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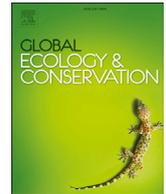
Light availability, soil phosphorus and different nitrogen forms negatively affect the functional diversity of subtropical forests

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A R T I C L E   I N F O

A B S T R A C T

Understanding the relationship between functional diversity (FD) and species diversity changes and the effects of environmental factors on FD during succession is useful to improve forest management, conservation and restoration strategies. In this study, we measured 9 environmental factors related to light availability, soil water content and nutrients, and 19 leaf functional traits related to leaf light and nutrient utilization, growth and defense, water-use efficiency, and leaf respiration strategies in the dominant species during subtropical forest succession in southern China. Logarithmic function analysis and linear mixed model were used to explore the relationships between FD and species diversity and between FD and environmental factors. The results showed that FD and species diversity were not linearly correlated during succession. The light availability (represented by leaf area index), soil phosphorus, and different nitrogen forms were negatively related to the FD, suggesting these factors were the main environmental factors affecting FD during succession in the subtropical forest. By dividing FD into components corresponding to the diversity of different plant strategies, this study improves our understanding of the roles of light availability and soil nutrients in plant community functional structure, and provides useful information for forest conservation and restoration.

1. Introduction

After severe human disturbances, forest community will undergo a series of successional stages, accompanied by the changes in community structure and function. Although many recent studies on the dynamics of forest succession revealed that there might be multiple successional pathways (Tepley et al., 2013; Arroyo-Rodríguez et al., 2017; Hilmers et al., 2018), the key attributes of community structure, i.e., species diversity (SD) and functional diversity (FD), are inherently linked to the successional stages (Seidl et al., 2016; Hilmers et al., 2018). Understanding the site-specific environmental factors that affect

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the forest structure during succession is conductive to improve forest management, conservation and restoration strategies (Cadotte et al., 2011).

At the local scale (e.g., a small patch of abandoned land or stand), soil and microclimate conditions, such as, soil nutrient, light and water availability are considered to have significant effects on community structure with succession (Asner et al., 2014; Poorter et al., 2017; Yuan et al., 2018; Gong et al., 2020). For example, soil nutrient availability is a key factor affecting tropical forest growth across the Amazon (Feldpausch et al., 2016). Kleinebecker et al. (2010) found positive linear correlations between species richness and soil total nitrogen (N) and NH_4^+-N contents. Alvarez-Clare et al. (2013) also confirmed that soil phosphorus (P) greatly affects the process of plant colonization in a lowland subtropical forest. A similar result was reported, showing that high FD in terms of nutrient uptake and utilization strategies is associated with nutrient-poor soil (Lambers et al., 2010). These environmental factors might also have indirect effects on one FD via their effects on the others. For example, soil fertility could influence community CO_2 uptake diversity by influencing the diversity of leaf P and Ca contents (Asner et al., 2014).

Seasonal effects might also have an indirect effect on the processes of forest succession (Sugai and Schimel, 1993). Some important physiological functions of the forest community, e.g., soil and leaf respiration, and microbial activity, are strongly dependent on temperature and precipitation (McGroddy et al., 2004; Yan et al., 2009), which could be reflected by the seasonal changes. In generally, the temperature and precipitation are correlated, for example, high temperature mostly occurs simultaneously with high moisture in the wet season, and low temperature and moisture occurs in the dry season in the subtropical regions (Zhou and Yan, 2001). Many studies have shown that environmental factors such as soil nutrients and water availability have important effects on the community assembly processes during succession (Asner et al., 2014; Gong et al., 2020). However, few studies have investigated these influencing processes excluding the seasonal effect, which would provide an unbiased understanding of the roles of these abiotic factors on the process of forest succession.

It is theoretically predicted that a random or uniform distribution of species within a functional dissimilarity spectrum would support a proportional relationship between FD and SD (Naeem and Wright, 2003). That is, SD would have a linear relationship with FD when the functional traits of the species are equally complementary. However, such relationship is atypical because the functional traits of some pairs of species were functional redundancy in natural ecosystems, which was beneficial to the stability of forest community structure and function (Diaz and Cabido, 2001; Cadotte et al., 2011). Although positive linear relationships between FD and SD have been found in some ecosystems (Petchey and Gaston, 2002), this trend is not universal and additional field studies should be conducted under different environmental conditions to verify their common relationship. Since SD generally tends to increase and environmental conditions will change during the process of forest succession (Li et al., 2015b), successional forests could be a good system for studying the general relationship between them.

In this study, we investigated FD, SD and environmental factors at four successional stages in the Dinghushan National Reserve in southern China. The climax plant community in this region is monsoon evergreen broadleaved forest that was heavily disturbed by human activities in the 20th century (Yan et al., 2006). Extensive long-term studies of community structures, functions, and dynamics have been conducted in these communities, and plant functional traits have been found to be good predictors of community structure (Yan et al., 2006; Li et al., 2015a). To better clarify the effects of environmental factors on community structure excluding the seasonal effect, 9 environmental factors related to light conditions, soil water and nutrient contents (Table 1), and 19 leaf functional traits related to plant light and nutrient utilization, growth and defense, water use efficiency, and leaf respiration (Table 1, A1) of dominant species were measured in both dry and wet seasons. The questions we tried to address include: (i) What is the relationship between SD and FD during subtropical forest succession? (ii) Unentangling from the seasonal effect, which environmental factors mostly affected FD in subtropical forests?

2. Materials and methods

2.1. Research site

The study site was located in the moist subtropical forests in the Dinghushan National Nature Reserve, southern China (E 112°32′57″, N 23°9′51″) (Fig. 1). This region has a monsoon climate. The mean annual precipitation is 1788 mm, 80% of which falls from April to September (Lu et al., 2018). The mean annual temperature is 21.9 °C, the mean annual relative humidity is 80%, and the coldest mean monthly temperature, which occurs in January, is 12.6 °C (Lu et al., 2018).

The Dinghushan Reserve contains four successional communities (Table 2), including a coniferous forest (SUC-2, approximately 60 years old), a mixed coniferous broadleaved forest (SUC-3, approximately 100 years old), an old-growth monsoon evergreen broadleaved forest (SUC-4, approximately 400 years old), and a nonforested grassland (SUC-1, approximately 4 years old) (Yan et al., 2006). All communities selected in this study exprience similar elevation and meteorological conditions (the elevation difference is less than 100 m). The data of species composition and abundance of the three forests surveyed in 2015 were provided by Han et al. (2019a, 2019b). In each forest, five 30 m × 30 m plots were selected to determine the dominant species and to collect leaf and soil samples (Han et al., 2019a). All plots were characterized similar elevations, slopes and aspects. The dominant species of each forest were defined as the species for which the sum of the "importance values" exceeded 75% (Peng, 1996). The main dominance species of each successional stage were shown in Table 2.

To compare the successional forests with a pre-forest community (SUC-1), we investigated the species composition and coverage of a grassland community in five 5 m × 5 m plots. The land occupied by SUC-1 was previously occupied by a
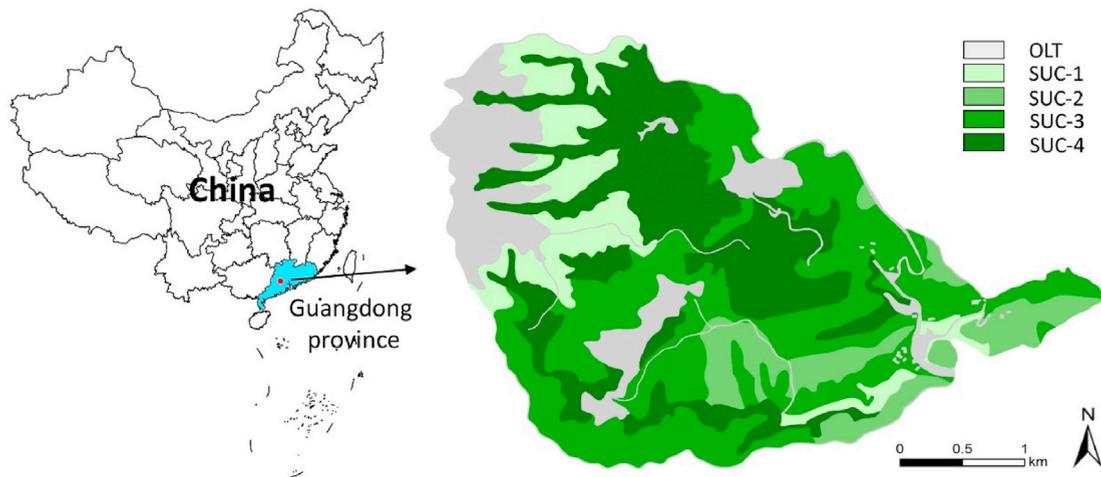
Fig. 1. Location of the Dinghushan National Nature Reserve. SUC-1 = grassland, SUC-2 = coniferous forest, SUC-3 = mixed coniferous-broadleaved forest, SUC-4 = monsoon evergreen broadleaved forest and OLT = other land use types.

coniferous forest that was degraded into a grassland. The dominant species in the SUC-1 were mainly grasses and herbs, such as *Chrysopogon aciculatus*, *Eleusine indica*, *Polygonum chinense*, and *Monochoria vaginalis*.

2.2. Leaf sampling and analysis

To quantify the effects of environmental factors on community functional structure excluding the seasonal effect, the leaf and soil sampling were conducted in both dry season (December to January) and in wet season (July to August) in 2016 and 2017. The plant functional traits were collected and measured following the standardized protocols of Perez-Harguindeguy et al. (2013). In each season, 50−100 fully expanded outer canopy leaves were sampled from five individuals per dominant species in each plot (at least two individuals were selected in and around the plot when the number of individual of the dominant species were less than five, the distribution data of dominant species in each plot was shown in Supporting information 1). The leaves were sealed in polyethylene bags and transported to the laboratory within 3 h. Leaf thickness (LT) and chlorophyll content per unit area (CHl) were measured using a thousandth digital thickness gauge (EXPLOIT, China) and a SPAD-502 Plus chlorophyll meter (Konica Minolta, China), respectively, from 15 to 20 leaves of each speceis in each plot (Rozendaal et al., 2006). Leaf area (LA) was determined on 50−80 leaves (leaf petioles were removed) with a LI-3000C (LI-COR, Inc., Lincoln, NE, USA), after which the leaves were oven-dried the leaves at 60 °C for 72 h to determine leaf dry weight (LDW). Leaf specific leaf area (SLA) was defined as LA/LDW, and leaf weight per area (LMA) was defined as 1/SLA (Li et al., 2015a). Leaf N and P contents (LNC, LPC) were determined via a modified Kjejdahl method, and a molybdenum anti-colorimetric method, respectively (Han et al., 2019a). Leaf carbon content (LCC) was determined with an IsoPrime100 (Elementar, Hanau, Germany) stable isotope ratio mass spectrometer.

Leaf maximum CO_2 assimilation rate per unit area (A_{area}), transpiration rate per unit area (T_{area}), and respiration rate per unit area (R_{area}) were measured with an LI-6400 Portable Photosynthesis System (LI-COR, Lincoln, NE, USA) in the morning between 8:30 and12:00 a.m. in each season of 2016 and 2017. To develop leaf photosynthesis-light response curves, we determined the photosynthesis rate as affected by light intensities of 1600, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, and 0 $\mu mol\ m^{-2}\ s^{-1}$ with a red-blue LED light source; the chamber temperature was set at 25 °C, and the reference CO_2 concentration was set at 400 $\mu mol\ mol^{-1}$ (Lu et al., 2018). In each community, 3−6 light response curves for each species were developed. The area-based leaf maximum net photosynthetic rate (A_{area}), maximum transpiration (T_{area}) and leaf dark respiration rate (R_{area}) were determined using a FvCB model and a SAS program (Dubois et al., 2007). Leaf mass-based physiological traits (i.e., A_{mass}, T_{mass}, and R_{mass}) were calculated as follows: $A_{mass} = A_{area}/LMA$, $T_{mass} = T_{area}/LMA$, and $R_{area} = R_{area}/LMA$ (Osnas et al., 2013). Water-use efficiency (WUE) was calculated as A_{area}/T_{area} (Gago et al., 2014). Photosynthetic N-use efficiency (PNUE) and photosynthetic P-use efficiency (PPUE) were determined as A_{mass}/LNC and A_{mass}/LPC, respectively (Wright et al., 2005).

2.3. Environmental factors sampling and analysis

Soil cores (5 cm diameter × 20 cm deep) were collected from six randomly selected locations in each plot in each season of 2016 and 2017. The six cores were combined to form one composite sample from each plot on each date, which were transported to the laboratory within 3 h. After the soil samples were passed through a 2 mm sieve and roots and stones were removed, the soil nitrate nitrogen content (NO_3^--N) and ammoniacal nitrogen content (NH_4^+-N) of the fresh soil samples were

Table 1

Environmental factors and functional diversities (FDs) used in this study.

Environmental factors	Abbreviations	FDs	Abbreviations
Soil bulk density	SBD	Leaf N allocation diversity	LNAD
Soil field capacity	SFC	Leaf P allocation diversity	LPAD
Soil total phosphorus content	TP	Leaf light and nutrient utilization diversity	LNUD
Soil total nitrogen content	TN	Leaf growth and defense diversity	GDD
Soil total carbon content	TC	Leaf water-use diversity	WUD
Soil organic matter content	SOC	Leaf respiration diversity	RD
Soil nitrate nitrogen content	NO_3^--N		
Soil ammoniacal nitrogen content	NH_4^+-N		
Leaf area index	LAI		

Table 2

The four successional stages of Dinghushan National Nature Reserve, China.

Successional stage	Age (yr)	Sampling elevation (m)	Main dominance species
Grassland (SUC-1)	4	130	*Monochoria vaginalis, Chrysopogon aciculatus, Polygonum chinense, Eleusine indica*
Coniferous forest (SUC-2)	60	135	*Pinus massoniana, Mallotus paniculatus*
Mixed coniferous-broadleaved forest (SUC-3)	100	200	*Castanea henryi, Schima superba, Pinus massoniana*
Monsoon evergreen broadleaved forest (SUC-4)	400	210	*Macaranga sampsonii, Schima superba, Blastus cochinchinensis, Machilus zuihoensis*

Notes: the dominance species information of each successional stage were shown in Han et al. (2019a, 2019b).

determined using the ultraviolet spectrophotometry method and the indophenol blue method, respectively (Wang et al., 2018). The soil available N content was the sum of soil NH_4^+-N and soil NO_3^--N. The soil total carbon content (TC), total nitrogen content (TN) and total phosphorus content (TP) of the air-dried soil samples were determined using the potassium dichromate method, the modified Kjejdahl method, and the molybdenum anti-colorimetric method, respectively (Liu, 1996). Soil organic matter content (SOC) was calculated as TC × 1.724 (Liu, 1996). Soil bulk density (SBD) was measured using the cutting-ring method, and soil water field capacity (SFC) was calculated as the ratio of the increase in soil weight after soaking for 48 h to the soil dry weight (Liu, 1996).

As one of the indicators of understory light environment, the leaf area index (LAI) was measured with a LAI-2200C plant canopy analyzer (LI-COR, USA) on a cloudless morning in each season of 2006 and 2007. In general, the higher LAI, the lower light availability in the understory forest floor. In each plot of each successional stages, 30 evenly distributed points of forest and 10 evenly distributed points of grassland were selected to record under canopy light to calculate the LAI, and in total 5 LAI measurements were taken for each successional stage (Han et al., 2020).

2.4. Data processing and statistical analysis

The sampling area sufficiency was accessed through the rarefaction curve between the number of individuals and the number of species in each successional stage and the distribution of Jaccard dissimilarity among four successional stages, and the results were shown in Fig. A1, A2. Because the distributions of most leaf functional traits and environmental factors were skewed, the data of these variables were log_{10} transformed before data analysis. Due to the wide range of values for most leaf functional traits among different species and the high species turnover during succession (Han et al., 2019a), the mean trait value of each functional trait for each dominant species was used in this study, although we recognized that intraspecific trait variation might be important in species adaptation (Lohbeck et al., 2013; Plourde et al., 2015). Additionally, the mean values from the two years for all variables were used to reduce the influence of the year.

2.4.1. Species diversity calculation

Hill numbers were used to estimate species richness (SPR), Shannon diversity (SHD) and Simpson diversity (SID) for all five plots of each successional stage in the R package iNEXT (see Fig. A3 for the estimations of SD at SUC-4) (Hsieh et al., 2016). The relationships between SD (i.e., SPR, SHD, and SID) and successional age (untransformed) were determined using the power function (Fig. A4, and Table A2).

2.4.2. Dimension reduction analysis (factor analysis) of functional traits

Preliminary results indicated multicollinearity among most leaf functional traits. Factor analysis, was therefore conducted to reduce the number (dimension) of variables. The functional traits were divided into four types of plant strategies based on their correlations according to factor analysis, which would make the correlations of these factors (strategies) relatively low (Fig. A5) (Tully et al., 2013). The four evaluated categories of plant strategies were leaf light and nutrient utilization strategies

(LNUD, including A_{area}, T_{area}, A_{mass}, T_{mass}, PNUE, and PPUE), leaf growth and defense strategies (GDD, including SLA, LT, and LMA), leaf water use efficiency strategies (WUD, including WUE), and leaf respiration strategies (RD, including R_{area}, and R_{mass}). The factor loading of each functional trait is shown in Tables A3-A5. The factor scores of these plant strategies were used as indicators of the functional traits of the plant strategies.

The leaf nutrient-related traits were also divided into two types of plant leaf nutrient allocation strategies according to factor analysis (Table A8): leaf nitrogen allocation strategy (LNAD, including LNC, and LCC/LNC), and leaf phosphorus allocation strategy (LPAD, including LPC, LNC/LPC, and LCC/LPC). The factor loading of each leaf nutrient-related functional trait is shown in Table A6. The factor scores of the leaf nutrient allocation strategies were used as indicators of the functional traits of leaf nutrient allocation strategies.

2.4.3. Community-level functional diversity calculation

The functional dispersion index represents the FD index in this study (Laliberté and Legendre, 2010; Chiang et al., 2016). The community-level abundance-weighted FD indexes (i.e., LNUD, GDD, WUD and RD, Table 1), were calculated for the four types of plant strategies (defined in section 2.4.2), respectively. The leaf total FD in each plot was calculated by combining all plant strategies using the function "dbFD" in the FD package (Laliberté and Legendre, 2010). The LNAD and LPAD were also calculated in each plot using the leaf N and P allocation strategies, respectively.

2.4.4. Analysis of the relationships between FD and SD, and between FD and environmental factors

The standardized effect size of functional diversity (SES.FD) was used to explore the relationship between FD and SD by controlling the effect of species richness on FD using a null model. The null model was constructed by shuffling the species information and retaining the species richness in each plot (Letcher et al., 2012). We constructed 999 random plots to determine SES.FD, which was defined as follows:

$$SES.FD = \frac{observed(FD) - mean(expected(FD))}{standard \; deviation \; of \; expected \; FD}$$

Observed (FD) is the abundance-weighted FD of each actual plot; expected (FD) is the abundance-weighted FD of each random plot; and the standard deviation of expected FD is determined using the expected (FD) of all 999 random plots. Based on the scatterplot distribution between the standardized effect size of functional diversity (SES.FD) and SD, the logarithmic function analysis was used to describe their relationship.

The linear mixed model was used to determine which environmental factor(s) mostly affected the FDs, with the environmental factors set as fixed effects and the season and species coordinate (site) set as random effects. The optimal model was determined using the Akaike information criterion (AIC).

One-way analysis of variance (ANOVA) was used to compare the differences in each soil nutrient-related factor and the FD between the dry season and the wet season. Two-way ANOVA was used to compare the differences between the effects of the successional stage, season, and their interaction on FD of each community. The statistical analyses in this study were conducted in the R 3.4.4 environment with the psych, smatr, ade4, dplyr, iNEXT, FD, mvstats, piecewiseSEM and lmerTest packages (Laliberté and Legendre, 2010; Warton et al., 2012; Chao et al., 2014; Lefcheck, 2016; Kuznetsova et al., 2017; Bougeard and Dray, 2018; Revelle, 2020).

3. Results

3.1. Relationships between FD and SD

Species diversity (i.e., species richness, Shannon diversity, and Simpson diversity) increased significantly with succession (Fig. A4). The relationships between the standardized effect sizes of FD and species richness were consistent. They all increased rapidly with species richness and the increase slowed when the species richness was large (Fig. 2). The relationships between the standardized effect sizes of FD and other SD showed similar trends (Fig. A6).

3.2. Relationships between FD and environmental factor

LNAD was significantly correlated with soil SOC, TN, TP and NH_4^+-N, which could explain 48% of its variance during succession (Table 3). Soil TP could explain 36% of the variance in LPAD in the process of succession (Table 3). LNUD was correlated with LAI, which explained 25% of its variance during succession (Table 3). GDD was correlated with TN and TP, both of which could explain 64% of its variance (Table 3). The 15% variance of WUD could be explained by NO_3^--N (Table 3). RD was positively correlated with LAI and 50% of its variance could be explained by the LAI during succession (Table 3).

3.3. Seasonal effects on relationships between FD and environmental factors

Soil NH_4^+-N and available N contents were negatively related to leaf total FD only in the dry season (Fig. 3a and b), and they were higher in dry season than in wet season in SUC-1 (Fig. 3c and d). Most of the FDs (e.g., WUD, LNUD) were significantly
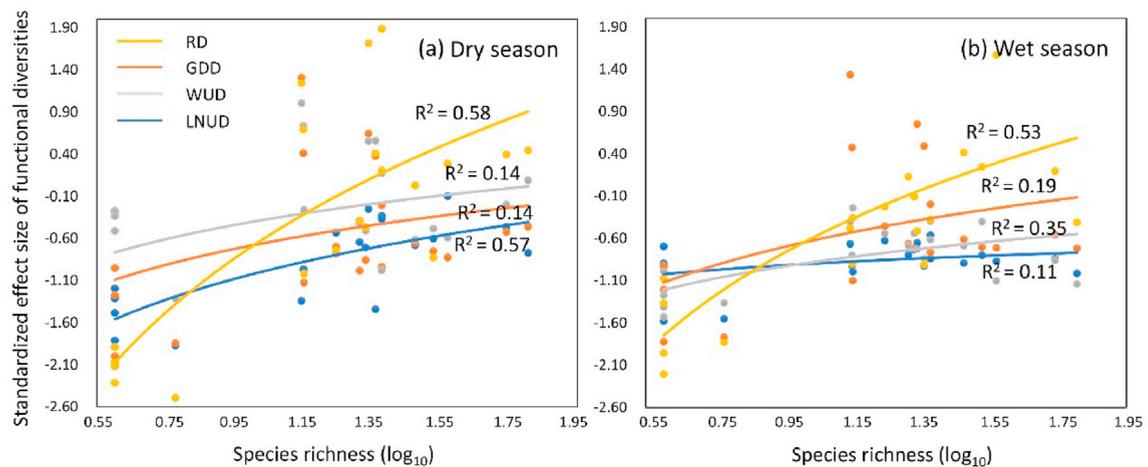
Fig. 2. Relationships between species richness and the standardized effect size of functional diversity in (a) the dry season and (b) the wet season. RD = leaf respiration diversity, GDD = leaf growth and defense diversity, WUD = leaf water-use diversity, LNUD = leaf light and nutrient utilization diversity.

Table 3
Equations expressing FD as a function of environment factors across all the dominant species with the season and site effects excluded during succession using the linear mixed model analysis.

Equations ($N = 80$)	R^2
Lg LNAD = 0.81 Lg SOC − 1.45Lg TN − 0.89 Lg TP − 0.28 Lg NH_4^+-N	0.48
Lg LPAD = −0.49 Lg TP	0.36
Lg LNUD = 0.19 Lg LAI + 0.28	0.25
Lg GDD = −0.53 Lg TN − 1.48 Lg TP	0.64
Lg WUD = −0.46 Lg NO_3^--N + 0.73	0.15
Lg RD = 0.58 Lg LAI + 0.29	0.50

Notes: All equations were significant ($P < 0.05$). LNAD = leaf N allocation diversity, LPAD = leaf P allocation diversity, LNUD = leaf light and nutrient utilization diversity, GDD = leaf growth and defense diversity, WUD = leaf water-use diversity, and RD = leaf respiration diversity. SOC = soil organic matter, TN = soil total nitrogen content, TP = soil total phosphorus content, NH_4^+-N = soil ammoniacal nitrogen content, NO_3^--N = soil nitrate nitrogen content, LAI = leaf area index.

affected by successional effect (Fig. 4a). The seasonal effect, however, only influenced RD, and the effect size was low (Fig. 4a). RD was higher in the dry season than in the wet season in SUC-2 (Fig. 4b).

4. Discussion

4.1. Relationships between FD and SD during succession

With the changing environmental factors and community structure (i.e., species diversity and functional diversity), the forest succession provided a good platform to study how the environmental factors affect the community structure in the process of succession. Results showed that SD (i.e., species richness, Shannon diversity, and Simpson diversity) increased with succession in the subtropical forest (Fig A4), which was also supported by previous studies (Petchey et al., 2002; Zhang et al., 2018). The FDs also showed similar trends to SD in the process of succession, e.g., RD, GDD and leaf total FD increased with succession (Fig. 4b, A7). One interesting finding, however, was that the slopes of the increasing trends of these FDs were not the same. For example, the RD increased rapidly with succession, while the leaf total FD seemed not to change markedly from SUC-2 to SUC-4, and the GDD was highest in the SUC-2 than other successional stages (Fig. 4b, A7). This indicated that the changes in different plant strategies were not always consistent with the processes of forest succession, e.g., the grasses and herbs in early-successional stage always have higher photosynthesis and respiration rates to support their rapid growth than the later successional stages in which the species had various growth strategies to occupied diversified niche space under relative high competition environments (Han et al., 2020), while the higher GDD value in SUC-2 was mainly due to the difference between angiosperms and gymnosperms. Many studies have also reported the inconsistencies in plant defense strategies (Han et al., 2019b), plant reproductive strategies (Han et al., 2019a), and plant light utilization strategies (Cornwell and Ackerly, 2009) during succession. Different from other studies that only used the leaf total FD to represent the community structure (Petchey and Gaston, 2002; Doxa et al., 2020), we believe that the study of different plant strategy diversities could improve our understanding of how plants adapt to different environmental conditions during succession.
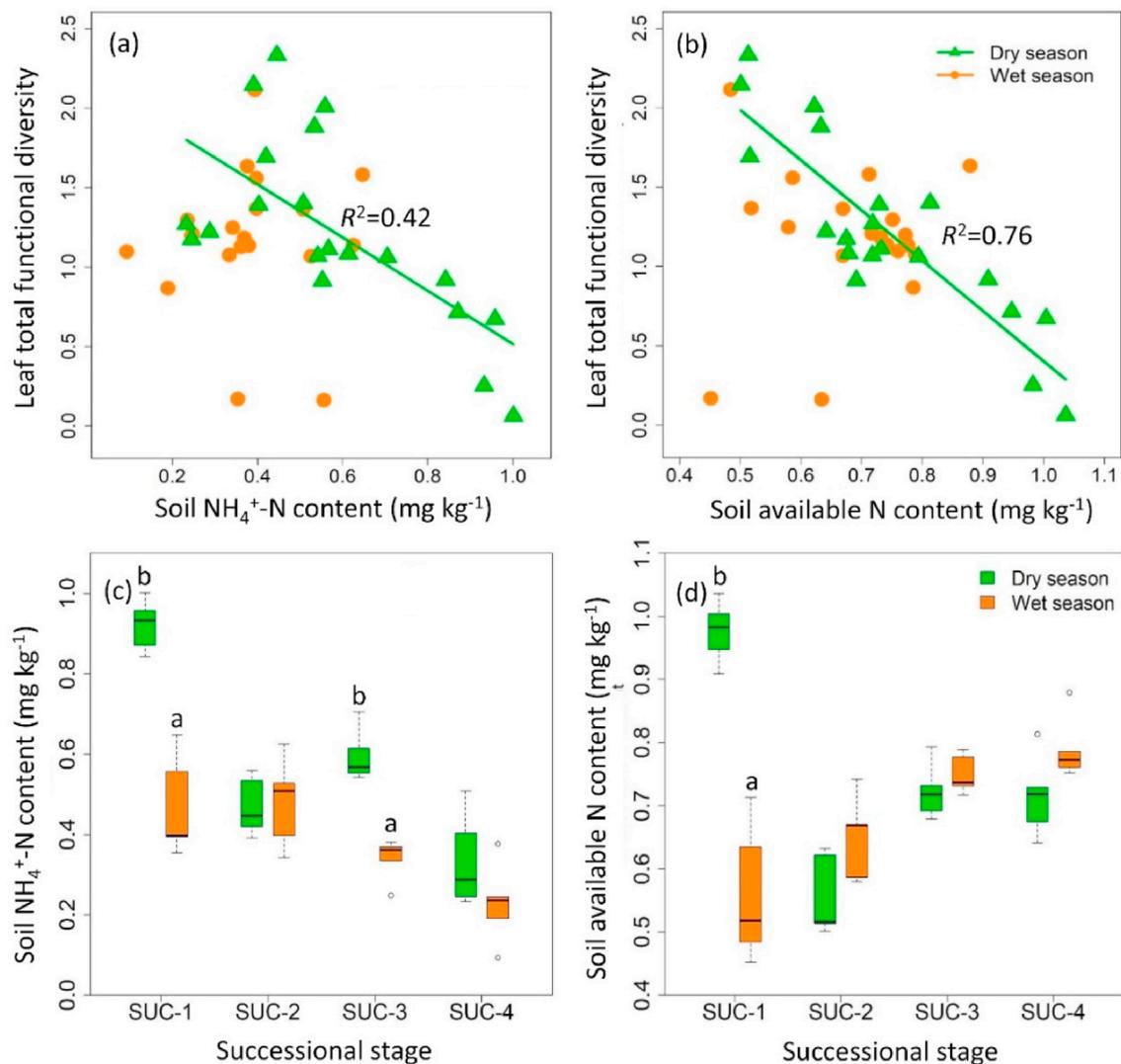
Fig. 3. Relationships between leaf total functional diversity and soil NH_4^+-N content (a), and soil available N content (b) in each season; and season differences of soil NH_4^+-N content (c), and soil available N content (d) in each successional stage. All data were log_{10} transformed before analysis. Different letters in (c) and (d) indicate significant differences ($P < 0.05$) in the dry vs. the wet season. SUC-1 = grassland, SUC-2 = coniferous forest, SUC-3 = mixed coniferous-broadleaved forest, SUC-4 = monsoon evergreen broadleaved forest.

The relationships between FD and SD were found positive and nonlinear in this study (Fig. 2, A6). For example, the RD increased rapidly with species richness, but slowed down when species richness was high. Cadotte et al. (2011) suggested that when the distribution of species along a functional dissimilarity spectrum is not random or uniform, FD and SD might have a positive nonlinear relationship, indicating the functional redundancy or functional trait clustering among species. From the plant function perspective, the nonlinear correlation between SD and FD during succession in this study indicated that the functional traits of the dominant species might be clustering in the later successional stages (e.g., SUC-3, and SUC-4). This is consistent with the study of Lasky et al. (2014) that in mid-successional stages, the negative selection effect cause the loss of past-growing pioneer species, resulting in the functional trait clustering in mid- and later successional stages. In theory, the environmental filtering could cause the functional trait clustering (redundancy) while the competitive exclusion would enhance the functional trait dispersion (Kraft and Ackerly, 2010), and the former might lead to a nonlinear relationship between SD and FD, while the later might lead to a linear relationship between them. However, Kraft et al. (2015) also claimed that the functional trait clustering within a community could result from both environmental filtering and competitive processes when the average fitness of species is associated with particular functional traits. Although our results did not support that there are two ecological processes on the community assembly process during succession, the different responses of SD and FD, e.g., RD showed a different response to species richness compared to WUD (similar increasing trend but
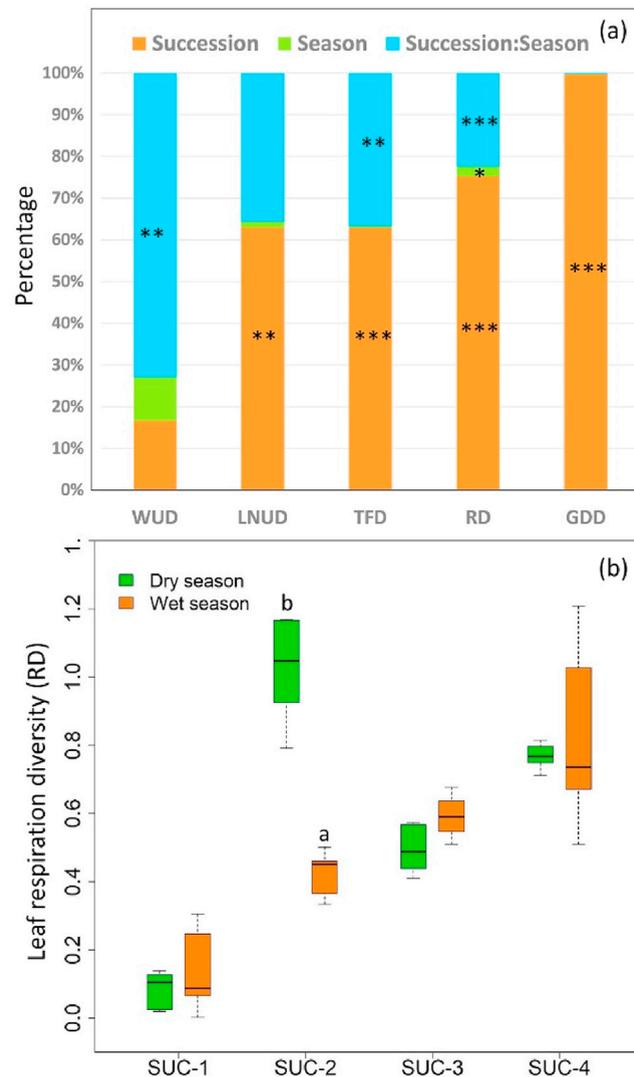
Fig. 4. The effect size of successional stage, season, and their interaction on the variation of each FD (a) and the seasonal difference of leaf respiration diversity (b). All data were $\log_{10}$ transformed before analysis. The significance of successional stage, season, or their interaction (a) is indicated by *, **, and *** ($P < 0.05$, 0.01, and 0.001), respectively. Different letters in (b) indicate significant differences ($P < 0.05$) in the dry vs. the wet season. LNUD = leaf light and nutrient utilization diversity, GDD = leaf growth and defense diversity, WUD = leaf water-use diversity, and RD = leaf respiration diversity. SUC-1 = grassland, SUC-2 = coniferous forest, SUC-3 = mixed coniferous-broadleaved forest, SUC-4 = monsoon evergreen broadleaved forest.

different slopes, Fig. 2, A6), might reveal indirectly that the two ecological processes (i.e., environmental filtering and competitive exclusion) both work on the community assembly in the process of succession in the subtropical forest.

4.2. The light availability, soil P and different N forms affected FD during succession

Rather than using only one measure of total FD, as found in some previous studies (Lambers et al., 2011), four different types of FD (i.e., LNUD, GDD, WUD, RD) were used to represent different plant strategy diversity in this study. The finding that these FDs were affected by different environmental factors showed the advantages of dividing FD into components corresponding to the diversity of different plant strategies (Table 3). In addition, the seasonal effect had an indirect effect on the processes of forest succession by influencing the effects of environmental factors on community structure and function (Sugai and Schimel, 1993). Therefore, it was necessary to study the relationship between environmental factors and FD with the seasonal effect excluded.

Some previous studies in tropical forests have emphasized that the decreasing light availability under canopy is the main reason for the transformation of plant growth strategy from plant acquisition to resource conservation over succession (Boukili and Chazdon, 2017; Lohbeck et al., 2015). In this study, the light availability under canopy (represented by LAI) was

found had significant relationships with the LNUD and RD (the two FDs were related to plant growth and competition strategy) (Table 3), indicating the important roles of light availability on the process of forest succession in the subtropical region. However, the SFC, as one of indicators of the soil water availability, was not found to have a significant relationship with FD (Table 3), suggesting that the soil water availability might not be limiting factor in driving the forest succession in subtropical forest.

For the soil-nutrient related factors, TP had significant effect on LNAD, LPAD and GDD (Table 3), indicating the importance of soil P in shaping the community functional structure during the succession of subtropical forests. Our results were consistent with the findings of Lambers et al. (2008), who found that soil P increasingly becomes a limiting factor during forest succession. In studying the relationship between SD and environmental factors, Lambers et al. (2011) reported that plant species richness is strongly correlated with decreases in TP. A similar result was also found in this study, in which TP was negatively correlated with Shannon diversity in both the dry and wet seasons (Fig. A8). It should be noted that TP was negatively related to LNAD, LPAD and GDD. That is, with the decrease of soil P, these FDs tended to increase. How can such negative relationships be explained?

In a study of Amazonian FD based on forest canopy chemical assembly, Asner et al. (2014) showed that the leaf P content, constraining the rates of canopy CO_2 fixation, was controlled by community-scale differences in soil P availability. Which was also found by the negative relationship between TP and LPAD in this study (Table 3). The trade-off between plant nutrient allocation and plant physiological function could be affected by two ecological processes. First, according to the niche-complementarity hypothesis, plants might diversify their P allocation strategies among photosynthetic, structural, and stored tissues to use P in a better form in P-limited environments (Diaz and Cabido, 2001). Hidaka and Kitayama (2009) also suggested that in soils with a low P content, plants increase their PPUE by increasing the fraction of P allocated to photo-synthetic tissue rather than to structural and storage tissues. Second, plants might invest more in defense strategies due to the severe environment of later successional stages (Han et al., 2019b). Therefore, with the decreasing nutrient utilization in growth and increasing investment in defense during succession, the FD increased due to the decrease of soil P content.

In a review paper, Alvarez-Clare et al. (2013) concluded that rather than being a question of N vs. P, nutrient limitation in tropical forests probably results from complex interactions among multiple nutrient cycles. Marklein and Houlton (2011) showed that N inputs may accelerate soil and root phosphatase activity. The finding of this study that LNAD and GDD were both affected by TP and TN (Table 3) could support the hypothesis that multiple nutrient cycles rather than P alone, determine FD in a subtropical forest.

In this study, the negative relationships found between soil NH_4^+-N and LNAD, between soil NO_3^--N and WUD, and between soil available N and leaf total FD (Fig. 3, Table 3) were in accord with the hypothesis that higher SD leads to more continuous use of soil available NO_3^--N and NH_4^+-N (Niklaus et al., 2001). Hooper and Vitousek (1998) also reported that the effects of soil available N on SD depend on the community composition and season. We found that seasonal effects on soil NH_4^+-N and available N mainly occurred in SUC-1 (Fig. 3c and d), indicating that the early successional stage show higher sensitivity to seasonal change than later successional stages. The transformation of soil available N (i.e., NO_3^--N and NH_4^+-N) generally depends on multiple factors and processes, e.g., soil structure and water status, root density, root NO_3^--N and NH_4^+-N uptake kinetics, microbial NO_3^--N immobilization rates, and nitrification and denitrification rates (Lambers et al., 2011). It is therefore difficult to determine how different forms of soil available N affect FD in different seasons. However, this study showed for the first time that different forms of soil available N might significantly affect the shaping of community functional structure in subtropical forests, especially in early successional stages.

When separating the effects of the season, successional stage, and their interaction on FDs, we found that successional effect explained large proportions of the variations in FDs (Fig. 4a), while seasonal effect only explained a small portion of the variation of leaf respiration diversity (Fig. 4b). Differences in RD between the dry and wet seasons were only detected in SUC-2 (dominated by *Pinus massoniana*, Fig. 6b). Huang et al. (2018) showed that subtropical pine forests could benefit from the dry season. Our results indicated that later successional communities with higher SD might be less disturbed by season changes than early successional communities.

5. Conclusions

This study generated several important findings. First, FD and SD were not always positive and linearly correlated. FD increased rapidly with SD and the increase slowed down when SD was high. Second, light availability, soil P and different N forms were the main factors shaping functional diversity during the succession of the subtropical forest. Third, distinguishing the diversity of different plant strategies provided more useful information about the interactions between plant species and environments. Fourth, the later successional communities with higher SD appeared to be disturbed less by season change than the early successional communities. By assessing the relationship between SD and FD and the effects of environmental factors on FD, our study provides community-level insights that are useful for predicting the possible consequences of regional environmental change on the functional structure of plant communities.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01334.

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