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SPECIALTY SECTION
This article was submitted to
Biogeochemical Dynamics,
a section of the journal
Frontiers in Environmental Science

RECEIVED 09 July 2022
ACCEPTED 19 August 2022
PUBLISHED 14 September 2022

CITATION
Su Y, Jia X, Zhang L and Chen H (2022),
Size-dependent associations of woody
plant structural diversity with soil C:N:P
stoichiometry in a subtropical forest.
Front. Environ. Sci. 10:990387.
doi: 10.3389/fenvs.2022.990387

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Size-dependent associations of woody plant structural diversity with soil C:N:P stoichiometry in a subtropical forest

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Woody plant structural diversity and soil C:N:P stoichiometry have widely been examined for their spatial patterns and changes across environmental gradients, but the interactions and relationship of these biotic and abiotic variables have not been well understood. Here, we investigated the associations of woody plant structural diversity variables with soil total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and their stoichiometry. We found only weak associations between soil C:N:P stoichiometry and species diversity variables, however, stronger significant associations were detected between C:N:P stoichiometry and species diversity variables for the adult trees and saplings when analyses were carried out with appropriate size stratification of woody plants. Most size diversity variables were significantly correlated with TOC, TN, TP, and their stoichiometric ratios, and the size diversity variables were greater in strength than species diversity in their associations with TOC, TN, TP, and C:N:P stoichiometric ratios. In most cases, C:N:P stoichiometric ratios were more sensitive than TOC, TN, or TP in predicting species diversity and size diversity. Our findings demonstrate that the associations of woody plant species diversity with TOC, TN, TP, C:N:P stoichiometry are size-dependent, and the size diversity is much more sensitive than species diversity in predicting the change of soil TOC, TN, TP, and C:N:P stoichiometric ratios. These findings also suggest that an appropriate size stratification will help demonstrate the linear relations between woody plant structural diversity and C:N:P stoichiometry and amplify the environmental signals from soil factors in predicting the biotic variables.

KEYWORDS

soil factor, C:N:P stoichiometry, species diversity, size diversity, random forest

Introduction

Soil organic carbon (C), nitrogen (N), and phosphorus (P) are important elements for sustaining forest ecosystem functions and for maintaining forest biodiversity (Kirkby et al., 2013; Di Palo and Fornara, 2015; Wilson et al., 2019), and the relationships of these elements with ecosystem functions and forest biodiversity may be usefully assessed based on C:N:P stoichiometry (Sterner and Elser, 2002; Cleveland and Liptzin, 2007). C:N:P stoichiometric study of biological resources has attracted increasing attention since the “Redfield ratio” was established with plankton in 1958 (Redfield, 1958; Cleveland and Liptzin, 2007). Since then, research on C:N:P stoichiometry has been applied to terrestrial higher plants, and a growing number of stoichiometric studies have been reported on scales ranging from individual plants to populations and communities, with some consistent findings for the C:N:P stoichiometric ratios in plant organs of specific species, especially in plant leaves (Cao and Chen, 2017; Li et al., 2017; Peng et al., 2017; Hu et al., 2018). The study of soil C:N:P stoichiometry is an important extension from biotic resource stoichiometry to environmental and ecosystem stoichiometry (Zhao et al., 2015; Soares et al., 2017; Farrell et al., 2018). To date, however, no specific soil type or ecosystem has been found to have a definite stoichiometric ratio. This is mainly because the soil ecosystem is affected by soil type and formation (Mendoza-Vega et al., 2003; Munoz-Rojas et al., 2012), vegetation cover (Egli et al., 2007; Oueslati et al., 2013), anthropogenic activities (Dintwe and Okin, 2018; Chang et al., 2019), climate change (Fantappie et al., 2011; Reynolds et al., 2015; Puissant et al., 2017), and many other biotic and abiotic factors (e.g., Zhang et al., 2013).

Studies on resource and environmental stoichiometry have mainly revealed the differences in the stoichiometric properties of plant species and soil composition under various

gradients related to biotic and abiotic factors (Su et al., 2012; Nottingham et al., 2015; Hu et al., 2018; Saeed et al., 2019; Xu et al., 2019). These biotic and environmental gradients involve latitude, altitude, land use types, climate, community types, and community successional stages (Di Palo and Fornara, 2015; Liang et al., 2018). At the community or stand level, however, few studies have determined how soil C, N, and P and their stoichiometric ratios are related to biotic variables such as species composition, community structure, and biodiversity. A recent study of a subtropical forest ecosystem of the same area showed a consistent pattern for the spatial heterogeneity of soil C:N:P stoichiometric ratios, which could predict the changes of certain community indicators to some extent and were sensitive in response to a negative elevation-dependent warming gradient (Su et al., 2020). From this point of view, an appropriate stratification of environmental gradients can help reveal the relationships between response variables and the weak environmental signals from abiotic or biotic factors.

By definition, the structural diversity of woody plant community comprises species diversity and tree size diversity (Zlatanov et al., 2013; He et al., 2017), and can be measured and described by species richness, abundance, species diversity indexes, and tree size (Fang et al., 2012; Zlatanov et al., 2013). While a variety of metrics have been used in quantifying species diversity, size diversity is commonly quantified by tree diameter at breast height (DBH) or basal area, a proxy variable of biomass or productivity widely used in forest ecological studies (Nguyen et al., 2012; Zhong et al., 2017). Woody plant structural diversity and soil C:N:P stoichiometry have been widely and yet independently examined for their spatial patterns and changes across environmental gradients, but the interactions and relationship of these biotic and abiotic variables have not been well understood. To clarify how woody plant diversity are associated with soil C:N:P stoichiometry will help understand the interactions of

TABLE 1 | Species composition of the woody plants (DBH \geq 1 cm) in the sample plot and forest communities. The values of number of stems per species, stem density, and species density have been rounded to whole numbers.

Indicator	Plot	TWINSPAN-based community			
		1	2	3	4
Number of quadrats	200	54	76	26	44
Number of species	141	91	93	102	108
Number of stems	37,778	9,895	14,654	6,351	6,878
Number of families	52	42	41	43	44
Number of stems per species	268	109	158	62	63
Stem density (stems/ha)	4,722	4,581	4,820	6,107	3,908
Species density (species/ha)	18	42	31	98	61

major biotic and abiotic factors in a forest ecosystem. Here, we focused on the patterns of woody plant structural diversity as related to soil total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and their stoichiometric ratios. Our study had three objectives: 1) to determine whether and how woody plant species composition is affected by the spatial distribution of soil TOC, TN, TP, and C:N:P stoichiometry; 2) to evaluate the relationships between woody plant species diversity and soil TOC, TN, TP, and C:N:P stoichiometry, and to determine whether these relationships are size-dependent; and 3) to determine the relative importance of abiotic variables in predicting the biotic variables, as well as the relative importance of biotic variables in predicting abiotic variables. To achieve these objectives, we carried out a field investigation in a subtropical forest to collect both vegetation and soil data

for analyses of their relationships using a variety of statistical and data-mining methods.

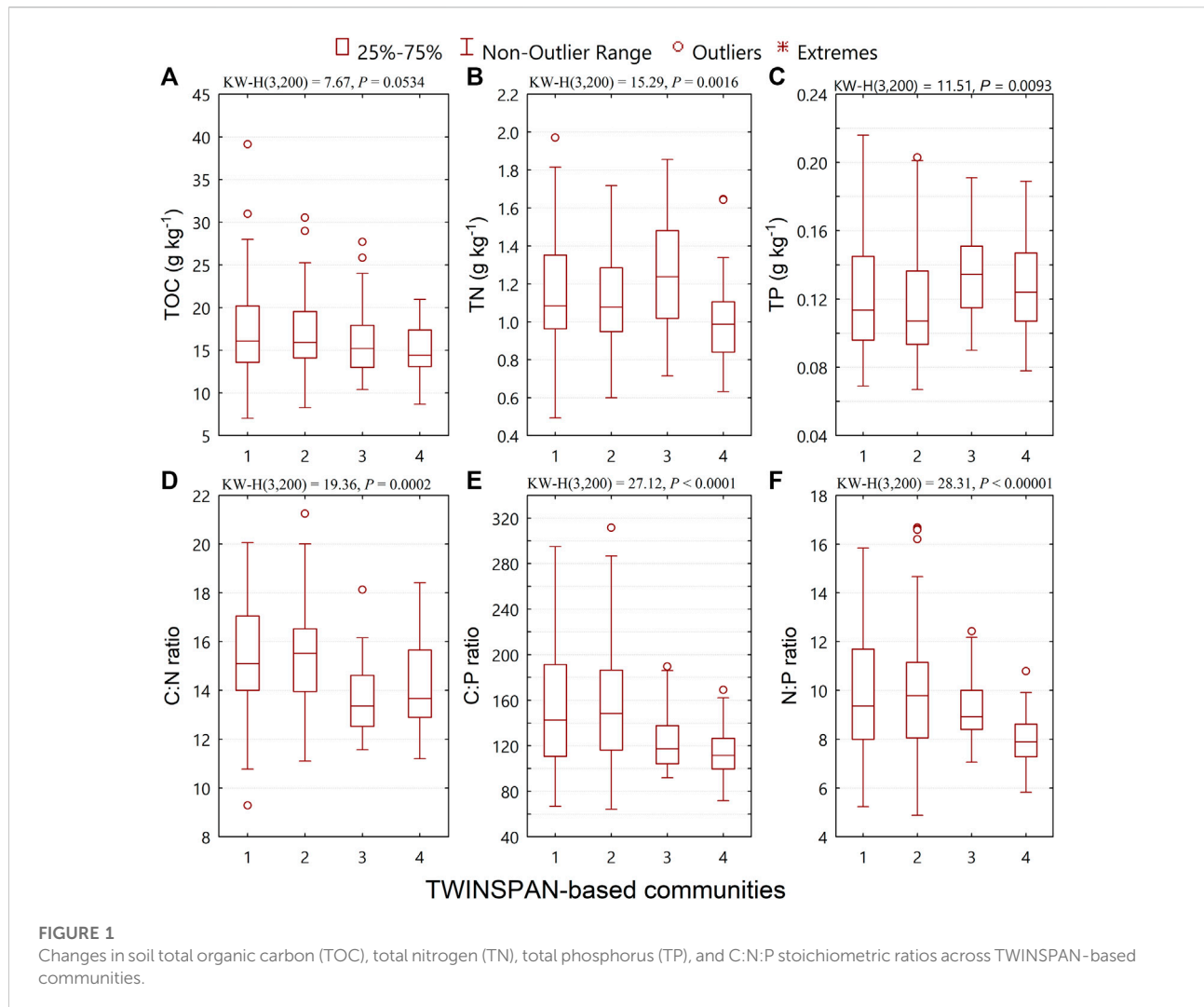
Materials and methods

Study area and sampling design

Our study site was located at the Kanghe Provincial Nature Reserve (23°44'37"–23°52'16" N, 115°04'27"–115°09'41" E) in the eastern part of Guangdong Province in south China. This area has a humid subtropical monsoon climate, with a mean annual temperature ranging from 20.3 to 21.1°C and a mean annual precipitation of 2,142 mm (Hu et al., 2015; He et al., 2017; Su et al., 2020). Soils in the area are predominantly clay loamy

TABLE 2 Pearson correlation coefficients of six vegetation-related biotic factors with soil total organic carbon (TOC, g kg⁻¹), total nitrogen (TN, g kg⁻¹), total phosphorus (TP, g kg⁻¹), and C:N:P stoichiometric ratios at the quadrat level. Asterisks (*, **, or ***) alongside a coefficient indicate statistical significance at $p < 0.05$, < 0.001 , or < 0.0001 , respectively.

Biotic factors	Abiotic factors					
	TOC	TN	TP	C:N ratio	C:P ratio	N:P ratio
Seedlings (1 cm ≤ DBH < 2.5 cm); 16,490 stems of 111 species						
Number of stems	0.09	0.06	0.08	-0.09	-0.09	-0.07
Number of species	0.03	0.03	0.01	0.01	-0.02	-0.02
Number of stems per species	0.04	0.00	0.07	-0.11	-0.13	-0.12
Shannon-Wiener index	-0.02	0.05	-0.03	0.08	0.08	0.08
Pielou's evenness	-0.06	0.04	-0.04	0.06	0.10	0.11
Berger-Parker index	0.01	-0.08	-0.01	-0.05	-0.07	-0.08
Saplings (2.5 cm ≤ DBH < 12.5 cm); 13,977 stems of 114 species						
Number of stems	0.09	0.20**	0.13	-0.11	0.00	0.07
Number of species	0.04	0.10	0.13	-0.15*	-0.13	-0.09
Number of stems per species	0.07	0.17*	0.05	-0.02	0.10	0.15*
Shannon-Wiener index	-0.02	-0.02	0.06	-0.12	-0.16*	-0.15*
Pielou's evenness	-0.06	-0.12	0.01	-0.09	-0.17*	-0.19**
Berger-Parker index	0.01	0.06	-0.02	0.11	0.14	0.13
Adult trees (DBH ≥ 12.5 cm); 7311 stems of 79 species						
Number of stems	0.13	0.25**	0.05	0.04	0.21**	0.26**
Number of species	-0.23**	-0.14	0.01	-0.23**	-0.27**	-0.21**
Number of stems per species	0.20**	0.25**	0.09	0.12	0.25**	0.24**
Shannon-Wiener index	-0.26**	-0.24	-0.04	-0.22**	-0.32***	-0.28***
Pielou's evenness	-0.22**	-0.30***	-0.06	-0.15*	-0.31***	-0.31***
Berger-Parker index	0.25**	0.26**	0.04	0.20**	0.33***	0.31***
Trees of all sizes (DBH ≥ 1 cm); 37,778 stems of 141 species						
Number of stems	0.11	0.17*	0.11	-0.10	-0.02	0.02
Number of species	-0.01	0.05	0.10	-0.13	-0.16*	-0.13
Number of stems per species	0.12	0.15*	0.05	-0.03	0.08	0.12
Shannon-Wiener index	-0.09	-0.05	0.03	-0.10	-0.17*	-0.15*
Pielou's evenness	-0.13	-0.12	-0.02	-0.07	-0.15*	-0.15*
Berger-Parker index	0.07	0.04	0.00	0.08	0.12	0.10



latosols developed from granite. The major vegetation type in the nature reserve is subtropical secondary forest dominated by hardwood tree species in the families of Fagaceae, Theaceae, and Iteaceae (He et al., 2017; Su et al., 2020). The forest ecosystem has been well protected since the founding of the nature reserve in 1991. As documented by the nature reserve's administration office, no major natural or anthropogenic disturbance occurred in this area in the past 50 years.

We used a total station (Nikon DTM-310, Nikon Geotecs Co. Ltd., Tokyo, Japan) to measure site topography and to establish an 8-ha rectangular plot (200 m × 400 m) on a forested slope in the nature reserve. The plot was divided into 200 contiguous square quadrats (20 m × 20 m) for field data collection. The quadrats were numbered and marked by placing PVC (polyvinyl chloride) tubes at the 20-m corners within the plot, and the elevation at each 20-m corner was recorded by the total station. The elevation of each quadrat was calculated by averaging the elevation values at its four

corners (Lai et al., 2009), and the mean elevation of the plot was 291.4 m.

Data collection

We collected data from all tree individuals ≥ 1 cm diameter at breast height (DBH) in each quadrat. All censused individuals were identified to species and recorded for species identity and DBH value measured to the nearest 0.1 cm. For exact DBH measurement, trees ≤ 5 cm DBH were measured with a dial caliper, and those > 5 cm DBH were measured with a diameter tape. Plant taxonomy and systematics followed Ye and Peng (2006).

A total of 200 composite soil samples (one per quadrat) were collected. To collect a composite soil sample for each quadrat, we first collected five subsamples of mineral soils to a depth of 25 cm in each quadrat. These subsamples of mineral soils were then evenly mixed to produce one homogenized

TABLE 3 The relative importance of soil total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and C:N:P stoichiometric ratios in predicting vegetation-related variables as determined by Random forest analysis. In this analysis, values range from 0.00 to 1.00, and higher values indicate greater relative importance.

Response variable	Predictor variable					
	TOC	TN	TP	C:N ratio	C:P ratio	N:P ratio
Number of stems	0.93	1.00	0.77	0.92	0.92	0.87
Number of species	0.81	0.64	1.00	0.91	0.94	0.92
Number of stems per species	0.96	0.88	0.95	0.80	1.00	0.99
Shannon-Wienetblr index	0.81	0.65	0.71	0.91	1.00	0.87
Pielou's evenness	0.89	0.87	0.74	0.93	0.95	1.00
Berger-Parker index	0.73	0.61	0.62	0.62	1.00	0.92
Basal area	0.73	0.71	0.71	1.00	1.00	0.97
Size diversity index	0.71	0.69	0.80	0.77	0.90	1.00
Size-dependent evenness	0.84	0.87	0.88	0.90	0.98	1.00
Size-dependent Berger-Parker index	0.67	0.70	0.79	0.69	1.00	0.87

composite sample per quadrat. Soil samples were transported to the laboratory and then air-dried, thoroughly ground, and passed through a 2-mm mesh sieve. Total soil organic carbon (TOC) and total nitrogen (TN) contents were determined by dry combustion using a vario-Max N/CN elemental analyzer (Elementar Analysensysteme GmbH, Germany), while total phosphorus (TP) content was determined by the ammonium molybdate colorimetric method (Bao, 2000). We calculated C:N:P stoichiometric values as the ratios of TOC to TN (C:N), TOC to TP (C:P), and TN to TP (N:P).

Data analysis

To determine whether and how woody plant species composition is related to the spatial distribution of soil TOC, TN, TP, and C:N:P stoichiometry, we first performed two-way indicator species analysis (TWINSPAN) to group the forest vegetation of the 8-ha plot into four communities. TWINSPAN is a generally recognized and widely-used approach for community classification based on species composition data, and the resulting communities or vegetation groups reflect the differences in species composition and community structure (McCune et al., 2002). We then used the Kruskal-Wallis test, a nonparametric method that is appropriate for use with field ecology data, to determine whether there were significant differences in TOC, TN, TP, and

C:N:P stoichiometric ratios across the TWINSPAN-based communities.

To evaluate the relationships between woody plant species diversity and soil TOC, TN, TP, and C:N:P stoichiometry, and to examine whether these relationships were size-dependent, we first grouped all tree individuals into three size classes, i.e., seedlings, saplings, and adults, as defined by DBH values using the following criteria: seedlings, 1 cm \leq DBH < 2.5 cm; saplings: 2.5 cm \leq DBH < 12.5 cm; and adult trees: DBH \geq 12.5 cm (He et al., 2017). We then calculated species richness (number of species), total abundance (number of stems), number of stems per species, the Shannon-Weiner diversity index, Pielou's evenness, and the Berger-Parker index by four size groups, i.e., all sizes (i.e., non-stratified data), seedlings, saplings, and adult trees, for each quadrat. Finally, we performed correlation analysis to determine the relationships between these species abundance-based diversity variables and soil TOC, TN, TP, and C:N:P stoichiometric ratios.

The Shannon-Wiener diversity index, Pielou's evenness, and the Berger-Parker index were calculated with the following formulas (Magurran and McGill, 2011):

$$H' = - \sum P_i \ln P_i \quad (1)$$

$$E = H' / \ln S \quad (2)$$

$$D_{B-P} = N_{max} / N \quad (3)$$

where H' is the Shannon-Wiener diversity index, and P_i is the relative abundance of the i th species in proportion to the total number of stems in a quadrat; E is the Pielou's evenness, and S is the number of species in a quadrat; D_{B-P} is the Berger-Parker index, N_{max} is the number of stems of the most abundant species, and N is the total number of stems in a quadrat.

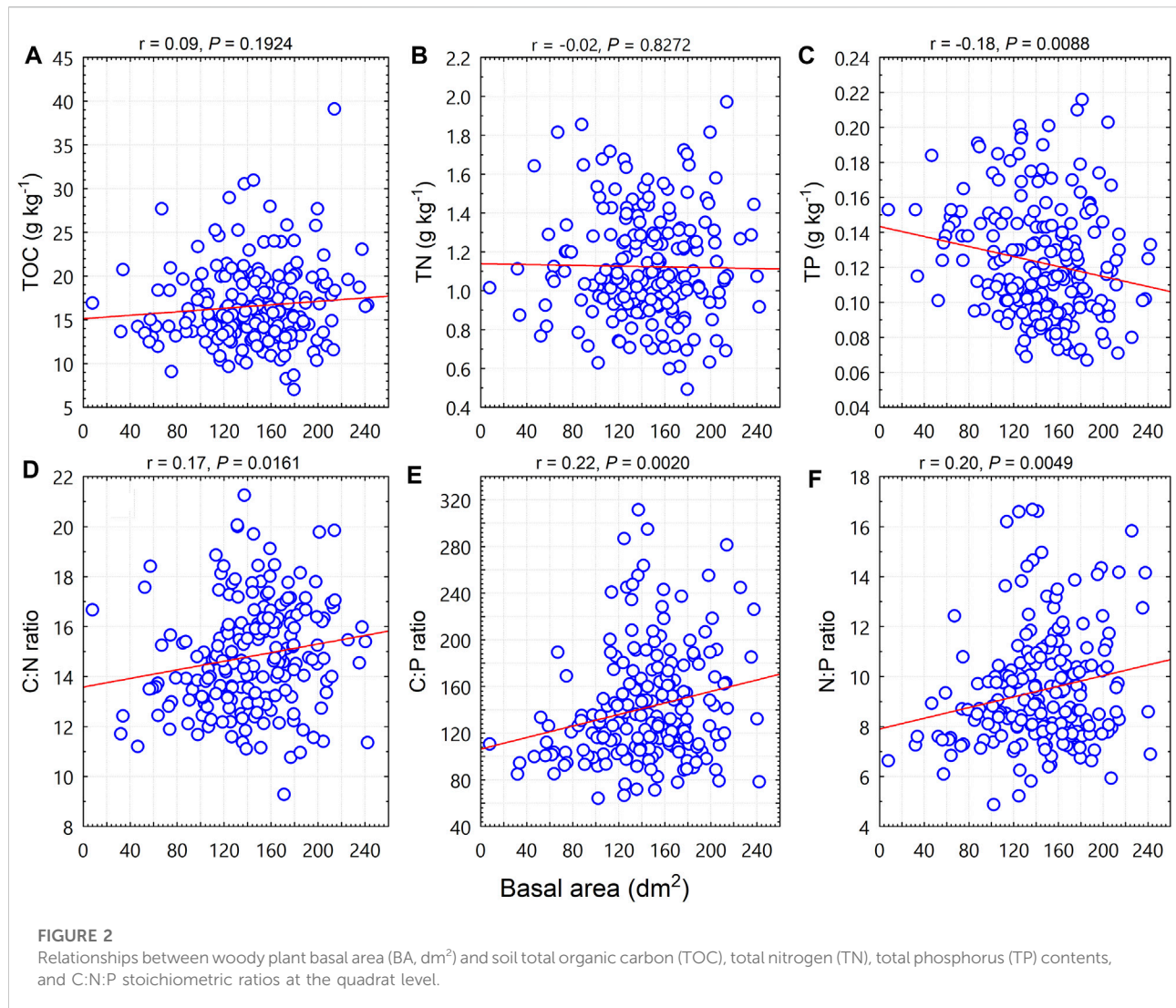
We performed correlation analyses to reveal the relationships between tree size diversity and soil TOC, TN, TP, and C:N:P stoichiometric ratios. We defined the size diversity as the variability in basal area (BA), size diversity index, size-dependent evenness, and the size-dependent Berger-Parker index across quadrats. We calculated the size diversity variables with the dataset for trees of all sizes. The size diversity index, size-dependent evenness, and size-dependent Berger-Parker index were calculated based on the Shannon-Wiener index, Pielou's evenness, and the Berger-Parker index, respectively, with the following formulas:

$$D_{size} = - \sum P_{BAi} \ln P_{BAi} \quad (4)$$

$$E_{size} = D_{size} / \ln S \quad (5)$$

$$D_{B-P(size)} = BA_{max} / BA_{Total} \quad (6)$$

where D_{size} is the size diversity index, and P_{BAi} is the relative basal area of the i th species in proportion to the total basal area of all



species in a quadrat; E_{size} is size-dependent evenness; $D_{B-P(size)}$ is the size-dependent Berger-Parker index, BA_{max} is the basal area of the most dominant species by size, and BA_{Total} is the total basal area of stems in a quadrat.

We used Random Forest to model the relationships between predictor variables and response variables. Random Forest is a data mining algorithm that does not require conventional statistical assumptions for variables (Breiman, 2001; Breiman et al., 2003). Because the relationships between the vegetation-related biotic variables and the abiotic variables (TOC, TN, TP, and C:N:P stoichiometric ratios) are interdependent, either the biotic variables or the abiotic variables can be used as predictor variables or response variables. We used the Random Forest regression model to assess the relative importance of the six abiotic variables in predicting the 10 biotic variables, as well as the relative importance of the biotic variables in predicting the

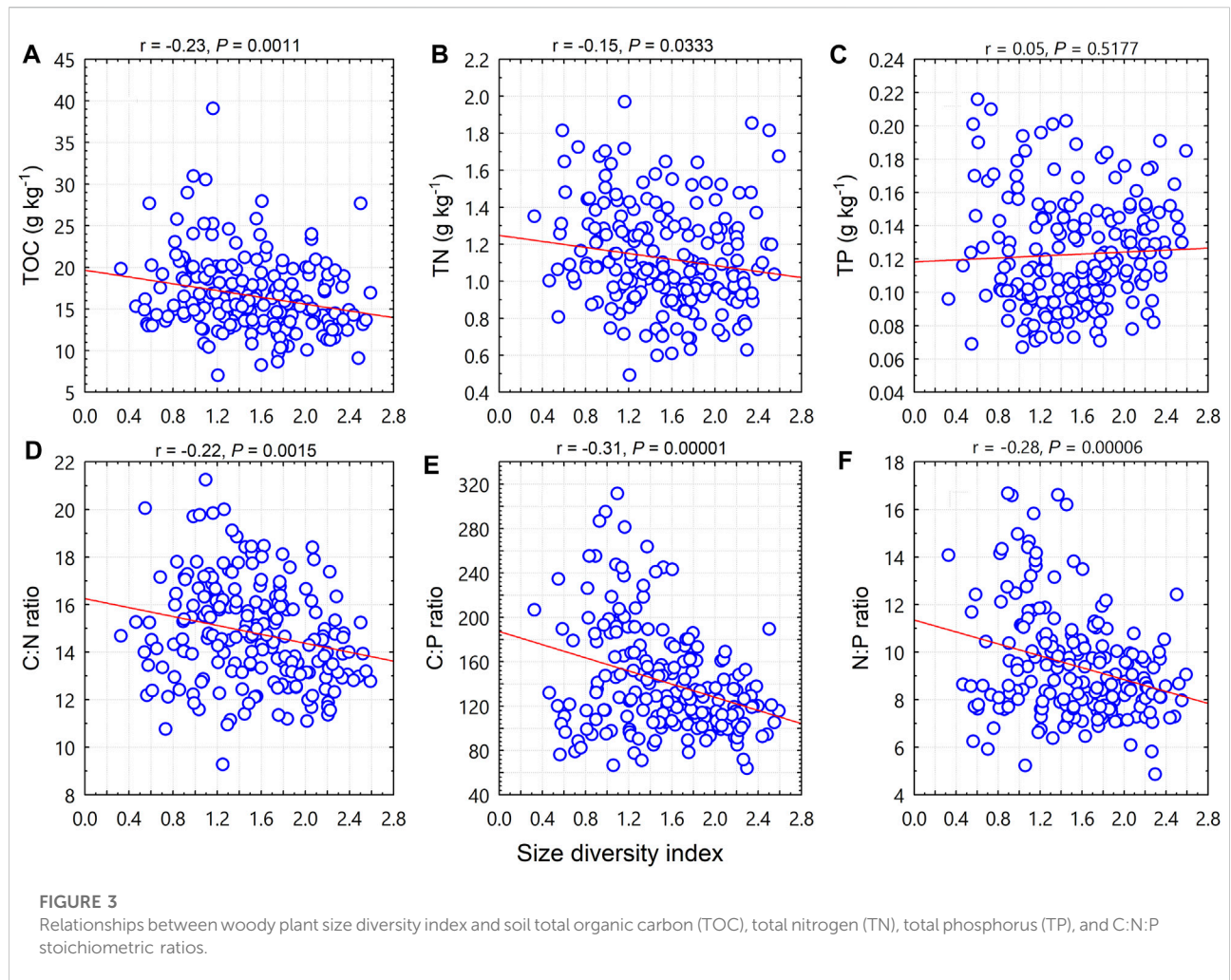
abiotic variables. The relative importance of predictor variables ranged from 0 (no importance) to 1 (substantial importance).

TWINSPAN and the calculation of diversity variables were carried out with PC-ORD version 7.0 (MjM Software, Gleneden Beach, Oregon, United States). Kruskal–Wallis tests, correlation analysis, and the Random Forest regression model were executed with Statistica version 8 (Statsoft, Inc. Tulsa, OK, United States).

Results

Species composition

We recorded a total of 37,778 stems ≥ 1 cm DBH of 141 woody plant species from 52 families in our census of



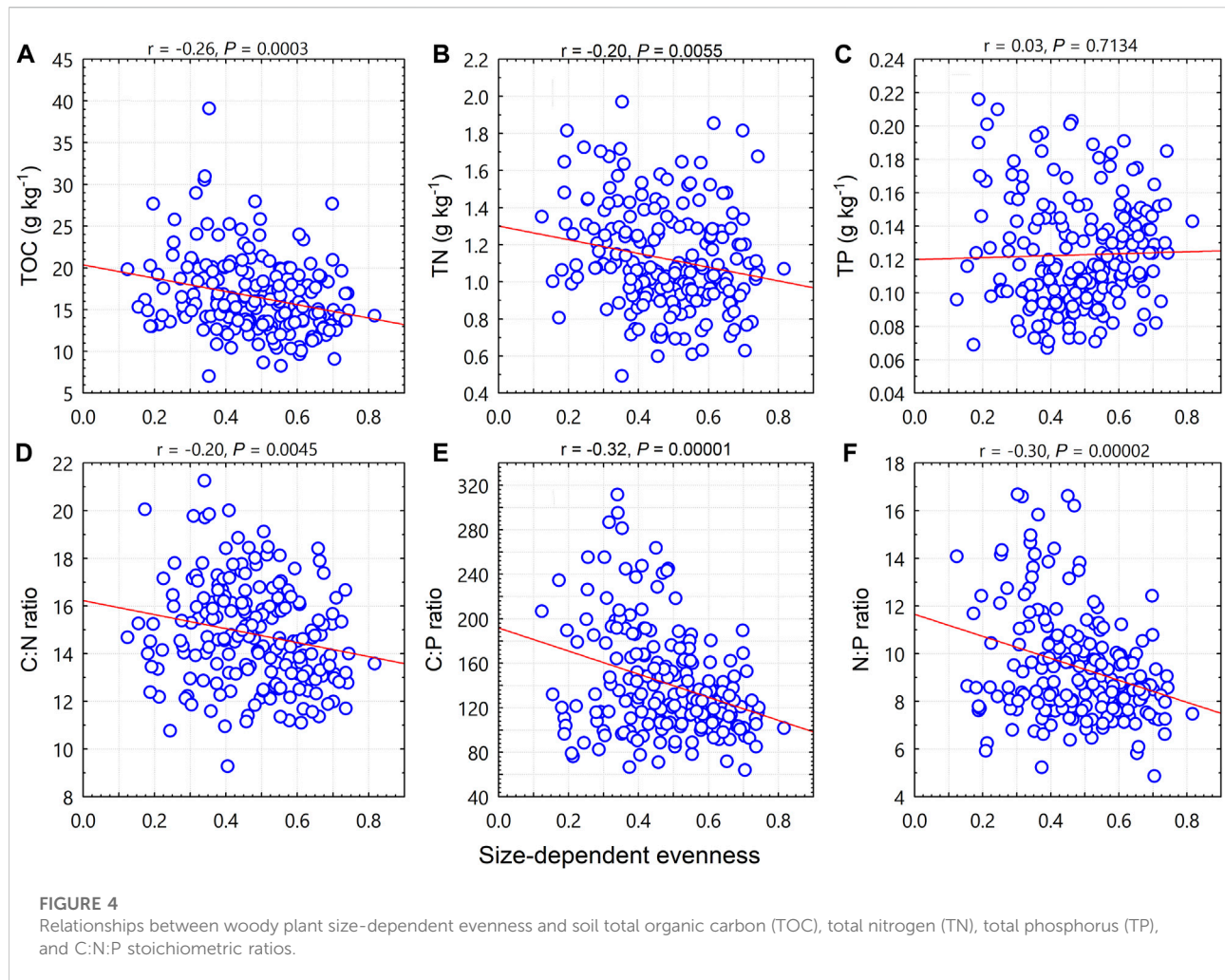
trees in the 8-ha plot. The four TWINSpan-based communities differed in terms of species composition, the number of stems per species, stem density, and species density (Table 1). The number of stems per species, also termed species-specific density (Niklas et al., 2003), exhibited different explanatory capability in separating the communities as compared with stem density and species density. The number of stems per species was highest for community 2 and lowest for both community 3 and 4, while the values of both stem density and species density were highest for community 3 (Table 1).

We found significant differences in soil total nitrogen (TN), total phosphorus (TP), and the C:N:P stoichiometric ratios across the TWINSpan-based communities (Figure 1). The difference in soil total organic carbon (TOC) across the communities was also marginally significant ($P = 0.0534$; Figure 1A). The values of the Kruskal–Wallis test statistics (KW-H) were higher for the C:N:P stoichiometric ratios than for TOC, TN, or TP (Figure 1), while the p -values for the significance level of the C:N:P stoichiometric ratios ($p < 0.001$)

were lower than for TOC ($p = 0.0534$; Figure 1A) or for TN or TP ($p < 0.01$; Figures 1B,C). These results indicated that the C:N:P stoichiometric ratios were more sensitive in predicting the change in species composition across communities than either TOC, TN, or TP.

Species diversity

We found size-dependent associations of woody plant species diversity with TOC, TN, TP, and the C:N:P stoichiometric ratios (Table 2). Linear relationships between species diversity variables and TOC, TN, TP, and C:N:P stoichiometric ratios were significant for sapling and adult tree size classes, but not for the seedling size class (Table 2). Only eight of 36 correlation coefficients were significant for the sapling size class, but 26 of 36 correlation coefficients were significant for the adult tree size class (Table 2). For the trees of all sizes, only 7 of 36 correlation coefficients were significant (Table 2), an outcome most probably due to the fact that the

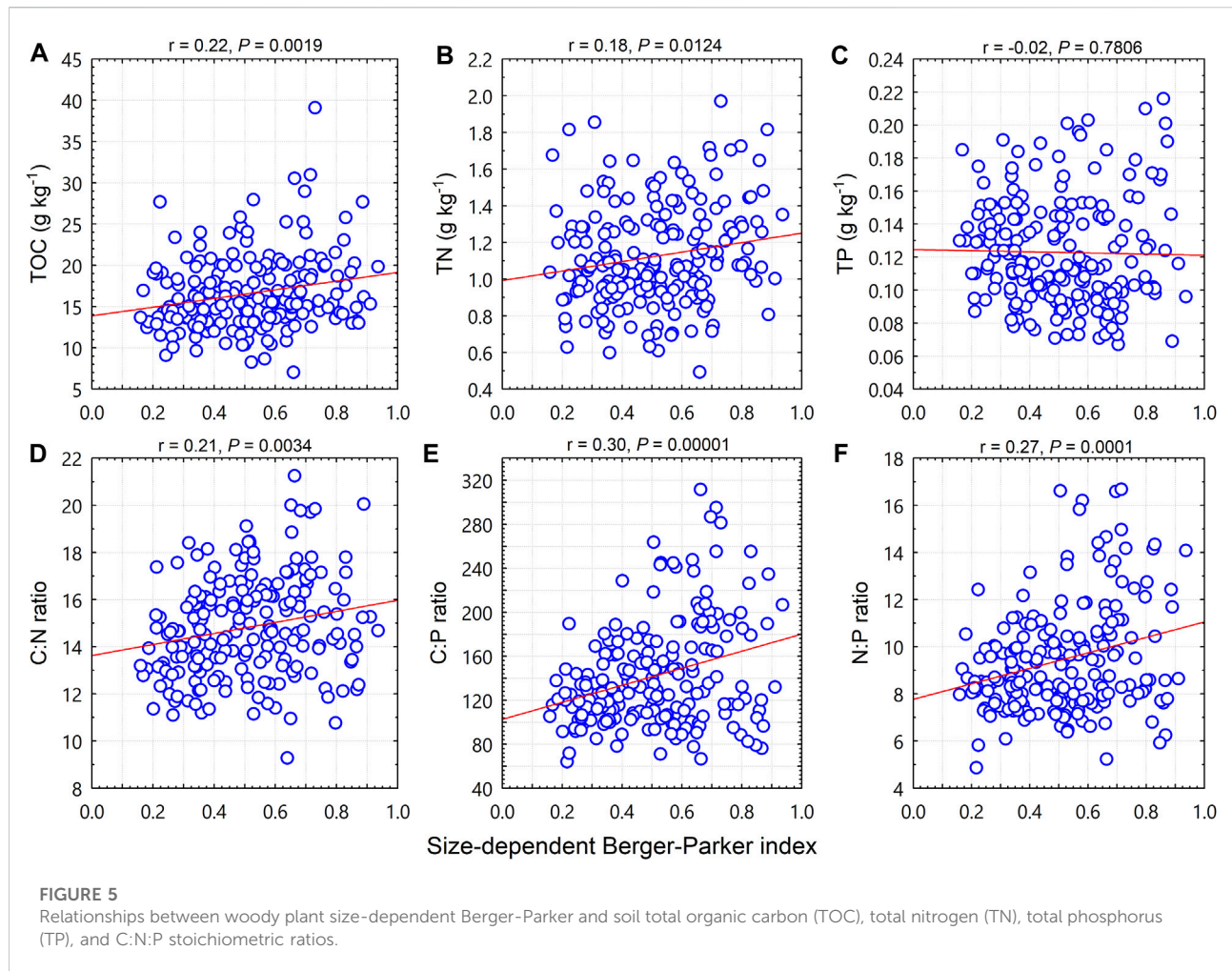


number of stems of the two most abundant size classes, i.e., seedlings (16,490 stems) and saplings (13,977 stems), together accounted for 80.6% of the total species abundance (Table 2).

The strength of the correlation coefficients in the relationships between species diversity variables and TOC, TN, TP, and C:N:P stoichiometric ratios was generally greater for the adult size class than for the sapling size class (Table 2). For the sapling size class, the relationship between the number of stems and TN was positive and highly significant ($p < 0.01$), whereas the relationship between Pielou's evenness and N:P ratio was negative and highly significant ($p < 0.01$). The number of stems per species was positively correlated with TN and N:P ratio ($p < 0.05$), while C:P was negatively correlated with the Shannon-Wiener index and Pielou's evenness ($p < 0.05$).

The relationships between diversity variables and TOC, TN, TP, and the stoichiometric ratios for the adult tree size class followed similar patterns (positive or negative) as

those of the sapling size class. Higher nutrient status and their stoichiometric ratios would favor the abundance-dependent variables, such as the number of stems, number of stems per species, and the Berger-Parker dominance index, resulting in a positive correlation, while these nutrient-related variables were negatively correlated with the richness-dependent diversity variables, such as number of species, the Shannon-Wiener diversity index, and Pielou's evenness. Among the positive correlations, the coefficient was highest for the relationship between the Berger-Parker index and the C:P ratio ($r = 0.33, p < 0.001$; Table 2), followed by the relationship between the Berger-Parker index and the N:P ratio. Among the negative correlations, the coefficient was highest for the relationship between the Shannon-Wiener index and the C:P ratio ($r = -0.32, p < 0.001$; Table 2), followed by the relationships between Pielou's evenness and the C:P ratio, Pielou's evenness and the N:P ratio, and Pielou's evenness and TN (Table 2).



Size diversity

Relationships with TOC, TN, TP, and C:N:P stoichiometric ratios for size diversity variables differed from those described in the previous section for species diversity variables. Basal area (BA) was negatively correlated with TP ($p < 0.01$; Figure 2C), and was positively correlated with the C:N ratio ($p < 0.05$; Figure 2D), the C:P ratio ($p < 0.01$; Figure 2E), and the N:P ratio ($p < 0.01$; Figure 2F); BA was not correlated with TOC ($p = 0.19$; Figure 2A) or TN ($p = 0.83$; Figure 2B).

The size diversity index was negatively correlated with TOC ($p < 0.01$; Figure 3A), TN ($p < 0.05$; Figure 3B), the C:N ratio ($p < 0.001$; Figure 3D), the C:P ratio ($p < 0.0001$; Figure 3E), and the N:P ratio ($p < 0.0001$; Figure 3F), but was not correlated with TP ($p = 0.52$; Figure 3C).

Like the size diversity index, size-dependent evenness was negatively correlated with TOC ($p < 0.001$; Figure 4A), TN ($p < 0.01$; Figure 4B), the C:N ratio ($p < 0.01$; Figure 4D), the C:P ratio ($p < 0.0001$; Figure 4E), and the N:P ratio ($p < 0.0001$; Figure 4F), but was not correlated with TP ($p = 0.71$; Figure 4C).

Unlike the size diversity index or the size-dependent evenness, the size-dependent Berger-Parker index was positively correlated with TOC ($p < 0.01$; Figure 5A), TN ($p < 0.05$; Figure 5B), the C:N ratio ($p < 0.01$; Figure 5D), the C:P ratio ($p < 0.0001$; Figure 5E), and the N:P ratio ($p < 0.001$; Figure 5F), but was not correlated with TP ($p = 0.78$; Figure 5C).

Predictability of variables

The relative importance of the biotic factors (i.e., the structural diversity variables), in predicting the spatial variability of TOC, TN, TP, and C:N:P stoichiometric ratios is shown in Figure 6. Among the 10 biotic predictor variables, the most important variable for predicting TOC was size-dependent evenness (Figure 6A); for predicting the C:N ratio was the size diversity index (Figure 6B); for predicting TN was Pielou's evenness (Figure 6C); for predicting the C:P ratio was the size diversity index and size-dependent evenness

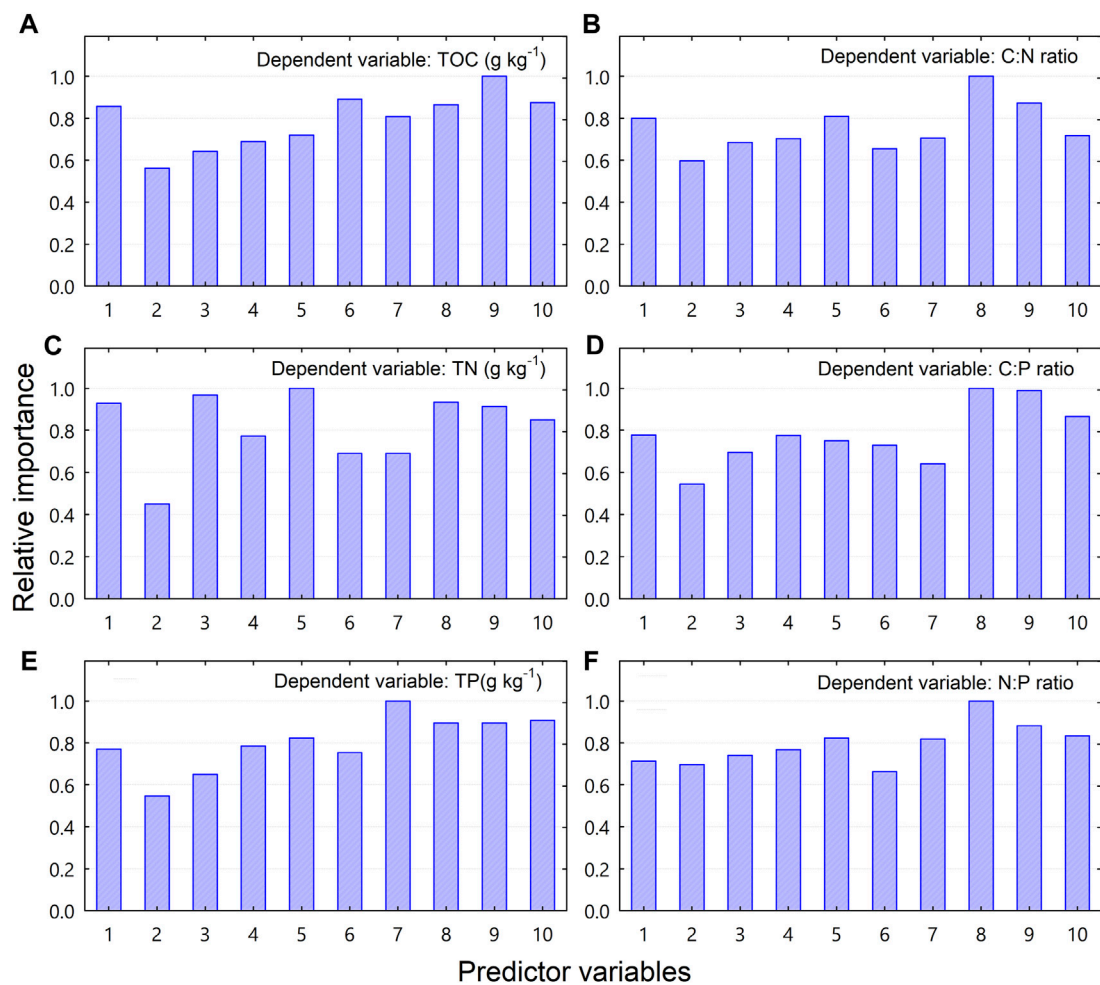


FIGURE 6

Relative importance of vegetation-related variables in predicting soil total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and C:N:P stoichiometric ratios as determined by the Random Forest regression model. Code for predictor variables: 1 = number of stems; 2 = number of species; 3 = number of stems per species; 4 = Shannon-Wiener index; 5 = Pielou's evenness; 6 = Berger-Parker index; 7 = basal area; 8 = size diversity index; 9 = size-dependent evenness; 10 = size-dependent Berger-Parker index.

(Figure 6D); for predicting TP was basal area (Figure 6E); and for predicting the N:P ratio was the size diversity index (Figure 6F).

When using the abiotic factors as predictor variables and the biotic factors as response variables, we found that the C:N:P stoichiometric ratios were much more important than TOC, TN, or TP (Table 3). TN and TP were the most important variables for predicting the number of stems and number of species, respectively. The C:N ratio was the most important variable for predicting total basal area. Both the C:P and N:P ratios were the most important variables for predicting a number of structural diversity variables (Table 3). In most cases, predictor importance was greater for C:N:P stoichiometric ratios than for TOC, TN, or TP.

Discussion

We found that associations between woody plant structural diversity and soil C:N:P stoichiometry were size-dependent, i.e., depended on the size of the woody plants. To our surprise, correlations between woody plant species diversity variables and topsoil TOC, TN, TP, and their stoichiometric ratios were not significant for seedlings but were significant for adult-sized trees. It would be expected that seedlings, which are small and have shallow root systems, should be more closely related with topsoil nutrient variables than were saplings and adult trees (Lin et al., 2016; Scholten et al., 2017; Chen et al., 2019). Relative to adult trees and saplings, seedlings are likely to be more susceptible to biotic and non-soil abiotic factors, such as the

competition from canopy trees, understory radiation, pests and pathogens, and animal damage. Therefore, the associations of woody plant seedlings with topsoil TOC, TN, TP, and their stoichiometric ratios will be weakened by non-soil habitat factors.

At the population level, plant individuals can change their chemical composition to some extent so as to adapt to the chemical composition of the soils that support them (Fanin et al., 2017; Hu et al., 2018), but such changes will be quite limited because during long-term evolution, plants have formed homeostatic mechanisms that keep the chemical composition of their organisms relatively constant (Fanin et al., 2017; Bai et al., 2019). Because the coupling of C, N, and P differs among plant species, changes in species composition, richness, abundance, and diversity metrics will be an effective mechanism of plants at the community level to respond to the spatial changes of soil C, N, P, and their stoichiometric ratios. As shown by our results, higher resource availability reduced species diversity, size diversity, Pielou's evenness, and size-dependent evenness, because increases in TOC, TN, and TP will promote community dominance (Alberti et al., 2015; Aanderud et al., 2018).

The C:N:P stoichiometric ratios rather than TOC, TN, or TP showed consistent trends for predicting changes in woody plant structural diversity. For species diversity variables of the adult trees, the C:N:P stoichiometric ratios were negatively associated with species richness, the Shannon-Wiener index, and Pielou's evenness, but were positively with Berger-Parker index. Both the number of stems and number of stems per species were positively associated with the C:P ratio and the N:P ratio. For size diversity variables, both basal area and the size-dependent Berger-Parker index were positively associated with the C:N:P stoichiometric ratios, while both the size diversity index and size-dependent evenness were negatively associated with the C:N:P stoichiometric ratios. The C:N:P stoichiometric ratios not only showed consistent trends in their associations with woody plant structural diversity variables, but they significantly differed among communities, indicating that C:N:P stoichiometry is closely associated with plant community type and species composition. The C:N:P stoichiometric ratios were more sensitive than soil C, N, or P content in response to the changes in community type. This may reflect a greater influence of the coupling of two or more nutrient elements on the species composition and community structure than a single nutrient element, because C:N:P stoichiometric ratios represent the coupling and balance among the elements (Sterner and Elser, 2002).

Although the correlation analysis does not predict causal relationships between woody plant community and soil TOC, TN, TP, and their stoichiometric ratios, the

strength of the associations between them does reflect their interdependencies (Zemunik et al., 2018). Soil N and P are the major nutrients for plants to grow, while soil organic matter, which is the major source of soil organic carbon, is a reserve of the N and other nutrients required by plants (Craswell and Lefroy, 2001). On the other hand, forest plants affect soil C, N, P and their stoichiometry by forming heterogeneous habitats, regulating soil surface microclimate conditions (Toledo et al., 2011) and nutrient return, and by affecting soil microbial diversity through root metabolism (Bergkemper et al., 2016) and other process such as shading effect provided by adult trees. Given that the associations of woody plant structural diversity with soil C, N, P, and their stoichiometry were dependent on tree size, and the woody plant size diversity and productivity metrics rather than abundance-based species diversity can better reflect changes in soil C, N, P, and their stoichiometry, it could be inferred that the associations of a forest community with soil C, N, P, and their stoichiometry are driven by community productivity.

Conclusion

Associations between soil C:N:P stoichiometry and woody plant species diversity variables were weak when plant size was ignored but were strong when plant size class (seedling, sapling, and adult) was accounted for. Most size diversity variables were correlated with TOC, TN, TP, and C:N:P stoichiometric ratios, and the correlations with TOC, TN, TP, and C:N:P stoichiometric ratios were stronger with the size diversity variables than with species diversity. In most cases, C:N:P stoichiometric ratios were more sensitive than TOC, TN, or TP in predicting the spatial variability of diversity variables. Our findings demonstrate that the associations of woody plant species diversity with TOC, TN, TP, and C:N:P stoichiometry are size-dependent, and that size diversity is much more sensitive than species diversity in predicting soil TOC, TN, TP, and C:N:P stoichiometric ratios. These findings also suggest that an appropriate size stratification will help demonstrate the linear relations between woody plant structural diversity and C:N:P stoichiometry and amplify the environmental signals from soil variables in predicting the biotic variables.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

HC and YS conceived and designed the study. YS, XJ, and LZ collected the data. YS analyzed the data and wrote the paper. HC edited the paper. All authors discussed the results and approved the paper for submission.

Funding

This research was supported by the Forestry Department of Guangdong Province, China, for non-commercial ecological forest research (890-2020-XMZC-2744-01-0001).

Acknowledgments

We thank Mingfeng Xu for his help with field work. We also thank the staff of the Kanghe Provincial Nature Reserve of

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Guangdong Province, China, for logistic support during field survey.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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