor of functional richness and Fdis (Table 3). The effect of slope was shown by increasing functional richness and dispersion on steeper sites, with 16% ($p = .036$) and 45% ($p < .001$) of explained variance respectively (Figure 5). On the other hand, altitude and RRI were final selected predictors for functional evenness and functional divergence, respectively (Table 3). Functional evenness decreased significantly with increasing altitude (12% of explained variance; $p = .031$) while functional divergence declined significantly with increasing RRI (11% of explained variance; $p = .042$) (Figure 5). Overall, results consistently suggest that taxonomic diversity patterns are not easily identifiable at local scale and are less responsive to topographical variation than functional and structural diversity measures.

Discussion

Diversity patterns at global, regional, and local scales are still being increasingly debated in recent studies (Allen & Gillooly, 2006; Ricklefs, 2004; Ricklefs & He, 2016). We analyzed the patterns of taxonomic diversity, functional diversity, and structural diversity, in relation to environmental factors such as slope, altitude, and radiation in the Woodbush—De Hoek natural forest, a Northern Mistbelt forest type under strict and legal protection and with relatively limited human disturbances. From the results, (a) only Shannon evenness among taxonomic diversity metrics showed significant and positive response to increasing slope; (b) structural and functional diversity, unlike taxonomic diversity metrics, varied along environmental gradients; (c) diameter class-based Shannon evenness declined with increasing slope while skewness and coefficient of variation of diameter distribution increased with increasing slope; (d) functional evenness and divergence decreased with increasing altitude and radiation, respectively; (e) functional richness and dispersion increased with increasing slope; and (f) taxonomic diversity measures were less responsive to topographical variation than functional and structural diversity.

Table 1. Model Selection Table Resulting From Multiple Regression Models of Altitude, Slope, and Relative Radiation Index Effects on Taxonomic Diversity.

| Subset model | Altitude | RRI | Slope | df | logLik | AICc | Delta | Weight |
|--------------------------|----------|--------|--------------|----------|---------------|--------------|-------------|--------------|
| <i>Species richness</i> | | | | | | | | |
| 1 | | | | 2 | -74.728 | 153.9 | 0.00 | 0.337 |
| 5 | | | 0.195 | 3 | -74.144 | 155.2 | 1.31 | 0.175 |
| 7 | | 0.398 | 0.483 | 4 | -72.908 | 155.4 | 1.52 | 0.158 |
| 2 | -0.090 | | | 3 | -74.605 | 156.1 | 2.23 | 0.110 |
| 3 | | 0.050 | | 3 | -74.690 | 156.3 | 2.40 | 0.101 |
| 6 | 0.045 | | 0.223 | 4 | -74.124 | 157.8 | 3.95 | 0.047 |
| 8 | 0.015 | 0.397 | 0.491 | 5 | -72.906 | 158.3 | 4.41 | 0.037 |
| 4 | -0.150 | 0.123 | | 4 | -74.429 | 158.5 | 4.56 | 0.035 |
| <i>Shannon diversity</i> | | | | | | | | |
| 5 | | | 0.297 | 3 | -15.00 | 36.9 | 0.00 | 0.287 |
| 1 | | | | 2 | -16.38 | 37.2 | 0.28 | 0.250 |
| 7 | | 0.275 | 0.495 | 4 | -14.39 | 38.4 | 1.46 | 0.139 |
| 2 | -0.161 | | | 3 | -15.99 | 38.9 | 1.97 | 0.107 |
| 3 | | -0.082 | | 3 | -16.27 | 39.5 | 2.56 | 0.080 |
| 6 | 0.031 | | 0.315 | 4 | -14.99 | 39.6 | 2.66 | 0.076 |
| 8 | 0.010 | 0.274 | 0.501 | 5 | -14.38 | 41.3 | 4.35 | 0.033 |
| 4 | -0.159 | -0.004 | | 4 | -15.99 | 41.6 | 4.65 | 0.028 |
| <i>Shannon evenness</i> | | | | | | | | |
| 5 | | | 0.396 | 3 | 36.575 | -66.2 | 0.00 | 0.343 |
| 3 | | -0.347 | | 3 | 35.947 | -65.0 | 1.26 | 0.183 |
| 7 | | -0.129 | 0.303 | 4 | 36.716 | -63.8 | 2.39 | 0.104 |
| 6 | -0.067 | | 0.355 | 4 | 36.626 | -63.7 | 2.58 | 0.095 |
| 2 | -0.283 | | | 3 | 35.277 | -63.6 | 2.60 | 0.094 |
| 1 | | | | 2 | 34.023 | -63.6 | 2.62 | 0.092 |
| 4 | -0.149 | -0.274 | | 4 | 36.242 | -62.9 | 3.34 | 0.064 |
| 8 | -0.058 | -0.123 | 0.272 | 5 | 36.754 | -61.0 | 5.22 | 0.025 |

Note. RRI = Relative Radiation Index; df = degree of freedom; logLik = log-likelihood; AICc = second-order Akaike Information Criterion. Bold values indicate selected optimal models.

Table 2. Model Selection Table Resulting From Multiple Regression Models of Altitude, Slope, and Relative Radiation Index Effects on Structural Diversity.

| Subset Model | Altitude | RRI | Slope | df | logLik | AICc | Delta | Weight |
|---|----------|--------------|---------------|----------|---------------|--------------|-------------|--------------|
| <i>Diameter class-based Shannon diversity</i> | | | | | | | | |
| 1 | | | | 2 | 18.119 | -31.8 | 0.00 | 0.429 |
| 5 | | | -0.128 | 3 | 18.365 | -29.8 | 1.99 | 0.159 |
| 2 | -0.038 | | | 3 | 18.142 | -29.4 | 2.43 | 0.127 |
| 3 | | 0.011 | | 3 | 18.121 | -29.3 | 2.47 | 0.125 |
| 6 | -0.185 | | -0.240 | 4 | 18.698 | -27.8 | 4.00 | 0.058 |
| 7 | | -0.168 | -0.249 | 4 | 18.574 | -27.5 | 4.25 | 0.051 |
| 4 | -0.058 | 0.039 | | 4 | 18.160 | -26.7 | 5.07 | 0.034 |
| 8 | -0.173 | -0.151 | -0.343 | 5 | 18.869 | -25.2 | 6.56 | 0.016 |
| <i>Diameter class-based Shannon evenness</i> | | | | | | | | |
| 3 | | 0.554 | | 3 | 46.983 | -87.0 | 0.00 | 0.294 |
| 5 | | | -0.536 | 3 | 46.555 | -86.2 | 0.86 | 0.191 |
| 7 | | 0.350 | -0.284 | 4 | 47.843 | -86.1 | 0.96 | 0.182 |

(continued)

Table 2. Continued

| Subset Model | Altitude | RRI | Slope | df | logLik | AICc | Delta | Weight |
|--|---------------|--------|--------------|----------|-----------------|--------------|-------------|--------------|
| 8 | −0.265 | 0.376 | −0.426 | 5 | 48.884 | −85.3 | 1.78 | 0.121 |
| 6 | −0.237 | | −0.680 | 4 | 47.315 | −85.0 | 2.01 | 0.107 |
| 4 | −0.121 | 0.613 | | 4 | 47.227 | −84.9 | 2.19 | 0.098 |
| 1 | | | | 2 | 41.474 | −78.5 | 8.54 | 0.004 |
| 2 | 0.177 | | | 3 | 41.954 | −77.0 | 10.06 | 0.002 |
| <i>Skewness of tree diameter distribution</i> | | | | | | | | |
| 5 | | | 0.484 | 3 | −33.044 | 73.0 | 0.00 | 0.381 |
| 6 | −0.225 | | 0.347 | 4 | −32.409 | 74.4 | 1.41 | 0.188 |
| 2 | −0.436 | | | 3 | −33.882 | 74.7 | 1.68 | 0.165 |
| 7 | | 0.096 | 0.553 | 4 | −32.958 | 75.5 | 2.51 | 0.109 |
| 4 | −0.378 | −0.119 | | 4 | −33.679 | 77.0 | 3.95 | 0.053 |
| 8 | −0.234 | 0.119 | 0.427 | 5 | −32.272 | 77.0 | 4.03 | 0.051 |
| 3 | | −0.303 | | 3 | −35.594 | 78.1 | 5.10 | 0.030 |
| 1 | | | | 2 | −37.040 | 78.5 | 5.51 | 0.024 |
| <i>Coefficient of variation of tree diameter</i> | | | | | | | | |
| 5 | | | 0.444 | 3 | −127.638 | 262.2 | 0.00 | 0.470 |
| 6 | 0.107 | | 0.509 | 4 | −127.504 | 264.6 | 2.41 | 0.141 |
| 7 | | −0.037 | 0.417 | 4 | −127.626 | 264.9 | 2.65 | 0.125 |
| 3 | | −0.338 | | 3 | −129.108 | 265.1 | 2.94 | 0.108 |
| 1 | | | | 2 | −130.926 | 266.3 | 4.10 | 0.061 |
| 8 | 0.110 | −0.048 | 0.476 | 5 | −127.483 | 267.5 | 5.27 | 0.034 |
| 2 | −0.203 | | | 3 | −130.295 | 267.5 | 5.31 | 0.033 |
| 4 | −0.050 | −0.313 | | 4 | −129.075 | 267.8 | 5.55 | 0.029 |

Note. RRI = Relative Radiation Index; df = degree of freedom; logLik = log-likelihood; AICc = second-order Akaike Information Criterion. Bold values indicate selected optimal models.

Table 3. Model Selection Table Resulting From Multiple Regression Models of Altitude, Slope, and Relative Radiation Index Effects on Functional Diversity.

| Subset Model | Altitude | RRI | Slope | df | logLik | AICc | Delta | Weight |
|----------------------------|---------------|--------|--------------|----------|----------------|---------------|-------------|--------------|
| <i>Functional richness</i> | | | | | | | | |
| 7 | | 0.423 | 0.668 | 4 | 161.075 | −312.5 | 0.00 | 0.343 |
| 5 | | | 0.364 | 3 | 159.517 | −312.1 | 0.44 | 0.276 |
| 1 | | | | 2 | 157.391 | −310.3 | 2.21 | 0.114 |
| 8 | −0.003 | 0.423 | 0.667 | 5 | 161.075 | −309.6 | 2.90 | 0.081 |
| 6 | 0.028 | | 0.381 | 4 | 159.526 | −309.5 | 3.10 | 0.073 |
| 2 | −0.203 | | | 3 | 158.025 | −309.1 | 3.42 | 0.062 |
| 3 | | −0.059 | | 3 | 157.445 | −308.0 | 4.58 | 0.035 |
| 4 | −0.228 | 0.052 | | 4 | 158.056 | −306.5 | 6.04 | 0.017 |
| <i>Functional evenness</i> | | | | | | | | |
| 2 | −0.393 | | | 3 | 30.084 | −53.2 | 0.00 | 0.391 |
| 4 | −0.333 | −0.124 | | 4 | 30.294 | −51.0 | 2.26 | 0.126 |
| 6 | −0.464 | | −0.116 | 4 | 30.236 | −50.9 | 2.37 | 0.119 |
| 3 | | −0.286 | | 3 | 28.842 | −50.8 | 2.48 | 0.113 |
| 1 | | | | 2 | 27.562 | −50.7 | 2.57 | 0.108 |
| 8 | −0.441 | −0.303 | −0.321 | 5 | 31.038 | −49.6 | 3.67 | 0.062 |
| 5 | | | 0.166 | 3 | 27.983 | −49.0 | 4.20 | 0.048 |
| 7 | | −0.346 | −0.083 | 4 | 28.897 | −48.2 | 5.05 | 0.031 |

(continued)

Table 3. Continued

| Subset Model | Altitude | RRI | Slope | df | logLik | AICc | Delta | Weight |
|------------------------------|----------|---------------|--------------|----------|---------------|---------------|-------------|--------------|
| <i>Functional divergence</i> | | | | | | | | |
| 3 | | −0.372 | | 3 | 23.514 | −40.1 | 0.00 | 0.256 |
| 2 | −0.366 | | | 3 | 23.435 | −39.9 | 0.16 | 0.237 |
| 4 | −0.242 | −0.254 | | 4 | 24.314 | −39.0 | 1.08 | 0.150 |
| 1 | | | | 2 | 21.281 | −38.1 | 1.99 | 0.095 |
| 5 | | | 0.273 | 3 | 22.443 | −38 | 2.14 | 0.088 |
| 7 | | −0.365 | 0.010 | 4 | 23.515 | −37.4 | 2.68 | 0.067 |
| 6 | −0.317 | | 0.080 | 4 | 23.505 | −37.4 | 2.70 | 0.067 |
| 8 | −0.293 | −0.336 | −0.147 | 5 | 24.470 | −36.4 | 3.67 | 0.041 |
| <i>Functional dispersion</i> | | | | | | | | |
| 5 | | | 0.686 | 3 | 55.241 | −103.6 | 0.00 | 0.416 |
| 6 | −0.252 | | 0.532 | 4 | 56.420 | −103.2 | 0.32 | 0.354 |
| 7 | | −0.043 | 0.655 | 4 | 55.266 | −100.9 | 2.63 | 0.112 |
| 8 | −0.251 | −0.018 | 0.519 | 5 | 56.425 | −100.3 | 3.21 | 0.083 |
| 4 | −0.426 | −0.308 | | 4 | 53.485 | −97.4 | 6.19 | 0.019 |
| 2 | −0.576 | | | 3 | 51.770 | −96.6 | 6.94 | 0.013 |
| 3 | | −0.515 | | 3 | 50.346 | −93.8 | 9.79 | 0.003 |
| 1 | | | | 2 | 45.722 | −87.0 | 16.56 | 0.000 |

Note. RRI = Relative Radiation Index; df = degree of freedom; logLik = log-likelihood; AICc = second-order Akaike Information Criterion. Bold values indicate selected optimal models.

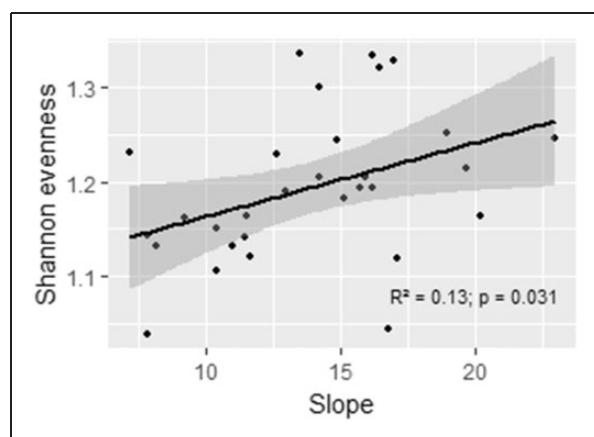


Figure 3. Bivariate relationship between taxonomic diversity metrics and variables retained by the final model; statistics are obtained from the results of the subset regression analysis presented in Table 1. Graphs were not displayed for species richness and Shannon–Wiener diversity as they were not significant.

Our analyses revealed little evidence of environmental effects on local-scale taxonomic diversity patterns. A plausible reason might be that species distributions are rather most likely governed by large-scale climatic and edaphic tolerance range and adaptations to physical conditions of the environment. Local species richness reportedly reflects, to a significant extent, regional characteristics, including geographical and geological history, that influence evolutionary diversification and regional

extinction (Ricklefs & He, 2016). The variation of Shannon evenness with increasing slope supports the view that local taxonomic diversity patterns are outcome of complex interactions of local and regional processes. The local diversity of the studied forest trees species is presumably codetermined by local processes (human interventions against fire, competition among species for limiting resources) and regional processes including large-scale dispersal mechanism and climatic variation.

The result of significant association between Shannon evenness and slope gradient is in line with report from past studies (Cui & Zheng, 2016; Homeier, Breckle, Gunter, Rollenbeck, & Leuschner, 2010; Takyu, Aiba, & Kitayama, 2002). For instance, Cui and Zheng (2016) and Homeier et al. (2010) observed significantly higher tree species diversity at lower slope position in comparison with upper slope sites. However, a study by Zhang et al. (2016) in mountain forest in China showed such relationships nonsignificant. These outcomes suggest that the effects of slope on taxonomic diversity may partly depend on other factors such as the scale of the study and the magnitude of the slope gradient.

Unlike Shannon evenness, species richness and Shannon index did not vary with slope, and neither did they respond to variations in altitude and RRI. Thus, these outcomes may also reflect the specific dimension of the taxonomic diversity measure used. Accordingly, it is important to mention that Shannon evenness is a standardized version of the Shannon index and is less affected by range and quantifies the degree of evenness

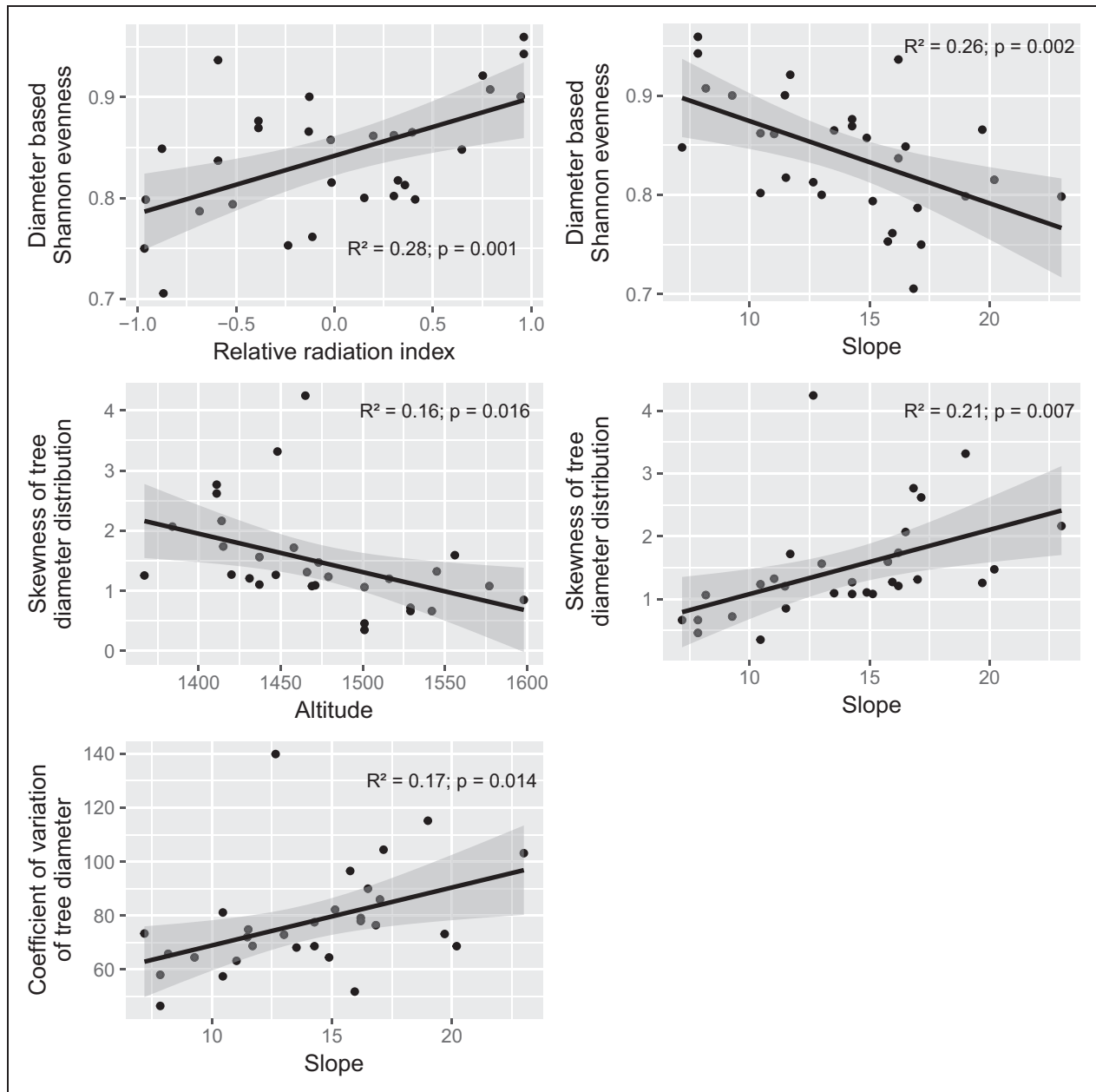


Figure 4. Bivariate relationship between structural diversity metrics and variables retained by the final model; statistics are obtained from the results of the subset regression analysis presented in Table 2.

in taxonomic diversity. As such, Shannon evenness could stand as a more appropriate measure not only for comparison purposes in plots with varying species pool (Pretzsch, 2009) but also for testing local environmental effects on taxonomic diversity.

Failure to detect taxonomic diversity patterns can also partly be attributed to spatial coverage of the data and methodological caveats such as usage of samples or plot sizes that are too small to adequately characterize the diversity of local assemblages (Baraloto et al., 2013),

given that smaller plot sizes would tend to reflect homogeneity and may obscure the effects of environmental variables on taxonomic diversity patterns.

Most structural diversity metrics varied with environmental factors; diameter class-based Shannon evenness declined with increasing slope while skewness and coefficient of variation of diameter distribution increased with increasing slope. Ultimately, because tree size is inherently related to tree growth and resources availability, local environmental effect can be mediated through

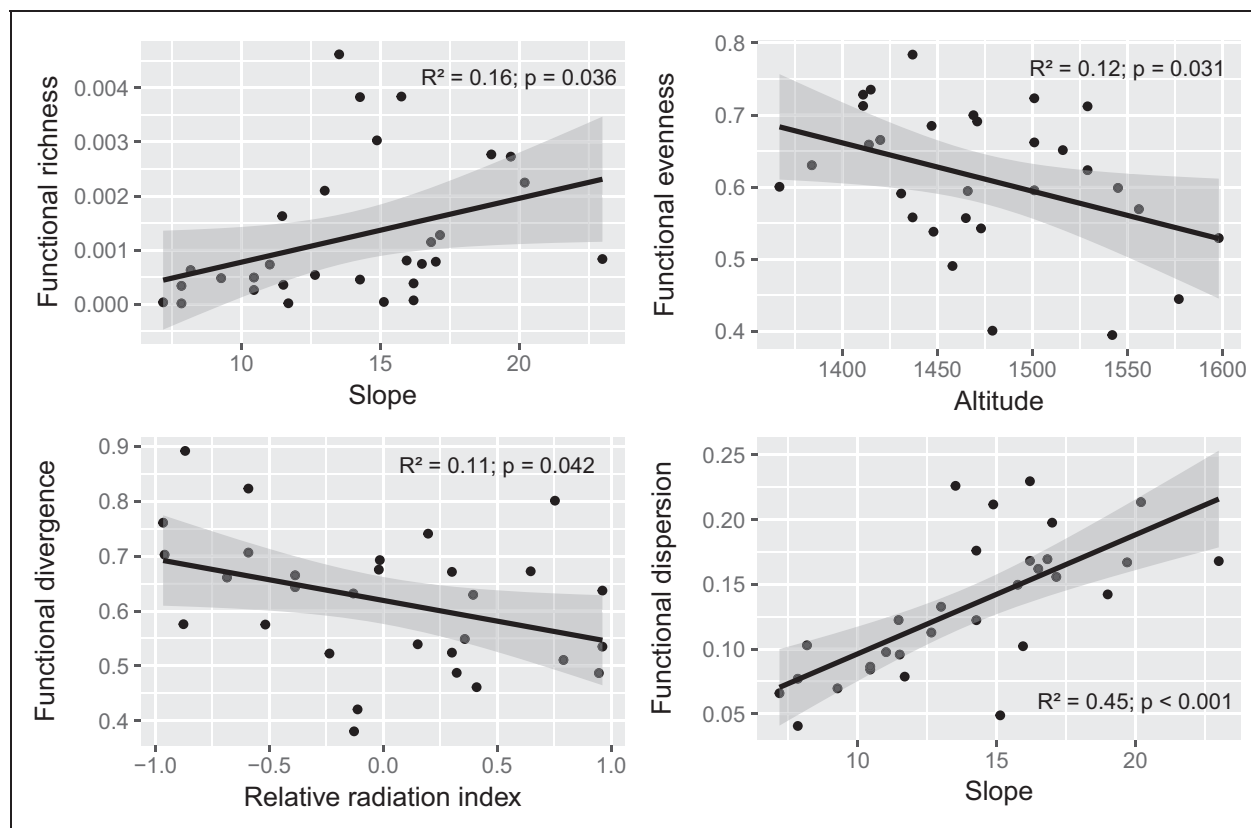


Figure 5. Bivariate relationship between functional diversity metrics and variables retained by the final models; statistics are obtained from the results of the subset regression analysis presented in Table 3.

light radiation (which is partly dependent on radiation index), temperature, moisture, runoff, infiltration, and soil properties (Tsui et al., 2004; Yirdaw et al., 2015). For instance, in a lowland rain forest of southern Taiwan, Tsui et al. (2004) observed higher organic carbon, available N and K, extractable Fe and exchangeable Na at upper slope position, and highest pH, available P, exchangeable Ca and Mg on the footslope. Further, a negative correlation between basal area and the percent of slope is expected because of the stability of trees that grow on steeper slopes and gravity-driven processes (Sefidi et al., 2016). Thus, water exigent species would likely be more abundant and dominant on flat and gentle slope sites, while steeper slopes (with limited water availability and soil nutrients) would tend to challenge tree growth and size. Our results corroborate with the expectations on environment-structured tree size variability and suggest that local environmental variation played substantial role in tree size variability in the studied area. The large values of coefficient of variation and skewness of diameter distribution on higher slope sites suggest that environmental filtering associated with increasing slope favors highly structured stands. This is presumably a

result of efficient use of limited resources by competing species characterized by conservative traits associated with high water stress tolerance on higher slope.

Functional diversity metrics also responded better to local-scale environmental variation compared to taxonomic diversity indices. More specifically, higher slope was significantly associated with higher functional richness and dispersion, while functional evenness and divergence decreased with increasing altitude and radiation, respectively. Our results suggest that functional trait composition is also likely dictated by small-scale topographical variables such as radiation index and altitude. In addition, incoming radiation is often considered a surrogate for moisture availability (Stohlgren & Bachand, 1997).

Harsh conditions (higher slopes, lower water-retention capacity, increased soil erosion, etc.) will tend to reduce the range of functional and growth strategies that lead species to persist, thus leading to functional clustering and low functional diversity (Asefa et al., 2017). Contrary to this, we found an opposite pattern, which can also be explained by shift in plant species composition as a result of environmental filtering associated with

slope variation. On lower or gentle slope, environmental filtering effect may be weak, and lower functional diversity could result from competitive exclusion and dominance of phenotypically similar species with acquisitive traits, which is in line with the limiting similarity theory (Abrams, 1983). As such, milder conditions in lower slopes may promote the proliferation of a few fast-growing competitive and phenotypically similar species, leading to functional clustering and lower functional diversity. On the other hand, high values of functional diversity at upper slope position suggest that environmental filtering seems to promote coexistence of species with conservative traits, probably because these species are best adapted to harsh conditions.

Concluding Remarks, Limitations, and Perspectives

We assessed the patterns of species diversity, in relation to environmental factors such as slope, altitude, and RRI in the Northern Mistbelt forests in South Africa. At local scale, there was little evidence of environmental effects on taxonomic diversity patterns. Nevertheless, differences in functional and structural diversity seemed to be caused by topological constraints, particularly difference in slope, altitude, and radiation. Thus, it was concluded that taxonomic diversity was less responsive to topographical variation than structural and functional diversity. Both structural diversity and functional diversity result from environmental filtering and exclusion based on competitive interaction between species. The results further suggest that functional diversity metrics especially functional evenness, divergence, and dispersion are good species diversity proxies to be considered in studies addressing diversity response to local-scale environment.

This study addressed an important aspect of the diversity–environment relationship, yet there is need to acknowledge the small plot size and subsequent sampling effects, which may overrule the effect of the extent of species occurrence patterns and range of taxonomic diversity. Structural diversity metrics in contrast might have better reflected both positive and negative interactions between and within species. It is also important to note that only few environmental variables (slope, aspect, and topography) were considered while others (e.g., edaphic, soil nutrients) might also be of significance; factors such as soil depth, for example, shallower on steep slopes versus deeper on flat or undulating slopes may well influence tree size and species distribution. Similarly, soil moisture content or plant available water might also be of significance. Research investigating how edaphic factors and soil fertility measures such as cation exchange capacity in interaction with topography influence diversity variables would contribute additional insights into our

understanding of the patterns and processes behind diversity and environment relationship.

Implications for Conservation

Northern Mistbelt forests are one of the few natural vegetation habitats in South Africa that have expanded into potentially suitable areas due to protection of the larger landscape against fire, for timber plantations and intensive agriculture. Today, these forests despite their limited extent are important habitats for wild animals, pollinators, and many tree species. Taking into account the historical fire disturbance, the present study suggests that the relatively strict conservation of these forests and fire management interventions (protection of surrounding land uses against fire) have reduced the human disturbance impacts and contributed to a recovery of these forests and more particularly to predominance of functionally similar species on lower slope sites. Our study showed higher functional diversity (coexistence of species with functionally divergent traits) on higher slope sites, suggesting that these environmental characteristics are suitable for conservation areas. However, in addition to the biodiversity component, a better understanding of the structures of these forests is important to develop further conservation strategies for enhancing their service provision.

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