

Shifts in community leaf functional traits are related to litter decomposition along a secondary forest succession series in subtropical China

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Abstract

Aims

We investigated shifts in community-weighted mean traits (CWM) of 14 leaf functional traits along a secondary successional series in an evergreen broadleaf forest in subtropical southeast China. Most of the investigated traits have been reported to affect litter decomposition in previous studies. We asked whether changes in CWMs along secondary succession followed similar patterns for all investigated traits and whether the shifts in CWM indicated a change in resource use strategy along the successional gradient. Using community decomposition rates (*k*-rates) estimated from annual litter production and standing litter biomass, we asked whether the dynamics of litter decomposition were related to changes in leaf functional traits along the successional series.

Methods

Twenty-seven plots were examined for shifts in leaf CWM traits as well as in *k*-rates along a series of secondary forest succession covered in the framework of the BEF-China project. We investigated whether the changes in CWMs followed similar patterns for all traits with ongoing succession. Three alternative linear models were used to reveal the general patterns of shifts in CWM trait values. Moreover, multiple regression analysis was applied to investigate whether there were causal relationships between the changes in leaf functional traits and the dynamics of litter decomposition along secondary succession. We furthermore assessed which traits had the highest impact on community litter decomposition.

Important Findings

Shifts in CWM values generally followed logarithmic patterns for all investigated traits, whereas community *k*-rates remained stable along the successional gradient. In summary, the shifts in CWM values indicate a change in community resource use strategy from high nutrient acquisition to nutrient retention with ongoing succession. Stands with higher CWM values of traits related to nutrient acquisition had also higher CWM values of traits related to chemical resistance, whereas stands with higher CWM values of traits related to nutrient retention exhibited higher CWM values in leaf physical defense. Moreover, high values in CWM values related to nutritional quality (such as high leaf phosphorus concentrations) were found to promote community *k*-rates, whereas high values in physical or chemical defense traits (such as high contents in polyphenols or high leaf toughness) decreased litter decomposition rates. In consequence, litter decomposition, which was simultaneously affected by these characteristics, did not change significantly along succession. Our findings show that leaf decomposition within the investigated communities is dependent on the interplay of several traits and is a result from interactions of traits that affect decomposition in opposing directions.

Keywords: secondary forest succession, BEF-China, nutrient cycling, plant polyphenols, multiple regression analysis

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INTRODUCTION

Secondary succession is defined as a directional change in community composition after disturbance (Finegan 1984; Horn 1974). While early studies focused on the successional changes in plant species composition (e.g. Guariguata and Ostertag 2001; Odum 1960, 1974; Peña-Claros 2003; Vitousek and Reiners 1975), more recent studies have also taken functional traits into account. The investigated plant characteristics often comprised functional leaf traits such as specific leaf area (SLA) and leaf dry matter content (LDMC), leaf nitrogen content (LNC), which commonly exhibit directional changes during succession. Trait shifts in the course of succession have frequently been described. Typically, fast-growing species with low LDMC but high SLA and leaf nutrient content are replaced by slow-growing species with high LDMC and low SLA (e.g. Caccianiga *et al.* 2006; Garnier *et al.* 2004; Raavel *et al.* 2012; Vile *et al.* 2006b). In a global analysis Wright *et al.* (2004) demonstrated that SLA, LNC and LDMC, among other traits, determine the leaf economics spectrum (LES) which is defined by a trade-off between productivity and resource conservation. In general, high investment into plant structural compounds, as e.g. reflected in high values in LDMC, were found to be related to low-productive species, whereas high values in SLA or LNC typically characterize highly productive species. In contrast to most other studies, Mason *et al.* (2011) detected an increase in SLA and a decrease in leaf secondary metabolites (e.g. polyphenolics) along secondary succession of a temperate rain forest in New Zealand. The authors concluded that these shifts resulted in an increase in leaf palatability as well as in leaf decomposability with ongoing succession, indicating that the shift toward a strategy of nutrient conservation during secondary succession does not hold true for every ecosystem. However, the majority of successional studies have reported the opposite trend, and thus, the New Zealand rainforest study seems to describe an exceptional system.

Irrespective of the directional shifts in leaf traits along succession, a corresponding change in leaf litter decomposability in subtropical rainforest systems has not explicitly been shown yet. Decomposition can be considered as one of the most important processes in terrestrial ecosystems (Aber *et al.* 1991) as the physical, biological and chemical breakdown of organic matter releases biologically bound nutrients and makes them available for plant growth (Berg and McClaugherty 2008; Swift *et al.* 1979). Interestingly, the traits of the LES related to resource conservation, such as LDMC, have also been found to be closely related to rates of litter decomposition (e.g. Fortunel *et al.* 2009; Garnier *et al.* 2007; Quested *et al.* 2007). However, as indicated by the contrasting results found by Mason *et al.* (2011) and other works (e.g. Garnier *et al.* 2004), litter decomposition may increase or decrease along succession, depending on the identity and importance of the leaf traits that change with ongoing succession. If the changes in community-weighted means (CWM,

i.e. species-specific mean leaf trait values weighted by the species' abundance in the community) of leaf traits are related to nutrient conservation, litter decomposition can be expected to decrease with ongoing succession. Conversely, if changes in CWM leaf traits are related to high productivity, litter decomposition should increase. However, as litter decomposition does not depend on a single trait, and in addition to LES traits litter breakdown has also been reported to depend on leaf secondary compounds (e.g. Hättenschwiler *et al.* 2005; Kraus *et al.* 2003), traits that promote or slow down litter decomposition might oppose or even outweigh each other, resulting in little or no net effects on leaf litter decomposition during succession. Besides functional and abiotic characteristics as well as stand age, leaf-litter species richness may affect decomposition rates (e.g. Wardle *et al.* 2003). In natural ecosystems, leaf litter is unlikely to consist of single species debris but is merely a mixture of litter types from all species growing in the respective community. Recent studies have shown that decomposition rates of leaf litter mixtures of different species often differed from those expected from the decomposability of single species leaf litter (see e.g. Gartner and Cardon 2004; Hoorens *et al.* 2003; Wardle *et al.* 2003). Non-additive effects, resulting from an impact of one litter type on the decomposition of another may either accelerate (synergistic effects) or reduce mixed litter decomposition (antagonistic effects). Such litter mixing effects on decomposition rates may be substantial. For example, mass loss in mixed grass litter was reported to be 37% higher than expected from mass losses of monospecific litter decomposition (Hector *et al.* 2000). Whether species mixing has synergistic or antagonistic effects was found to be highly dependent on which litter types were combined (see e.g. Wardle *et al.* 2003). Depending on the traits of the species combined, synergistic and antagonistic effects of species mixtures may outweigh each other, and may thus have or have not a net effect on rates of community decomposition.

In contrast, leaf chemical defense traits such as e.g. polyphenol contents were found to negatively affect decomposition rates (Hättenschwiler and Vitousek 2000). Similarly, leaf traits referring to physical resistance such as leaf toughness (LT), LDMC and leaf carbon content (LCC) have been reported to slow down litter decomposition (e.g. Hättenschwiler *et al.* 2005). As stated above, most of these traits, in turn, were also reported to change in communities undergoing secondary succession; thus litter decomposition rates can be expected to change accordingly. Based on the rationale of the mass-ratio hypothesis (Grime 1998), it may be anticipated that the most abundant species in a community exerts the highest impact on ecosystem properties (see also Díaz *et al.* 2007; Garnier *et al.* 2004, 2007; Quested *et al.* 2007). Following this argumentation, it can be expected that leaf traits of the most dominant species should have the highest influence on ecosystem processes such as decomposition. As demonstrated in a study on changes in community leaf trait composition along a successional series investigated by Garnier *et al.* (2004), CWM trait values offer a convenient metric to describe shifts in

functional trait values and may be used to relate functional characteristic of plants to ecosystem properties. In most cases, CWMs are aggregated species mean trait values, using the same species trait value across the different communities that are compared (but see Auger and Shipley 2013). However, such a procedure is only valid under the assumption that the trait variability within a certain species is low in comparison to the variability among species (see Albert et al. 2010, 2011), which is true for some traits such as phenolics and tannin as well as LT (Eichenberg et al. 2014, D. Eichenberg, O. Purschke, H. Bruelheide (in preparation)) but might not be for other traits. CWMs calculated in this way for diverse plant communities have successfully been used to predict ecosystem-specific above-ground net primary production along a gradient of secondary succession (Vile et al. 2006a). Thus, changes in CWM traits along secondary succession, which have been postulated to be indicative for community resource use strategy (e.g. Mason et al. 2011; Raavel et al. 2012) may also be used to investigate the relationships between leaf functional traits and community properties such as litter decomposition rates.

In the present study we analyzed shifts in CWM traits along a gradient of secondary succession established in the BEF-China project (Bruelheide et al. 2011). We examined 27 communities along a gradient covering ~120 years of secondary forest succession. For a total of 143 species we assessed mean values of 14 traits that have been reported to be related to litter decomposition in the literature (e.g. Perez-Harguindeguy et al. 2000). We made use of species mean values because most of the traits studied by us have been reported to be largely invariable to changes in *in-situ* conditions within a species, such as LCC, as seen in the study of Garnier et al. (2007), which covered 11 climatically and edaphically different sites across Europe and Israel. In contrast, some traits (such as LNC) were found to strongly covary with site conditions. For such more variable traits over-all species mean values may be less representative, and thus, the use of site-specific mean values for every species has been suggested to take intraspecific trait variability into account (de Bello et al. 2011; Lepš et al. 2006). However, Kröber et al. (2012) who studied the same communities as investigated by us found changes in community trait values to be predominantly related to differences in community composition and only to a negligible degree to intraspecific differences across sites. Moreover, as the environmental gradient covered by our succession series is relatively short compared to the continent-wide study by Garnier et al. (2007), intraspecific trait variation would be expected to be only moderate, which justified to employ over-all species mean values across all communities.

To evaluate the dynamics of litter decomposition for each community, we measured rates of leaf litter decomposition (k -rates) as a community property along the gradient. In addition to assessing the effect of successional age we also tested for effects of tree and shrub species richness on changes in CWM values of different traits and on k -rates of litter decomposition. In particular, we hypothesized that (i) along secondary

succession, there is a shift from communities dominated by species with high productivity, high leaf nutrient contents and short-lived leaves with low physical or chemical resistance to communities consisting of species with low productivity, low leaf nutrient contents and more persistent leaves (i.e. higher investment into structural compounds and chemical defense). We expected these shifts to remain significant after accounting for species richness. We also tested whether these shifts followed a linear, logarithmic or quadratic pattern (see Mason et al. 2011). We further hypothesized that (ii) community litter decomposition rates decline with successional age and that (iii) the changes in litter decomposition along the successional series can be explained by the observed shifts in CWMs. More precisely, we predict that traits relating to high nutrient content and high productivity increase litter decomposition rates, whereas traits related to physical and chemical resistance decrease litter decomposition rates. To our knowledge this is the first study that relates shifts in community trait composition to leaf litter decomposition in the course of a subtropical secondary forest succession.

MATERIALS AND METHODS

Research location and species inventory

The Gutianshan National Nature Reserve (GNNR) is located in the Zhejiang Province in southeast China. It comprises >80 km² of laurophyllous rainforests undergoing secondary succession. With a mean annual temperature of 15.1°C and mean annual precipitation accumulating to 1964mm, the climate is characterized as typically subtropical, exhibiting a wet season from May to June (see Geißler et al. 2012 as well as Hu and Yu 2008 for further information). The bedrock is acidic, mainly formed by a granite intrusion. A total of 27 plots of 30 m by 30 m ('Comparative Study Plots', in short CSPs) have been established along a gradient of secondary succession. This series covers communities with a range of duration in secondary succession from ~20–120 years (67.4 ± 26 years, mean \pm standard deviation) after periodic logging by the local population. Thus, the secondary succession series represents a succession on previously forested terrain. In all 27 CSPs a census was carried out in 2008 and 2009 and all individuals exceeding 1 m in height were counted and identified to the species level. A total of 148 woody species were recorded across all 27 CSPs, with plot species richness varying between 25 and 69 species per plot (Table S1, see online supplementary material). Age determination was accomplished by counting tree rings from core drillings (see Bruelheide et al. 2011 for further details). Plant species names follow the nomenclature of the 'Flora of China' (www.efloras.com).

Leaf traits assessment

In the present investigation, we focused on the shifts of leaf CWM traits from tree species along the successional gradient, for practical reasons. The importance of herbaceous species in the herb layer and their impact on forest-ecosystem

functioning is well known (e.g. Tchouto *et al.* 2006). However, with respect to the successional gradient established within the BEF-China project, Both *et al.* (2012) found that, in contrast to recruits of woody species, herbaceous species played a minor role in species composition in all 27 CSPs.

We compared the shifts in CWM values for 14 leaf traits (see Table 1), which have been related to litter decomposition in other studies. Nine of these leaf traits were compiled from Kröber *et al.* (2012) and further five traits were determined in the present study (see Table 1). In general, we investigated traits that can be grouped into four groups of different effects on ecosystem functioning: firstly, we included traits related to productivity and photosynthetic efficiency of plants such as SLA, leaf calcium content (LCaC) and stomatal density (StoD). While LCaC was found to be significantly correlated with the maximum rate of photosynthesis (Reich *et al.* 1995), StoD has been related to the efficiency of a plant's adaptation to the water vapor deficit and thus to the efficiency of photosynthesis (Carpenter and Smith 1975; Kröber *et al.* 2012). Secondly, we aimed at assessing leaf traits concerning the nutritional value of the plant tissue by including information on leaf nutrient concentrations of nitrogen (LNC), phosphorus (LPC) and sulfur (LSC). A third group of traits were those related to chemical leaf defense. To this end, we included leaf total phenolics and tannin concentrations. These secondary metabolites have frequently been related to nutrient turnover dynamics in terrestrial ecosystems and litter decomposition

(see e.g. Hättenschwiler *et al.* 2005). The fourth group of leaf functional traits can be summarized under the aspect of physical resistance due to investment into structural components: we included LT, LDMC as well as the carbon-to-nitrogen ratio (C/N) and LCC. The latter two traits may also be regarded as chemical traits, relating to the nutritional value of a plant but have also been reported to scale positively with prominent aspects of physical defense in previous studies (Eichenberg *et al.* 2014; Villar *et al.* 2006). Similarly, other traits may also affect multiple functions simultaneously, and thus the assignment to these four groups and the specific functions of each trait in Table 1 can only be taken as a rough guide.

The protocol for assessing the traits related to productivity and nutritional value are described in Kröber *et al.* (2012). In short, leaf C and N contents were measured by gas chromatography (elementar vario EL), using leaves from five plants per species. Calcium, potassium, sulfur and phosphorus as well as magnesium contents were analyzed by atom absorption spectrometry (AAS Vario 6, Analytik Jena, Jena, Germany), using 15 leaves from three individuals per species. Stomata were counted on three leaves from three individuals per species on a minimum of 50 000 mm². These traits were available for 143 out of the total of 148 tree species.

Information on leaf polyphenolic content were determined by us for 101 species. Fifty milligrams of dried leaf powder were extracted in 20 ml of 50% aqueous acetone, according to the procedures described in Torti *et al.* (1995). Leaf

Table 1: list of traits investigated in this study and a selection of their ecological functions

Trait	Type of trait function	Other ecological functions
SLA (mm ² ·g ⁻¹) ^a	Productivity	Adaption to light regime, leaf life span, structural defense, relative growth rate, photosynthetic rate, productivity ^[1,2,3,4]
LCaC (µgg ⁻¹) ^a	Productivity	Leaf transpiration, leaf life span, nutritional quality, productivity, photosynthetic rate ^[12,13]
StoD (1 µm ⁻²) ^a	Productivity	Adaption to vapor pressure deficit, photosynthetic rate ^[11,12,13]
LNC (%) ^a	Nutritional value	Nutritional quality, photosynthetic rate, productivity ^[1,9]
LPC (µg·g ⁻¹) ^a	Nutritional value	Nutritional quality, photosynthetic rate, productivity ^[1,9]
LSC (µgg ⁻¹) ^a	Nutritional value	Chloroplast construction, rate of photosynthesis, nutritional quality, productivity ^[9,10]
Phenolics (mg·g ⁻¹)	Chemical defense	Chemical defense, decomposability ^[13,15]
Tannin (mg·g ⁻¹)	Chemical defense	Chemical defense, decomposability ^[13,15]
C/N (%) ^a	Physical resistance	Nutritional state of plant, physical resistance, disturbance regime, nutritive value, leaf longevity, decomposability, productivity ^[5,6]
LCC (%) ^a	Physical resistance	Structural components, physical defense, relative growth rate ^[1,2]
LDMC (mg·g ⁻¹) ^a	Physical resistance	Physical defense, leaf life span, relative growth rate ^[1,7,8]
LT (N·mm ⁻¹)	Physical resistance	Physical defense, decomposability ^[14,15,16]
Evergreen	—	Leaf longevity ^[17,18]
Pinnate	—	Adaptation to light regime ^[17]
k rate	—	Decomposition ^[19]

References: ^[1]Cornelissen *et al.* (2003), ^[2]Wright *et al.* (2004), ^[3]Poorter and Garnier (1999), ^[4]Reich *et al.* (1999), ^[5]Matsuki and Koike (2006), ^[6]Tateno and Chapin III (1997), ^[7]Poorter and Garnier (1999), ^[8]Grime *et al.* (1997), ^[9]Aerts and Chapin III (1999), ^[10]Terry (1976), ^[11]Kröber *et al.* (2012), ^[12]Gindel (1969), ^[13]Carpenter and Smith (1975), ^[14]Eichhorn *et al.* (2007), ^[15]Hättenschwiler and Vitousek (2000), ^[16]Perez-Harguindeguy *et al.* (2000), ^[17]Roloff (2004), ^[18]Graca *et al.* (2005), ^[19]Cornwell *et al.* (2008). Evergreen = evergreen leaf habit; phenolics = leaf total phenolics concentration; pinnate = leaf pinnation; tannin: leaf tannin concentration.

^aTrait information compiled from Kröber *et al.* (2012).

total phenolics concentrations were determined using the Prussian blue method (Price and Butler 1977) as modified by Graham (1992). Total tannin concentrations were determined using the radial diffusion method for increased sensitivity as described by Hagerman (2002). Both secondary metabolites were quantified by standardization against tannic acid (Roth, Germany, Charge Nr. 250153788) and expressed as milligrams per gram dry weight of tannic acid equivalents (for further details see Eichenberg et al. 2014).

LT was assessed as leaf tensile strength for a total of 91 species according to the methods described by Hendry and Grime (1993). Briefly, leaf fragments of 1–5 mm width were cut from the central part of the leaves (avoiding the midrib and major veins) along the longitudinal axis. These fragments were fixed between two clamps in the tearing apparatus and slowly pulled apart. The force needed to tear apart the leaf fragment was measured with a spring balance (Cornelissen et al. 2003). In total, 1725 single leaves were analyzed.

Moreover, information on life form (evergreen or deciduous) and leaf type (pinnate or entire) for 143 out of the 148 species was compiled from field observations and the Flora of China.

Assessment of community decomposition rates

For each of the 27 CSPs, the community decomposition constant k was estimated according to Olson (1963) as presented in equation 1:

$$k = \frac{\text{Annual leaf litter production} [\text{Mg} \cdot \text{ha}^{-1}]}{\text{Forest floor leaf litter mass} [\text{Mg} \cdot \text{ha}^{-1}]} \quad (1)$$

Leaf litter production (Mg ha^{-1} , oven-dried at 80°C until constant weight) was assessed using five litter traps evenly spread across each plot. To account for interannual variation in monthly collected litterfall, we calculated annual mean leaf litter production based on data obtained in two subsequent years (2010 and 2011). Mean forest floor litter mass (Mg ha^{-1}) was seasonally determined (spring 2009, summer 2009, autumn 2009 and winter 2010) by sample cores taken in undisturbed litter patches in each CSP, excluding twigs with diameter >0.6 cm. In parallel we measured litter thickness at 12 additional points per CSP to correct for spatial variation of forest floor litter mass. The obtained k -rates do not only integrate over decomposition dynamics influenced by species abundance and composition at the community level, but also account for potential non-additive litter mixture effects that have been observed during decomposition (Gartner and Cardon 2004; Hättenschwiler et al. 2005) as well as abiotic differences such as *in-situ* microclimatic and edaphic conditions.

Functional trait data

Mean trait values and CWMs

For each of the 12 continuous trait variables (see Table 1) species mean values were calculated. Dichotomous categorical variables (evergreen/deciduous, pinnate/entire) were 1/0

coded and treated as numeric variables to obtain community-weighted relative proportions of evergreen and pinnate species within the respective communities. Community mean traits (CWM) were computed on the basis of species mean trait values and species abundances in the plot according to equation 2.

$$\bar{x} = \frac{\sum_{i=1}^n x_i a_i}{\sum_{i=1}^n a_i} \quad (2)$$

with \bar{x} = community-weighted aggregated mean trait; x_i = mean trait value of species i , a_i = abundance of species i and n = species richness of the community.

We used the FD-package (Laliberté & Shipley 2011) in R for CWM calculation. All statistical computations were performed using the statistical program R (Version 3.0.1; R Development Core Team 2011). In Table S1 (see online supplementary material) we provide information on the plot-specific CWMs as well as on plot age and species richness.

Tests for shifts in CWM trait values along the successional gradient

According to the original design of BEF-China, the 27 CSPs were established along two crossed gradients: species diversity and stand age (see Bruelheide et al. 2011 as well as Table S1, see online supplementary material). To assess whether shifts in CWM trait values may be related to changes in species richness in addition to successional age, we conducted regression analyses including plot species richness in addition to plot age in each linear model. To assess the general patterns of shifts in CWMs along secondary succession we ran three alternative types of linear models. These models were used to determine whether shifts in CWM values for each single trait were best reflected by (i) linear, (ii) logarithmic or (iii) quadratic patterns along the successional gradient. In each model, the respective CWM was used as response, whereas the successional stand age as well as species richness were used as predictor variables. The most informative model was selected according to the Akaike Information Criterion (AIC) criterion.

Relating CWM shifts to decomposition along the successional gradient

To test for correlations between the changes in CWM traits and litter decomposition rates along the successional gradient we ran multiple regression analysis. According to hypothesis (iii), we only included CWMs calculated from continuous traits from the four types of traits with different functional roles as presented above. Thus, the variables ‘evergreen’ and ‘pinnate’ were excluded from these analyses. We used principal components analyses (PCA) to assess multidimensional CWM interrelationships prior to multiple regression analyses in order to characterize all 27 communities according to their CWM as well as to screen for potential problems of multicollinearity in the multiple regression analysis.

Model selection of the most informative model was based on stepwise backward selection applying the stepAIC routine available in the MASS-package (Venables and Ripley 2002) for R. Potential model inconsistencies due to multicollinearity were assessed using variance inflation analysis available in the R package faraway (Faraway 2011). To assess the relative strength of the CWM trait values affecting community litter decomposition we used standardized trait values (mean = 0, SD = 1) in multiple regression analyses.

RESULTS

Shifts in CWM traits and litter decomposition along the successional gradient

Fig. 1 shows the patterns of all significant changes of the CWMs of all determined traits along the secondary succession. According to the AIC criterion, species richness was not included as an informative predictor affecting shifts in any final CWM model. Observed changes in litter carbon (LCC) and LSC concentrations, LDMC and the percentage of pinnate individuals did not change significantly with successional age. Most significant changes in the CWMs followed a logarithmic pattern, whereas community k -rates followed a quadratic pattern with ongoing secondary succession, which, however, was not statistically significant. In general, CWMs related to high community productivity and to nutritional quality decreased along the successional gradient, whereas in the group of CWM traits that were related to physical resistance, C/N and LT as well as the proportion of evergreen species increased. Surprisingly, we detected a decrease of total phenolics and tannin concentrations with increasing stand age.

The interrelationships of the CWM values of the 13 traits used in the multiple regression analysis on community litter k -rates are shown in Fig. 2. The first two axes of the PCA comprised ~70% of the over-all variance in CWM trait values. Along the first axis, communities were arranged from those indicating high

productivity with leaves of high nutritional content and chemical defense on the left-hand side to those with leaves of high carbon content and LT on the right-hand side. The CWMs of traits related to productivity and nutritional value (with the exception of LSC) as well as those related to chemical defense show a high degree of collinearity. The second axis mainly reflected differences in community LDMC, which was the most uncorrelated CWM trait to the main trait gradient on the first PCA axis.

Relationships between CWM traits and decomposition rates along succession

The most informative multiple regression model included the predictor variables SLA, LCC, LCaC, LPC, LSC, total phenolics and tannin concentrations as well as LDMC and LT. However, variance inflation factor analysis indicated multicollinearity with the highest variance inflations in the CWMs of tannin and LPC (see also Fig. 2). Tannin concentrations were strongly positively correlated to phenolic concentrations ($r = 0.72$, $P < 0.001$) and LPC was strongly positively correlated to LCaC ($r = 0.65$; $P < 0.001$). We thus used linear models to residualize tannin vs. total phenolics concentrations and LPC vs. LCaC, respectively. Multiple regression analyses based on the residuals of tannin and LPC from the linear models of phenolics and LCaC resulted in a more informative and accurate model (lower AIC values) than when computed from the original values ($R^2 = 0.35$, $P < 0.05$ and $R^2 = 0.21$, $P = 0.12$, respectively). As indicated by the regression coefficients, LPC_{resid} had the strongest positive, whereas $Tannin_{resid}$ had the strongest negative effect on community litter decomposition rates (see Table 2). LCC had a strong positive effect, whereas LDMC and LT decreased litter decomposition. LSC was also included in the final model although this variable affected litter decomposition rates with only marginal significance. However, removal of LSC decreased R^2 and increased over-all P values in the reduced model. Moreover, variance inflation factor

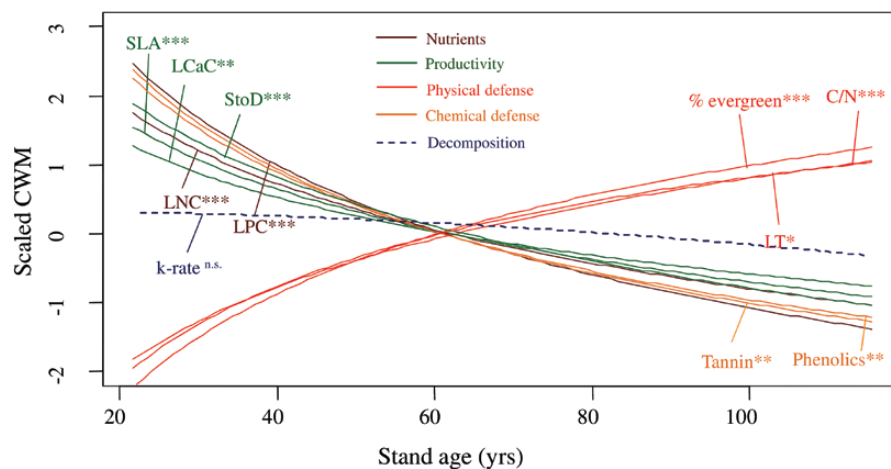


Figure 1: shifts of standardized community leaf functional traits and decomposition rates along secondary succession. Only significant trait changes are displayed. Colors indicate the different types of trait functions (see Table 1). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s.: not significant.

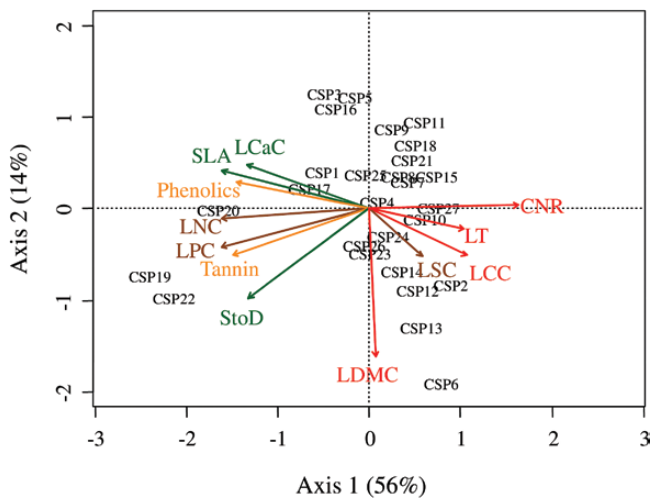


Figure 2: principal components of functional traits included in the study. Colors indicate the different types of traits functions as indicated in Fig. 1. Numbers in parentheses indicate the proportion of variance accounted for by the respective axis.

Table 2: leaf functional traits affecting community leaf decomposition in the best model according to AIC

Trait	Coefficient	Significance
LPC _{resid}	0.97	*
LCC	0.81	**
LSC	0.34	'
Tannin _{resid}	-0.75	*
LDMC	-0.62	*
LT	-0.61	**

Regression coefficients were calculated from standardized trait values. Thus, the absolute value of the coefficients shows the importance of this predictor on leaf decomposition. Removal of LSC increased AIC values, indicating less appropriate models. Note: LPC_{resid} and Tannin_{resid} depict the residuals from linear regression analyses against LCaC and total phenolics concentrations, respectively.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' $P < 0.1$.

analysis did not indicate severe multicollinearity between the remaining predictors (data not shown).

DISCUSSION

In the present investigation we detected shifts in CWM values of traits along a gradient of secondary succession. None of these shifts were found to be significantly related to differences in plot species richness. Traits related to productivity, nutrient quality and chemical defense decreased along succession. In contrast, C/N and LDMC, traits with known impact on physical defense (Eichenberg et al. 2014; Villar et al. 2006), increased with ongoing succession, whereas community litter decomposition rates did not change significantly. These results are in full accordance with the findings of

Kröber et al. (2012) who investigated the importance of abiotic vs. biotic factors in trait shifts along the secondary successional gradient of the BEF-China experiment. The traits not studied by Kröber et al. (2012) were total phenolics and tannin concentrations as well as LT and litter decomposition. The authors encountered the same directional tendencies in shifts of those traits values that were also included in our study. In addition to the directions of change described by Kröber et al. (2012), we were able to specify which mathematical relationship best described the changes in trait values, which in all cases followed a logarithmic pattern. We found that LT increased in parallel to C/N with increasing stand age, while traits related to physical resistance (LCC and LDMC) did not change along the successional gradient. Surprisingly, CWMs related to chemical defense such as total phenolics and tannin contents decreased with successional change. Moreover, as indicated by the increase in the proportion of species with evergreen leaf habit, late successional communities tended to be composed of species with more persistent leaves. While communities of young successional age were dominated by highly productive species with leaves of high nutritional value, old stages were characterized mostly of species with leaves of low productivity and nutritional quality. This points to a change in resource use strategy from high nutrient acquisition to nutrient retention, thus, confirming our first hypothesis. Multiple regression analysis revealed causal relationship between shifts in CWMs and community litter decomposition rates. Therefore, our second hypothesis, predicting a decrease in community litter decomposition rates has to be rejected. Thus, litter decomposition showed a different pattern in Chinese subtropical forests than Mediterranean old-field succession as described by Garnier et al. (2004). However, in accordance with Garnier et al. (2004) our study provides evidence that CWM values of species leaf traits can be successfully used to predict ecosystem processes such as litter decomposition. Using multiple regression analysis we demonstrated that along the successional gradient encountered in the GNNR, rates of community leaf litter decomposition were positively related to traits of community leaf nutritional quality such as LPC, and negatively to community leaf physical resistance and chemical defense traits (i.e. LT and leaf tannin concentrations). Surprisingly, in contrast to our expectations, LCC had a strong positive effect on litter decomposition. In contrast, Perez-Harguindeguy et al. (2000) reported a negative effect of litter carbon content on litter decomposability. In addition to leaf carbon, the authors also reported a negative effect of C/N and LT on litter decomposition rates for a wide variety of species. However, as opposed to the results of the present study, Perez-Harguindeguy et al. (2000) used separate linear models to relate each single trait to litter decomposability. In the multiple regression analysis, LCC positively affected litter decomposition whereas LT and LDMC slowed down this process. We initially assigned both former traits to the group of leaf traits related to physical defense. Although the collinear arrangement of LT and LCC in the PCA indicated

that LT was affected by the same leaf structural compounds as LCC, both traits had opposing effects on leaf litter decomposition. As variance inflation factor analysis of the most informative multiple regression model did not indicate detrimental influences of multicollinearity between LT and LCC, the positive effect of LCC might rather be related to more labile carbon fraction than to structural carbon compounds (see Kraus *et al.* 2003). Such labile compounds might be readily used by the decomposer community, thus resulting in higher leaf litter decomposition rates. Support of this interpretation can be found in the increasing carbon leaching rates from leaf litter with increasing total phenolics concentrations as described by Madritch and Hunter (2004). Furthermore, Lin *et al.* (2006) argued that in particular low molecular weight phenolics might be leached from leaf litter and then, as readily available carbon source, may stimulate microbial growth and activity (see also Rahman and Motiur 2012).

Similar to our study, Wardle *et al.* (2003) used multiple regression analysis to relate leaf traits to rates of litter decomposition. The authors used a wide variety of leaf functional traits, including tissue nitrogen content, lignin, cellulose, fiber and leaf polyphenol content in their analyses and reported a positive effect of leaf nitrogen concentrations on litter decomposition. In contrast to our results, Wardle *et al.* (2003) reported tissue tanning capacity to be positively related to decomposition rates, which contradicts other decomposition studies (e.g. Hättenschwiler *et al.* 2005; Hoorens *et al.* 2003; Salamanca *et al.* 1998). Among many other studies, Perez-Harguindeguy *et al.* (2000) highlighted the negative effect of tannins and total phenolics content on decomposition when investigating decomposability of 52 Argentinean and 15 species from UK. Moreover, Coq *et al.* (2010) analyzed a wide variety of different condensed tannins and provided evidence that these have an important influence on litter decomposition and nutrient dynamics. This is in line with our findings that tannins decrease rates of litter decomposition. Hättenschwiler *et al.* (2005) provided information on the mode of action of tannins on litter decomposition such as the inhibition of nitrification or on the complexation of nutrients, thereby reducing nutrient availability for decomposers (see also Kraus *et al.* 2003). However, in contrast to our expectations, differences in community productivity (as indicated by the traits related to productivity) did not affect community decomposition rates. Nevertheless, this might be due to strong multicollinearities among the traits related to productivity and those related to the nutritional value, as depicted in the PCA.

We are not aware of any other study investigating shifts in leaf functional traits in forest communities along secondary succession that directly linked these shifts to community litter decomposition rates. In summary, we conclude that along secondary succession in the species-rich subtropical forest ecosystem under study, leaf traits that promote litter decomposition decreased in importance, whereas traits that reduce the community *k*-rates did not consistently increase in importance along the succession. Based on our results

we suggest that future studies that aim at relating shifts in leaf functional traits on a community basis to community properties such as litter decomposition along secondary succession should use multiple regression analyses rather than separate linear models to analyze causal relationships. We found that, while leaf physical resistance increased, chemical defense traits decreased in older forest communities. Other traits that were found to be important in the dynamic of litter decomposability in the multiple regression analysis (such as LDMC, LCC and LSC) did not change significantly with ongoing succession. However, these traits affected litter decomposability in opposing directions. In consequence, litter decomposition rates remained stable along secondary succession. The adverse effects of polyphenolic substances on litter decomposition are most prominent in young successional stages, whereas in the late successional stages, structural components dominated decomposition. We therefore conclude that decomposition dynamics along the successional gradient under study can be explained by CWM values of traits (our hypothesis 3).

SUPPLEMENTARY MATERIAL

Supplementary Table S1 is available at *Journal of Plant Ecology* online.

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