



# „Litter quality and tree species richness effects on litter decomposition in subtropical forest“

## Bachelorarbeit

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## 1. Introduction

Photosynthetic organisms are able to transform water and carbon dioxide into glucose and oxygen by the transformation of photonic energy to chemical potential in chemical bonds (Croce & van Amerongen 2014). This chemical potential will then be the driving force of the plant anabolism and growth. This newly produced organic matter can serve as food for the plant itself but also for herbivores. Those herbivores (i.e. primary consumer) can then get eaten by predators (i.e. secondary consumers). Senesced, the dead organic matter from primary producers and consumers feed another group of organisms: the decomposers. The decomposition of dead organic matter, like leaf litter, releases among other carbon to the atmosphere and nutrients to the soil, making those elements available for primary producers (Rees *et al.* 2006). The good functioning of an ecosystem depends on the cycling of carbon, energy and nutrients across the system. Therefore, the understanding of leaf litter decomposition is necessary to understand the circle of energy, carbon and nutrients, as well as the whole functioning of an ecosystem.

Leaf litter decomposition is controlled by three main factors: environmental conditions, decomposer community and litter quality (Pérez-Harguindeguy *et al.* 2000, Toledo Castanho & Adalardo de Oliveira 2008). Environmental conditions, for example climate (wet and warm) and soil (e.g. neutral soil pH) are known to be strong predictors of litter decomposition (Aerts *et al.* 1997, Currie *et al.* 2010). The decomposer community, for example a high diversity of bacteria and fungi, positively affect decomposition processes (Bastian *et al.* 2009). A high litter quality, for example high content of phosphorus in the litter increases decomposition (Ostrofsky *et al.* 1997). However, these three factors often interact in driving decomposition processes, complicating the identification of the contribution of single factors to the process.

This bachelor thesis aims to explore the influence of litter quality on decomposition, by controlling for environmental conditions and decomposer community composition. Litter quality can be described by the amounts of available nutrients and the accessibility by decomposers. The amount of nutrients, i.e. litter chemical composition, is known to positively affect litter decomposition. For example, a high nitrogen and phosphorus to carbon ratio has been proven to increase decomposition (Ostrofsky *et al.* 1997). In contrast, chemical structure compounds like high content of lignin, phenolics and tannins hinder the decomposition process (Kainulainen and Holopainen 2002). Thus, a high leaf chemical quality can be defined by high amounts of nutrients (e.g. nitrogen and phosphorus) and low amounts of structure compounds (e.g. phenolics and tannins).

The chemical content of a leaf can only affect the decomposition, if the decomposers can get access to this content. It has been shown that the possibility of direct access of leaf litter internal content increases the decomposition (Wagai *et al.* 2012). The nutrient accessibility can be linked to the physical stability of the leaf (i.e. leaf toughness). Strong predictors of this leaf toughness are specific leaf area (SLA, Santiago *et al.* 2007) and leaf dry matter content (LDMC, Quested *et al.* 2007). A high SLA reduces leaf toughness, whereas a high LDMC increases leaf toughness. An increasing decomposition rate has been shown with low leaf toughness (Hansen and Coleman 1998, Pérez-Harguindeguy *et al.* 2000), meaning with a high SLA and a low LDMC (Quested *et al.* 2007, Bakker *et al.* 2011).

Decomposition increases with a high litter surface where decomposition can occur. The surface increases with fragmentation of litter pieces and positively influences the access to substrates and nutrients (Salamanca *et al.* 1998, Hector *et al.* 2000). It was shown that many small fragments of litter get decomposed faster than bigger pieces with the same chemical composition (Yang *et al.* 2012). Therefore, leaf litter with a high likelihood to break into fragments (further called fragmentability) is expected to decompose faster.

One way of describing decomposition is based on the biomass ratio hypothesis (Grime 1998) which predicts litter decomposition effects by community weighted mean (CWM) traits (Garnier *et al.* 2004) and not by species interactions (i.e. additive effects). The CWMs describe the average trait values calculated from the species-specific values and the abundance of the species in the mixture. For example, Tardif *et al.* (2014) showed with a species litter diversity experiment, that the difference between the CWM prediction and the occurring decomposition rate was not significant. This proved that CWM traits, so additive effects, are well predictors of the decomposition.

However, in forests, trees do not grow in isolation but are surrounded by neighbouring trees. The interaction between a tree and its neighbours can influence the litter quality already in the growth process, for example the nitrogen and phosphorus content of the leaves (Novaplansky *et al.* 2009, Violle *et al.* 2009). Furthermore, interactions between leaf litter species on the ground (i.e. non-additive effects) can increase decomposition (Gartner and Cardon 2004, Hättenschwiler *et al.* 2005). These non-additive effects (i.e. species mixture decomposition shows a different decomposition rate than predicted from the occurring species) have been shown in decomposition experiments using species-rich mixtures (Lecerf *et al.* 2011, Trogisch *et al.* 2016). They were rather related to species composition than to the number of tree species present (Barantal *et al.* 2014, Handa *et al.* 2014). The non-additive effects resulted from

differences in species-specific physical and chemical litter traits represented in litter mixtures. These effects were forecasted theoretically by Epps *et al.* in 2007 and have been empirically proven for example by Trogisch *et al.* (2016), who showed also an indirect positive effect of leaf species richness on decomposition. Non-additive effects are the most commonly reported outcomes of litter diversity experiments (Gartner and Cardon 2004, Makkonen *et al.* 2013, Vos *et al.* 2013, Trogisch *et al.* 2016). In litter mixtures, weighted variance of species traits (i.e. functional dissimilarity, FDis) has been shown to promote litter interaction during decomposition (Heemsberg *et al.* 2004, Schleuter *et al.* 2010). The FDis can be calculated by using one specific trait or a set of various traits. Barantal *et al.* (2014) showed increasing decomposition with high species dissimilarity in their carbon, nitrogen and phosphorus content. This chemical quality is often species-specific (Güsewell *et al.* 2004, Speed *et al.* 2015).

To test leaf litter quality and diversity effects on decomposition, a “Common Garden” experiment was set up in a Chinese subtropical forest plantation. This experiment was designed to control for environmental conditions such as biotic (e.g. microbial community composition and abundance) and abiotic (e.g. humidity, temperature and soil properties) parameters variability.

Litter-bags with an increasing diversity of tree species up to nine species were used to test the following hypothesis:

- Hypothesis 1 (H1): A high leaf litter chemical quality will increase leaf-litter decomposition.
- Hypothesis 2 (H2): The decomposition will increase with low leaf toughness.
- Hypothesis 3 (H3): A high fragmentability of leaf litter will increase decomposition.
- Hypothesis 4 (H4): The decomposition will increase with high leaf litter diversity.



## 2. Materials and Methods

### 2.1 Experimental design

To investigate leaf trait-based litter decomposition a Common Garden decomposition experiment was set up. Therefore, 360 litterbags with specific leaf litter were distributed in a *Schima superba* plantation in the Jiangxi province located in south-east China, near the town Xingangshan (29.12°N, 117.90°E). The climate is subtropical, with warm wet summers and cool dry winters. The local mean annual temperature is 16.7 °C with an annual precipitation of 1800 mm (Yang *et al.* 2013). In September 2019, soil properties such as a soil water holding capacity of 80 % and a soil moisture of 24 % were measured.

Fallen leaves of twelve native broad-leaved tree species were used to fill the litter bags. The leaves were collected in the experimental Site A of the BEF China experiment (Bruehlheide *et al.* 2014), from 180 tree pairs in 68 plots with a tree species richness ranging from one to twelve. The tree pairs are henceforth called tree species pairs (TSPs). The TSPs are combinations of these twelve species with two replicates of each TSP in the plots where the species occurs. Six deciduous species: *Castanea henryi*, *Koelreuteria bipinnata*, *Liquidambar formosana*, *Nyssa sinensis*, *Sapindus mukorossi* and *Sapium sebiferum* and six evergreen species: *Castanopsis sclerophylla*, *Choerospondias axillaris*, *Cyclobalanopsis glauca*, *Lithocarpus glaber*, *Quercus fabri* and *Quercus serrata* were used.

To collect the leaves, litter-traps between each TSP were set up in September 2018 (**Figure 1**). Each litter-trap covered an area of approximately one square meter between the two trees and



**Figure 1:** Litter-trap between a tree species pair to collect fallen leaves between September and December 2018.

collected the litter of the TSP as well as from the surrounding tree neighbours. After four months in the field, the litter was collected in December 2018.

The litter for each TSP was split by species and air-dried in paper bags at 40 °C in a drying oven for three days. The dry weight of the leaf litter of each species was measured (+/- 0.01 g) to calculate the percentage of each species in the litter-trap. Litter-bags with a

0.005 mm<sup>2</sup> mesh size were filled with a total of 2 g (+/- 0.001 g) of dry litter. The litter-bags mirrors the amount of species-specific litter in the litter-trap of the TSP in the specific plot. For each TSP, two litter-bags were filled and labelled, resulting in a total number of 360 litter-bags that were prepared.

For a standardized litter control 8 teabags of green tea and 8 teabags of red tea were dried in the same way as the leaf litter, labelled and weighted.



**Figure 2:** The two blocks of the Common Garden in the beginning of the experiment (12/2018). Each block contains 180 litter-bags (white squares) with one replicate of a litter-trap. Yellow sticks mark the position of the control points, where two teabags were added on the ground

The Common Garden experiment was set up in December 2018 in the evergreen *Schima superba* monoculture plot. For the set-up, two tree rows next to each other with a length of approximately 8 m (six trees) and a length shift of approximately 6 m between the rows were selected. Litter and big rocks were removed and the soil surface got smoothed. In each row, a block was formed with the litter-bags by using a pattern with 36 rows and

five columns. Each block contained one replicate of each TSP litter-bag placed randomly within the block (**Figure 2**).

To control the decomposition rate based on the soil microbial community in the Common Garden, four control points in each block with two teabags of standardized litter (red and green tea) on the soil-surface were added.

Ten mm mesh wire and steel hooks on the borders were used to fix the litter-bags of each block on the ground.

## 2.2 Sampling

In September 2019, the 360 litter-bags from the Common Garden were collected. First, the mesh wire was removed row by row, then, the litter-bags were transferred into paper bags and labelled with their unique number and position in the block. Most of the bags were covered with soil therefore the soil-cover was recorded for each litter-bag in percentage. Under each litter-bag 5 g of soil got sampled to measure the soil-moisture. The teabags were collected from the ground and got separately stored for each control point.

Afterwards, each litter-bag was transferred into a plastic box filled with water for 48 h to remove soil contamination from the bag and the litter inside. The litter-bags were opened and the content got cleaned by hand. Soil and non-litter material, like thin roots and faeces were removed and recorded, and the litter was gently brush-cleaned.

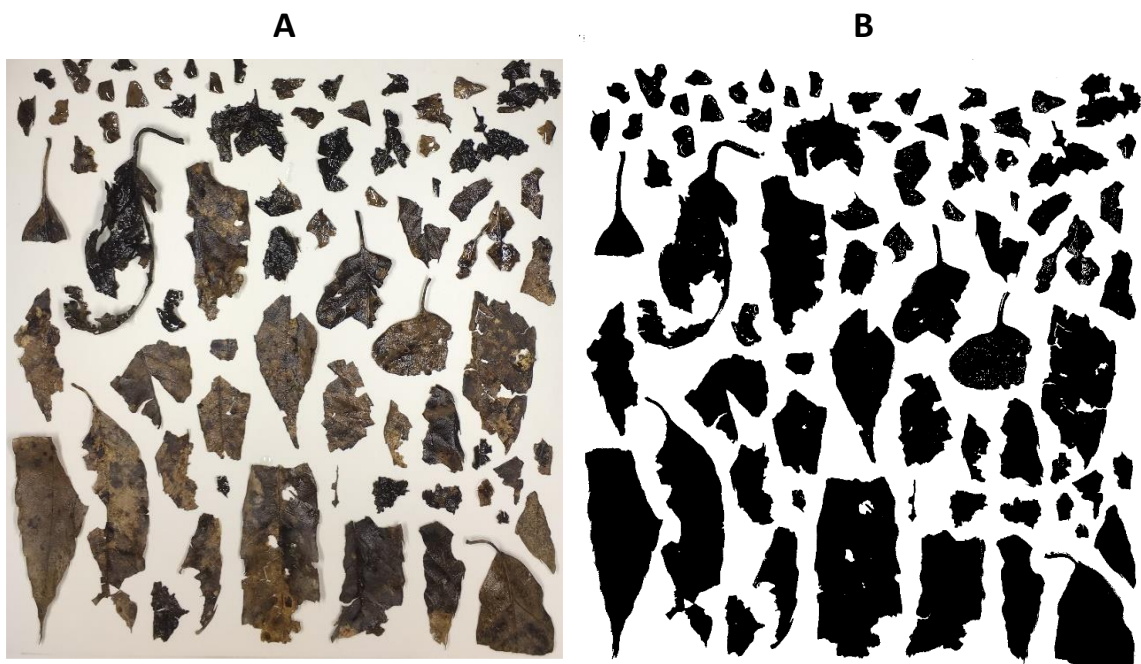


### 2.3 Litter fragmentability measurements

To analyse the litter fragmentation, photos of the wet litter were taken on a white, scaled background. Therefore, an eight-megapixel camera with a five-element lens and an optical image stabilization was mounted horizontally 40 cm above the scaled background. The litter from the litter-bag was sorted on the scaled background controlling for overlapping between litter pieces (**Figure 3.A**). Pieces with a size smaller than  $0.05 \text{ mm}^2$  were excluded from the record. Both small and big litter pieces were separately air-dried along with the teabags at  $40 \text{ }^\circ\text{C}$  for three days.

Photos of the litter fragments were analysed with the java-based program imageJ (version 1.52a, Java 1.8.0\_112). The photo was transformed to an 8-bit image, to use the function threshold (**Figure 3.B**). Threshold selects the pieces on the background and analyses particles to measure the area of each piece. Based on this measured area the piece average size (PAS) got calculated. Furthermore, the number of pieces in the litter-bag and the remaining litter mass was used to calculate the pieces per g of litter (PPG). The fragmentability got linked to a low PAS and high PPG.

The measured area is based on a scale which was set before for each photo. To test if the variation of setting the scale manually had an effect, the scale was set 75 times, and the occurring differences were calculated. By using the threshold function, only dark areas got selected.



**Figure 3:** A: photo of the leaf litter fragments of one litter-bag after removing non-litter material, brush-clean and removing pieces smaller than  $0.05 \text{ mm}^2$ . B: leaf litter fragments after processing with imageJ.

Areas with water reflections were lighter in colour and got not selected. To control if those non-selected areas change the measured area significantly, in 20 sample photos the white error points were removed manually and the significance of the changed area was tested.

## 2.4 Litter carbon and nitrogen measurements

The dry litter content of each bag was milled at 26 shakes per second for 5 min and filled in labelled plastic tubes. Four mg of the litter powder was filled in tin vials and shipped to the University of Göttingen for a total carbon and nitrogen analysis using an elemental analyser (Vario L, Elementar).

## 2.5 Soil-moisture measurements

The sampled 5 g of soil below each litterbag were weighted and afterwards dried for two days at 40 °C. The dried weigh was measured and the soil-moisture got calculated in percentage.

## 2.6 Data analyses

All calculations and statistical analyses were performed in R (version 3.6.1). Initial carbon and nitrogen content before decomposition were calculated as community weighted means (CWM) for each litter bag from fresh leaves on the experimental site in 2018 by using the FD package from the R package vegan. Specific leaf area (SLA), leaf dry matter content (LDMC), contents of phenolics and of tannins for each litter-bag were calculated in the same way from data based on a sampling on the experimental site between 2008 and 2012 by collaborators. The package was also used to calculate the species level and the functional dissimilarity (FDis). The species level is equally to the number of species in the litter-bags. To calculate the functional dissimilarity, first the traits of chemical quality and leaf toughness got rescaled (to have a mean of zero and variance of one) and then the Euclidean distance matrix of scaled traits got computed (Cadotte *et al.* 2009).

Decomposition was described as percentage of carbon loss. Therefore, the carbon loss was calculated by subtracting the initial carbon in fresh leaves by the carbon measured in the litter bags after decomposition and divided by the initial carbon content. For testing the hypothesis of chemical quality, leaf toughness and leaf fragmentability, the following linear model was used:

$$\text{carbon loss} \sim C:N + C:P + \text{Tannin} + \text{Phenolics} + \text{SLA} \times \text{LDMC} \\ + \text{piece average size} \times \text{pieces per g}$$

The model got tested on the whole dataset (species level from 1 to 9) as well as on the monocultures (species level equally 1). Significant explanatory variables were selected with the stepAIC function from the R MASS package. The stepAIC function tests all possible addition and removal of variables to the model and compares all different models to select the model with the lowest AIC (AIC is calculated from the log-likelihood and number of variables). The algorithm continues until reaching the model with the lowest AIC. To test the first hypothesis (the influence of chemical quality on decomposition), the leaf chemical traits were added to the model. For the second hypothesis (the influence of leaf toughness on decomposition), SLA and LDMC were used in the model, as well as the correlation between them. The third hypothesis, how fragmentability increase the decomposition, was tested by using the measurements from the analyses of the photo fragments. Piece average size, pieces per g and their correlation were added to the model. After adding all variables to the model, the stepAIC was used to select the significant ones. A variance partitioning analysis was performed to understand the importance of the litter traits on decomposition and to show which trait has the highest explanatory power.

For testing the possible prediction of carbon loss in species mixtures litter-bags from the monocultures, predicted carbon loss was calculated based on measured carbon loss from the monocultures. The calculated decomposition for each species got used to calculate the predicted carbon loss of species mixture litter-bags by sum the decomposition of each species related to the amount in the litter-bag. The models of selected traits and predicted decomposition got compared with the ANOVA and the AIC function.

To test the influence of species diversity on decomposition, the factors species richness and function dissimilarity (FDis) were added to the best model after model selection. The stepAIC function was used to keep the significant variables.

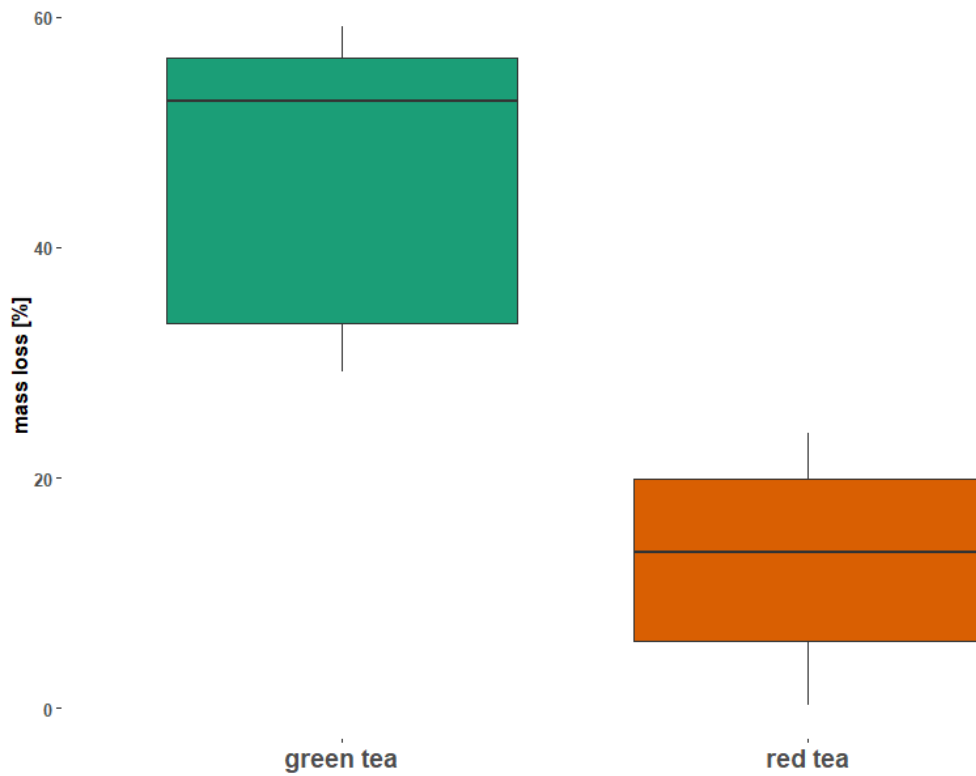
### 3. Results

#### 3.1 Validation of methodological assumptions

To evaluate the quality of the photos of litter fragments the same scale got remeasured 75 times. The measured scale for 25 cm had a mean number of 2435 pixels and the standard deviation of 9 px between the measurements (approx. 0.4 % of the mean). Then, the effect of removing white error points from the photos was tested, the area between the measured area and the area where the points were removed were compared. The chi-square-test between the two measurements showed a non-significant difference with a p-value of 0.24 (**Figure 9S**), meaning that the correction of white error didn't affect the measurement.

The homogeneity of the Common Garden experiment was controlled by the soil-cover, moisture and the decomposition of standardised litter (red and green tea). The measurements of the soil-cover on top of the litter-bags and the soil-moisture below the bags were modelled against the carbon loss. The model explained 0.02 % of the variation with a p-value for soil-cover of >0.25 and for soil-moisture of >0.28, with a model total F-value<sub>2,332</sub> of 1.402, indicating that the soil-cover and the soil-moisture at the sampling date did not explain decomposition.

The analysis of the teabags at the control points of the Common Garden showed a carbon loss for the green tea between 33 % and 60 %, with an average of 46 % (standard deviation to the mean of 13.17 %). For the red tea carbon loss was measured between 3 % and 22 %, with an average of 13 % (standard deviation to the mean of 9.36 %, **Figure 4**).

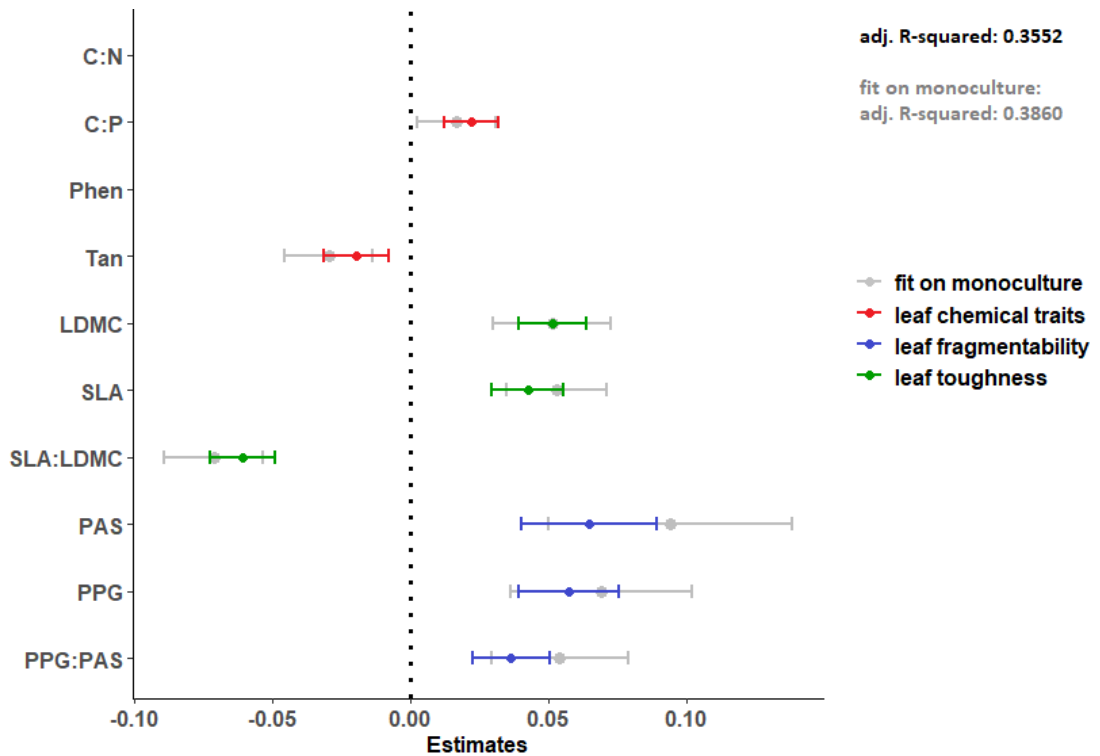


**Figure 4:** Mass loss of the teabags on the ground at the control-points in the Common Garden. Green tea with a mean mass loss of 45.86 % and a standard deviation to the mean of 13.17 %. The mean mass loss of the red tea was 12.74 % with a standard deviation to the mean of 9.36 %.



### 3.2 Leaf-litter quality effects on decomposition

The model of the all dataset showed a non-significant influence of the C:N ratio and the phenolics, these two traits were excluded during model selection. After model selection on AIC, all other traits stayed in the model with an adj. R<sup>2</sup> of 36 % (F-value<sub>8,327</sub> = 24.07, p-value < 0.001, **Figure 5**).



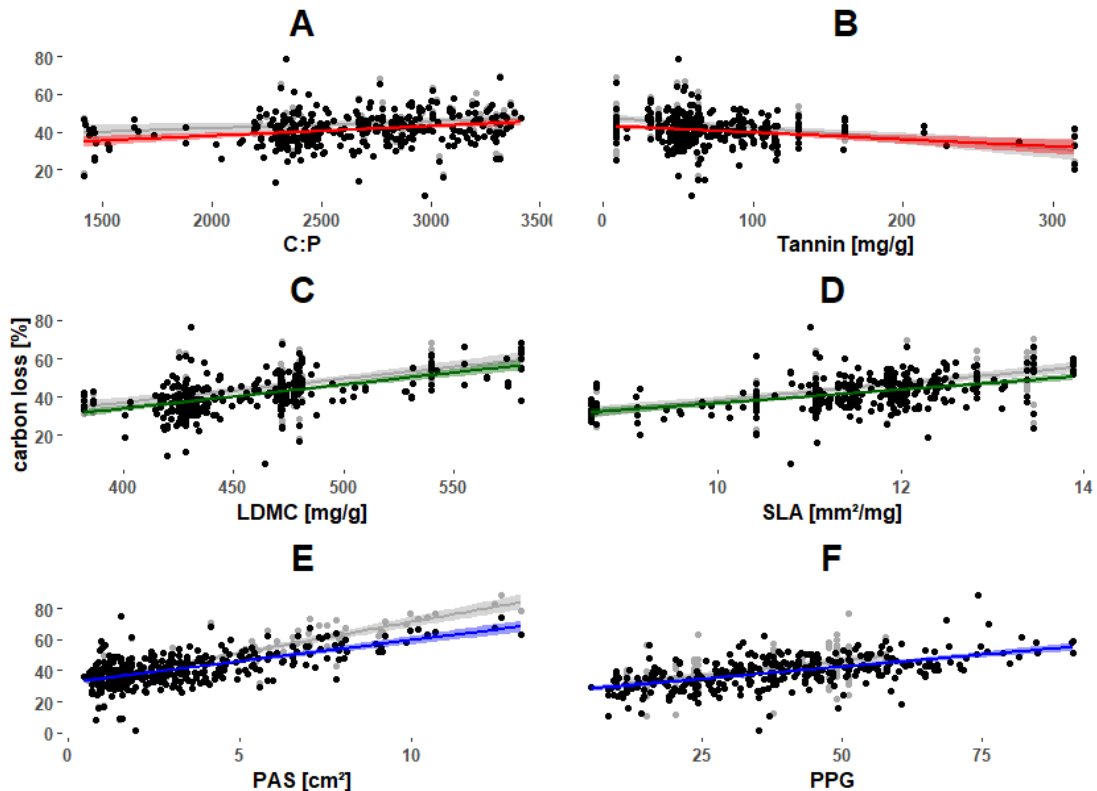
**Figure 5:** Estimates of calculated and measured values, non-significant values shown with empty rows. SLA:LDMC shows the interaction between these factors. PAS: piece average size, PPG: pieces per gram and PPG:PAS: the interaction between the two factors. The model on monoculture and mixture litter-bags had an adj. R-squared of 0.36 with a p-value < 0.001. Following p-values for the parameters were measured: C:P: < 0.001, Tan: 0.00151, LDMC: < 0.001, SLA: < 0.001, PAS: < 0.001, PPG: < 0.001.

The C:P ratio was positively correlated to the measured carbon loss (**Figure 6.A**). For example, if the C:P ratio increased from 1500 to 3000, the carbon loss increased approximately by 10 %. The amount of tannins was negatively correlated with decomposition (**Figure 6.B**). Between 0 and 300 mg tannins per g leaf, the carbon loss decreased by approximately 15 %.

Another predictor for the leaf litter quality was leaf toughness. A high LDMC (**Figure 6.C**) and a high SLA (**Figure 6.D**) increased carbon loss. Both parameters were highly significant with a p-

value below 0.001. For example, an increase of  $4 \text{ mm}^2 \text{ mg}^{-1}$  of the SLA increased the decomposition by 10 %.

The leaf-litter fragmentability was suggested to positively influence carbon loss. A higher carbon loss was measured with an increasing piece average size (p-value <0.001, **Figure 6.E**). Moreover, a higher number of pieces after decomposition was shown correlate positively with higher decomposition (p-value <0.001, **Figure 6.F**).

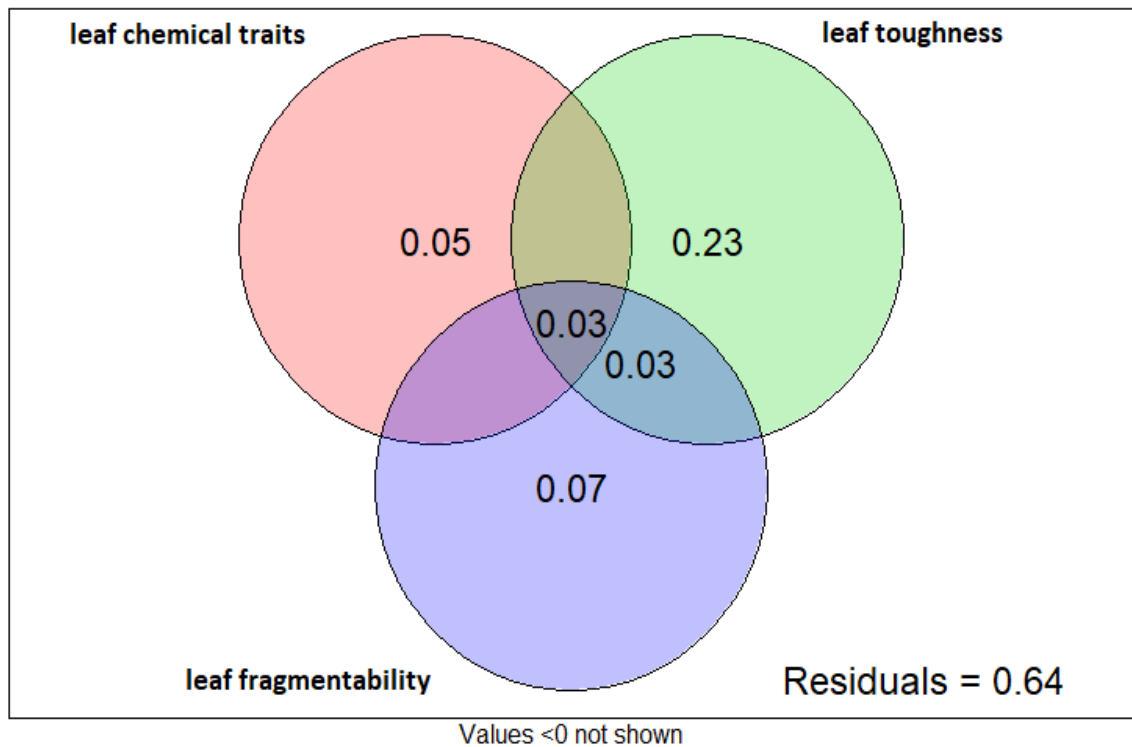


**Figure 6:** Carbon loss against all significant traits selected (each selected trait were plotted against carbon loss controlling for the effects of the other selected traits). Black points and the coloured line show the results for the whole dataset, grey points and lines the results of the samples with only one species. Carbon to phosphorus ratio (C:P): p-value < 0.001, Tannin: p-value = 0.00151, leaf dry matter content (LDMC): p-value < 0.001, specific leaf area (SLA): p-value < 0.001, piece average size (PAS): p-value < 0.001, pieces per g (PPG): p-value < 0.001.

For the subsamples of the monoculture litter-bags, the same traits with comparable effects were selected from the model. The adj.  $R^2$  was at 39 % (p-value > 0.001) and an  $F\text{-value}_{8,104}$  of 9.82. The p-values of all traits were similar to the ones measured for monocultures and mixture litter-bags, only the p-value of tannin for the monoculture was below 0.001. The similarity of the models of the monocultures and the mixtures showed that the response variables were explaining monocultures and mixtures in the same quality

### 3.3 Variance partitioning analyses of leaf-litter quality traits

For the leaf-litter quality traits, a variance partitioning analysis was performed to understand the importance of the litter traits on decomposition. The leaf toughness explained most of the variances with 23 %, leaf chemical content only explained 5 % and leaf fragmentability 7 %. The decomposition variability was explained with 3 % by the leaf toughness and leaf fragmentability, this is linked to the correlation between the two parameters.



**Figure 7:** Venn diagram of the three groups of explanatory variables and how much of variance they explain by their own and overlapping with the others. non-significant values (below 0) are not shown.

The correlation diagram (**Figure 10S**) showed higher correlations for the leaf toughness and fragmentability than the Venn diagram for explained decomposition. For example, specific leaf area (SLA) and litter piece average size (PAS), were negatively correlated (Pearson correlation = 31 %) and while SLA and pieces per g (PPG) were correlated up to 28 %. Furthermore, the diagram showed for the leaf dry matter content (LDMC) with piece average size a positive correlation of 49 % and a negative correlation with pieces per g of 75 %. A positive correlation was also shown for the chemical traits and leaf toughness, as well as for the leaf fragmentability.

The C:P ratio had a positive correlation between piece average size and pieces per g with 31 % and 26 %. The amount of tannins showed a positive correlation with SLA (58 %) and LDMC (20 %). But the overlapping of all three traits (**Figure 7**) explained only 3 % of the decomposition variance.

### 3.4 Prediction of decomposition in mixtures from the monocultures

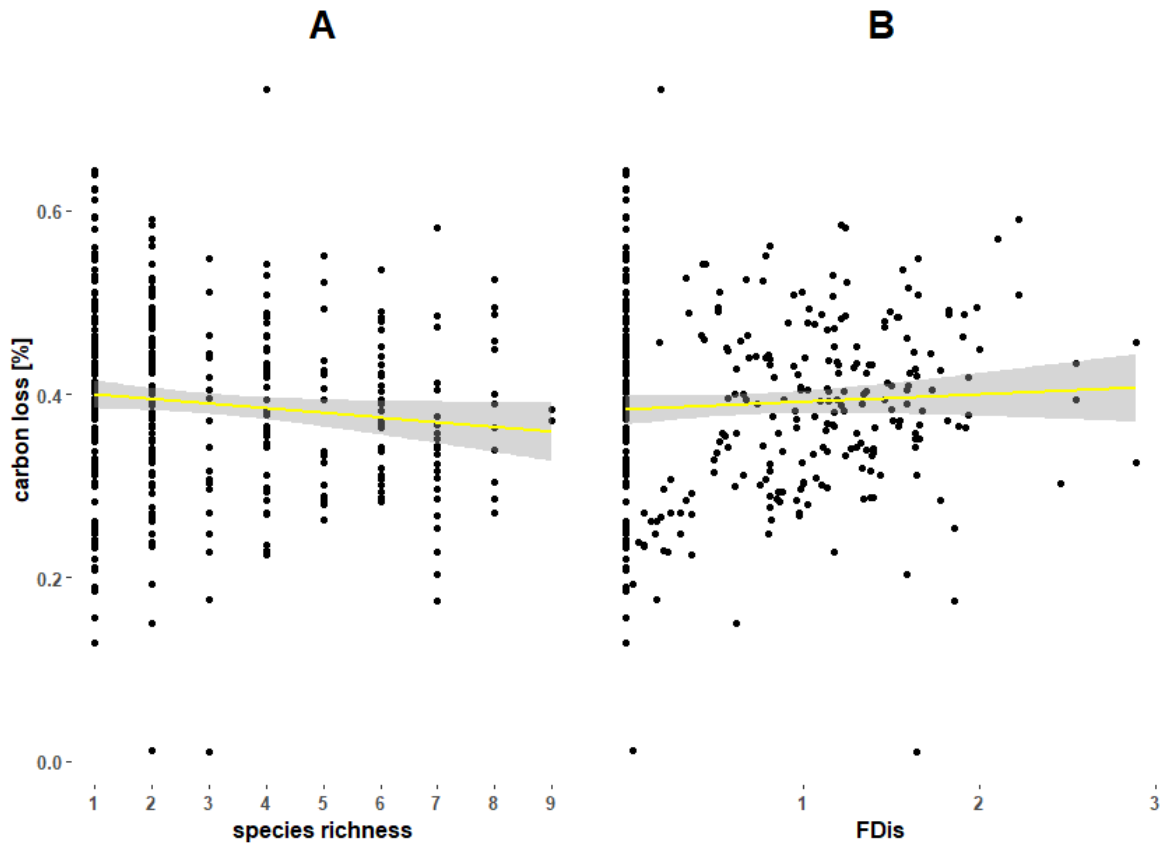
The calculation of the predicted decomposition was performed to estimate the importance of additive effects on decomposition. The predicted decomposition explained 23.26 % (F-value<sub>1,222</sub>: 68.6) of the variance of the measured decomposition with a p-value below 0.001 (**Figure 11S**).

### 3.5 Comparison of the trait-based and predicted decomposition model

The model of the traits explained a higher proportion of the variance (35.52 %, F-value<sub>8, 327</sub> = 24.07) than the model of predicted carbon loss from the monocultures (23.26 %, F-value<sub>1,222</sub> = 68.6). The ANOVA test showed that both models are significantly different (p-value < 0.001). The model based on leaf traits got selected with an AIC of -702.72 against the model of predicted decomposition from the monocultures with an AIC of -681.15.

### 3.6 Species leaf-litter diversity effects on decomposition

The species richness and the functional dissimilarity (FDIs) was added to the trait-based model after selection. After a model selection, the species richness and FDIs were excluded. The species richness had a p-value of 0.6562 and the FDIs a p-value of 0.1764.



**Figure 8:** Carbon loss in percentage against the two diversity traits: species richness and functional dissimilarity (FDIs).

## 4. Discussion

### 4.1 Method assumption of the Common Garden experiment

To evaluate the photo analysis with imageJ, two kinds of calibrations were done. The correction of the photo's scale measurement did not change significantly the area estimations. On average, on the 25 cm scale, the error was estimated to be 0.4 %. The chi-square-test between the areas with and without error-points did not show a significant difference (p-value of 0.24). Thus, conclude that the method how the picture was analysed can be accepted, because the error which occurs through those measurements is not significant.

The model of the soil-coverage of the litter-bags and the soil moisture below the litter-bags against the carbon loss, explained 0.02 % of the decomposition variance. The non-significant effect on the decomposition showed that these uncontrolled parameters did not significantly influence the decomposition in the Common Garden experiment.

To check for the homogeneous decomposition throughout the Common Garden experiment, teabags were used as standardised litter at four control-points in each block. The average mass loss of the green tea was 46 % (standard deviation: 13.17 %) and 13 % for red tea (standard deviation: 9.36 %) for teabags on the ground. This variance in mass loss could be explained by a potential coverage of the teabags with soil over the time in the field. It was shown that teabags, which were dug in or covered with soil had a higher decomposition rate than teabags without soil-cover lying on the ground (Fanin *et al.* 2019). This effect increased more for green tea than for red tea. Furthermore, Fanin *et al.* showed that the effect of climate is higher on green tea than on red tea, and the effect of surrounding tree species is lower on green tea, than on red tea. They proved that green tea shows a higher decomposition rate, as high-quality litter, than red tea. Also, the standard deviation increased with higher mean. The low standard deviation of red tea showed the low impact of the surrounding tree species *Schima superba*. Comparing the standard deviation of red and green tea, the green tea had a 4 % higher standard deviation. The higher decomposition variance of green tea could be explained by its higher mean decomposition rate, but also by its sensitivity to soil-cover and climate. The mass loss of the teabags did not show a high standard deviation, which suggests that conditions were very homogeneous in the Common Garden experiment.

## 4.2 Leaf-litter quality effects on decomposition

A high leaf quality (high content of nitrogen and phosphorus, low content of phenolics and tannins) was hypothesised to increase decomposition. The leaf-litter quality was described as the combination of the influence of the leaf chemical content, leaf toughness and the leaf fragmentability. The litter chemical quality was defined as the amount of nitrogen, phosphorus, phenolics and tannins. It was expected that a high chemical quality increases decomposition. Our analyses showed a significant increase of decomposition with a high carbon to phosphorus ratio (C:P ratio) and a low amount of tannin. The results of increasing decomposition with a high C:P ratio were in contrast with the literature. For example, Xu and Hirata (2005) showed an increasing decomposition with a low C:P ratio, meaning with a higher amount of phosphorus compared to carbon. This effect has been shown with high amounts of the carbon to phosphorus ratio, ranging between 1639 and 3811. The results from this bachelor thesis showed a range of C:P laying between 1500 and 3500. For the values below 2000, it could be that the carbon was more the limiting factor than the phosphorus. Therefore, an increase of decomposition was measured with an increasing of the C:P ratio.

We expected to observe an inhibitory effect of tannins on the decomposition. This inhibit effect can be explain by its enzyme inactivation effect on decomposers, especially fungi (Benoit & Starkey 1968). The negative effect of tannins was more significant in the analysis of the monocultures, than in the one of all litter-bags. This result goes in line with the literature. For example, Ristok *et al.* (2017) showed a positive influence of species mixtures on the decomposition of tannins. The increased decomposition of tannins in early stages of the decomposition process reduced their negative effect.

A positive effect of high nitrogen on decomposition was expected. The result showed a non-significant increase of the carbon to nitrogen ratio (i.e. C:N ratio) against decomposition. This result matches the findings from Porre *et al.* (2020), where no effects of litter nutrient concentrations were shown. The hypothesis of the positive influence of leaf chemical quality on leaf-litter decomposition were partly proofed by these results. The effect of phosphorus was depending on the limiting factor of the C:P. It is likely that carbon was mostly the limiting factor due to the possibly phosphorus rich soil of the experiment side. Another reason for the shown result could be that the experiment was not set up long enough to show an increasing decomposition with high phosphorus. Xu and Hirata (2005) showed an effect of phosphorus in the late phase of decomposition (total time of two years), and a higher effect of nitrogen in the initial phase (first three months). The results in this bachelor thesis could shown the process

between the initial phase and the long-term decomposition where the effects of phosphorus got stronger.

The second approach of defining leaf quality was related to leaf toughness. An increasing carbon loss was hypothesized with low leaf toughness. The positive effect of the specific leaf area (SLA) and a negative effect of leaf dry matter content (LDMC) were expected. Partly in contrast to our expectations, the results showed a positive influence of both SLA and LDMC on decomposition. The LDMC was calculated with the oven-dry mass (mg) divided by the water-saturated fresh weight (g) of a leaf. In studies where the LDMC was a strong predictor of decomposition, fresh leaves were used (Quested *et al.* 2007). For fresh leaves, a high LDMC means a high amount of structural content and a low amount of water. In this experiment, the oven-dry mass was used to fill the litter-bags. The used weight of leaf-litter was independent from the water content, and only the structural contents of the leaves were used. Considering this, the LDMC should have neither a positive nor a negative effect on decomposition. A reason for the positive effect could be that the structure of a leaf with a low water content does not have the possibility to store a high amount of water and has therefore less strong structural elements (Choong *et al.* 1992). The weaker structural elements could link to a higher fragmentability of the leaf-litter. The data showed a positive correlation between LDMC and the piece average size (PAS, **Figure 10S**).

A high impact of SLA got shown, whereas Quested *et al.* (2007) showed that the effect of LDMC on carbon loss was more significant than the one of SLA. The significant positive effect here could be linked again to the use of oven-dry leaf-litter. A high SLA means a high area and low leaf thickness. By using 2 g of dry weight, thin pieces of litter were used from a species with a high SLA instead of very thick pieces from a species with a low SLA. This could have increased the accessibility of nutrients and therefore the carbon loss. This relation was supported by the positive correlation between SLA and number of pieces per gram (PPG), as well as the negative correlation with the PAS (**Figure 10S**).

The leaf fragmentability was hypothesized to increase decomposition. Therefore, the piece average size and the pieces per g were measured after the decomposition in the field. The results showed an increasing decomposition with increasing piece average size and with a high number of pieces per g. Considering the results of Yang *et al.* (2012), the complete opposite was expected, because with less piece average size the total surface of the litter increases which leads to an easier access to the nutrients for the microbes. A reason for this contrary result could be the link to the SLA. When the piece average size was high, there was possibly a large but thin piece in the beginning instead of several area-small thick pieces. This thin litter piece



with a big surface had a lot of space for microbes and so possibly increased the number of microbes in the bag. In a litter-bag with a species mixture, this would lead to a faster decomposition of the additional small pieces of the same bag. The big pieces will remain in the bag and this is what was shown here. The pieces per g showed that still a lot of pieces remained when the carbon loss was high. The link to the positive correlation between piece average size and pieces per g means that the decomposition rate was higher when a lot of big pieces were remaining in the litter-bags. A reason for this result could be that the pieces in the beginning were much larger and broke into a lot of smaller pieces when the microbes started to decompose them. The higher surface gave more space for the microbes in the beginning instead of leaf-litter which broke really fast into small pieces maybe already before or in the first days of the litter-bags in the Common Garden. These results need to be examined more closely also because of the lag of publications by now. A measurement of piece average size and pieces per g before and after decomposition could on one hand, increase the accuracy of interpreting these results and on the other hand, make it possible to compare this data and evaluate the change of the values through decomposition. Here it was shown that piece average size and pieces per g are possibly good predictors of decomposition.

In this bachelor thesis, the calculation of the C:P ratio, phenolics, tannins, SLA and LDMC and their effects on carbon loss should not be overvalued, because they are based on species average values measured in the same study site between 2008 and 2012. This could also be a reason why the C:N ratio did not show any significant effect, because it was a species average calculation based on data from 2016. Summarised, this means that the data that was used, did not contain an effect of the surrounding trees and the interaction of the species from the litter collection sides. This could be the same for the effect of tannins or C:P ratio. The observed effect could come from the misinterpretation of the calculated values. This calculated amount could be much higher or lower than the amount in the litter-bags, and the effect which was shown could be random. This error could be determined if the data could be measured from samples of oven-dried leaf-litter from the same origin as the litter used in the litter-bags.

#### 4.3 Leaf-litter diversity effects on decomposition

A positive effect of species diversity on litter decomposition was hypothesized. To define diversity, species richness in the litter-bags and the functional dissimilarity (FD<sub>is</sub>) were measured. The model selection excluded both of the values as non-significant. Trogisch *et al.* (2015) showed that two thirds of the measured leaf-litter decomposition were positively

influenced by species mixtures and one third negatively. Furthermore, a decreased carbon loss with low species richness has been shown by Lopez-Rojo *et al.* (2018). The experiment of Trogisch *et al.* (2015) differed from the used method in this study. The litter-bags were set up in different plots with different occurring species and species levels. The different species levels and dominated tree species affected the occurring species-specific decomposers (Urbanová *et al.* 2015). In this bachelor thesis, the microbial community was controlled in the Common Garden. This means, in the Common Garden, species-specific decomposers of *Schima superba* were expected. This species was not part of the litter-trap design. For example, a litter-bag with species-mixture would decompose faster in a plot with a species which is in the bag instead of a plot without matching species (Fanin *et al.* 2016).

This showed that leaf-litter traits are stronger predictors in a Common Garden than the species level or the dissimilarity of these species. Related to the species richness effect one positive effect has been shown: the negative effect of tannins was lower in species-mixture litter-bags. Furthermore, the specific leaf area (SLA) and the leaf dry matter content (LDMC), so the leaf toughness was the strongest predictor of the measured decomposition. The piece average size and the pieces per g shown potential to explain decomposition, measurements of the values before decomposition and after could increase the explanatory strength of them.

## 5. Summary

The decomposition process of leaf litter can be affected by environmental conditions (such as temperature and humidity), the soil microbial-community and the leaf-quality. Here, we performed a Common Garden experiment in a subtropical forest to control for the effects of the environmental conditions and the microbial-community, and to investigate the effects of leaf-litter quality on decomposition. Leaf-quality was defined in this study by the leaf content of nitrogen, phosphorus, phenolics and tannins, as well as the leaf toughness and the fragmentability.

In the set-up of the Common Garden, 360 litter-bags were used with one to nine species mixtures, including one replicate per mixture. The litter-bags stayed in a monoculture plot for nine months. After collecting the litter-bags, the litter was brush-cleaned and pictured for measurements of litter piece average size and pieces per g. Furthermore, the litter was air-dried and carbon and nitrogen measurements were done.

As expected, a positive influence of leaf quality on decomposition was shown. Especially leaf toughness, defined by specific leaf area and leaf dry matter content, explained most of the variance of measured carbon loss. The measurements of fragmentability could be linked to the leaf toughness and explained significant proportion of the decomposition. For the chemical content of the leaves, only carbon to phosphorus ratio and the amount of tannins were significantly affecting decomposition. The negative effects of tannins on decomposition decreased in species mixture litter-bags. A significant effect of species richness or of the functional dissimilarity could not be shown in this experiment, suggesting that previously observed biodiversity effects may be mediated by the abiotic and biotic environment of more diverse tree stands.

This study showed potentially the use of the leaf litter fragmentability as predictor of decomposition. The benefit of this method has to be investigated more by measuring the values before and after decomposition. Furthermore, this study showed that the leaf toughness (specific leaf area (SLA) and leaf dry matter content (LDMC)) explained most of the variance of the measured decomposition. The carbon to phosphorus ratio (C:P) and the amount of tannin in the leaf before decomposition showed significant effect on decomposition. Overall, the structural traits, like leaf toughness and fragmentability were the stronger predictors of decomposition in this subtropical Common Garden experiment.

## References

- Aerts, R.** (1997) Climate, leaf litter chemistry and litter decomposition in terrestrial ecosystems: a triangular relationship. In *Oikos*, 79, pp. 439–449
- Alvarez-Sánchez, J.** and Becerra Enríquez, R. (1996): Leaf decomposition in a Mexican tropical rain forest. In *Biotropica*, 28, pp. 657–667
- Bakker, Maartje Anne, Carreño-Rocabado, Geovana, Poorter, Lourens** (2011): Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. In *Functional Ecology* 25 (3), pp. 473–483
- Barantal, Sandra, Schimann, Heidy, Fromin, Nathalie and Hättenschwiler, Stephan** (2014): C, N and P fertilization in an Amazonian rainforest supports stoichiometric dissimilarity as a driver of litter diversity effects on decomposition. In *Proceedings of the Royal Society B*.
- Barbe, Lou, Jung, Vincent, Prinzing, Andreas, Bittebiere, Anne-Kristel, Butenschoen, Olaf, Mony, Cendrine** (2017): Functionally dissimilar neighbors accelerate litter decomposition in two grass species. In *New Phytologist* 214 (3), pp. 1092–1102
- Bastian, M., Pearson, R. G., Boyero, L.** (2008): Effects of diversity loss on ecosystem function across trophic levels and ecosystems: A test in a detritus-based tropical food web. In *Australian Ecology*, 33(3), pp. 301–306
- Bastias, B. A., Anderson, I. C., Xuc, Z., Cairney, J. W. G.** (2007): RNA- and DNA-based profiling of soil fungal communities in a native Australian eucalypt forest and adjacent *Pinus elliotti* plantation. In *Soil Biology and Biochemistry*, 39, pp. 3108–3114
- Benoit, Robert E. and Starkey, Robert L.** (1968): Enzyme Inactivation as a factor in the Inhibition of Decomposition of organic matter by tannins. In *Soil Science*, Volume 105, Issue 4, pp. 203-208
- Blagodatskaya, E., Kuzyakov, Y.** (2008): Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. In *Biol Fertil Soils* 45 (2), pp. 115–131
- Bonanomi, G., Capodilupo, M., Incerti, G., Mazzoleni, S., Scala, F.** (2015): Litter quality and temperature modulate microbial diversity effects on decomposition in model experiments. In *Community Ecology* 16 (2), pp. 167–177
- Bruehlheide, H., Nadrowski, K., Assmann, T. et al.** (2014): Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. In *Methods of Ecology and Evolution*, 5, pp. 74–89

- Cadotte et al.** (2009): Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. In *PLoS ONE*, 4
- Cardinale**, Bradley J., Matulich, Kristin L., Hooper, David U., Byrnes, Jarrett E., Duffy, Emmett, Gamfeldt, Lars et al. (2011): The functional role of producer diversity in ecosystems. In *American Journal of Botany* 98 (3), pp. 572–592
- Chen**, Ruirui, Senbayram, Mehmet, Blagodatsky, Sergey, Myachina, Olga, Dittert, Klaus, Lin, Xiangui et al. (2014): Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories. In *Global change biology* 20 (7), pp. 2356–2367
- Choong**, M. F., Lucas, P.W., Ong, J. S. Y., Pereira, B., Tan, H. T. W. and I. M. Turner (1992): Leaf fracture toughness and sclerophylly: their correlation and ecological implications. In *New Phytologist* 121, pp. 597-610
- Croce**, R and **van Amerongen**, H. (2014): Natural strategies for photosynthetic light harvesting. In *Nature Chemical Biology*, 10, pp. 492-501
- Cusack**, Daniela F., Ashdown, Daniel, Dietterich, Lee H., Neupane, Avishesh, Ciochina, Mark, Turner, Benjamin L. (2019): Seasonal changes in soil respiration linked to soil moisture and phosphorus availability along a tropical rainfall gradient. In *Biogeochemistry* 145 (3), pp. 235–254
- Dangles**, Oliver and Malmqvist, Björn (2004): Species richness-decomposition relationships depend on species dominance. In *Ecology Letters*, Volume 7, Issue 5
- Epps**, K. Y., Comerford, N. B., Reeves, J.B., Cropper, W. P., Araujo, Q. R. (2007): Chemical diversity – highlighting a species richness and ecosystem function disconnect. In *Oikos*, 116, pp. 1831–1840
- Fanin**, N., Fromin, N. and Bertrand, I. (2016): Functional breadth and home-field advantage generate functional differences among soil microbial decomposers. In *Ecology*, 97, 4, pp. 1023–1037
- Fanin**, Nicolas, Bezaud, Sophie, Sarneel, Judith M., Cecchini, Sébastien, Nicolas, Manuel, Augusto, Laurent (2019): Relative Importance of Climate, Soil and Plant Functional Traits During the Early Decomposition Stage of Standardized Litter. In *Ecosystems* 88, p. 408
- Tracy B. **Gartner** and Zoe G. **Cardon** (2004): Decomposition dynamics in mixed-species leaf litter. In *OIKOS* 104, pp. 230–246

- Finerty**, G. E., de Bello, F., Bílá, K., Berg, M. P., Dias, A. T. C., Pezzatti, G. B. and Moretti, M. (2016): Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition. In *Journal of Ecology*, Volume 104, Issue 5
- Gotsch**, Sybil G., Powers, Jennifer S. and Lerdau, Manuel T. (2010): Leaf traits and water relations of 12 evergreen species in Costa Rican wet and dry forests: patterns of intra-specific variation across forests and seasons. In *Plant Ecology* 211, pp. 133-146
- Grime**, J.P., Cornelissen, J.H.C., Thompson, K. and Hodgson, J.G. (1996): Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. In *Oikos*, 77, pp. 489–494
- Guenet**, B., Moyano, F. E., Peylin, P., Ciais, P., Janssens, I. A. (2015): Towards a representation of priming on soil carbon decomposition in the global land biosphere model ORCHIDEE (version 1.9.5.2). In *Geoscientific Model Development Discussions* 8 (10), pp. 9193–9227
- Güsewell**, S., Gessner, M. O. (2009): N:P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. In *Functional Ecology*, 23, pp. 211– 219
- Handa**, I. Tanya, Aerts, Rien, Berendse, Frank, Berg, Matty P., Bruder, Andreas, Butenschoen, Olaf *et al.* (2014): Consequences of biodiversity loss for litter decomposition across biomes. In *Nature* 509 (7499), pp. 218–221
- Hättenschwiler**, Stephan, Tiunov, Alexei V., Scheu, Stefan (2005): Biodiversity and Litter Decomposition in Terrestrial Ecosystems. In *Annual Review of Ecology, Evolution and Systematics* 36 (1), pp. 191–218
- Hector**, A., Beale, A. J., Minns, A. *et al.* 2000. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos* 90: 357–371
- Hector**, A. *et al.* (2009): The analysis of biodiversity experiments: from pattern toward mechanism. In *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*. In *Oxford University Press*, pp. 105–120
- Heemsbergen**, D. A., Berg, M. P., Loreau, M., van Haj, J. R., Faber, J. H., Verhoef, H. A. (2004): Biodiversity effects on soil processes explained by interspecific functional dissimilarity. In *Science*, 306, pp. 1019–1020
- J.C. **Sharma** and Yogender Sharma (2004): Nutrient Cycling in Forestecosystems - A Review. In *Agriculture Reviews* 25 (3), pp. 157–172

- Jabiol**, Jérémy, Lecerf, Antoine, Lamothe, Sylvain, Gessner, Mark O., Chauvet, Eric (2019): Litter Quality Modulates Effects of Dissolved Nitrogen on Leaf Decomposition by Stream Microbial Communities. In *Microbial ecology* 77 (4), pp. 959–966
- Joly**, François-Xavier, Milcu, Alexandru, Scherer-Lorenzen, Michael, Jean, Loreline-Katia, Bussotti, Filippo, Dawud, Seid Muhie *et al.* (2017): Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. In *New Phytologist* 214 (3), pp. 1281–1293
- Judith A. **Schofield**, Ann. E. Hagerman and Andrew Harold (1998): Loss of Tannins and Other Phenolics from Willow Leaf Litter. In *Journal of Chemical Ecology* 24, No. 8
- Kainulainen**, P. and **Holopainen**, J. K. (2002): Concentrations of secondary compounds in Scots pine needles at different stages of decomposition. In *Soil Biology and Biochemistry*, Volume 34, Issue 1, pp. 37-42
- Kaneko**, N. and Salamanca, E. F. 1999. Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecol. Res.* 14: 131–138
- Lecerf**, A., Marie, G., Kominoski, J. S., Leroy, C. J., Bernadet, C., Swan, C. M. (2011): Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. In *Ecology*, 92, pp. 160–169
- López-Rojo**, Naiara, Martínez, Aingeru, Pérez, Javier, Basaguren, Ana, Pozo, Jesús, Boyero, Luz (2018): Leaf traits drive plant diversity effects on litter decomposition and FPOM production in streams. In *PloS one* 13 (5)
- Makkonen**, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M., Aerts, R. (2012): Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. In *Ecology Letter*, 15, pp. 1033–1041
- Makkonen**, M., Berg, M. P., van Logtestijn, R. S. P., van Hal, J. R., Aerts, R. (2013): Do physical plant litter traits explain non-additivity in litter mixtures? A test of the improved microenvironmental conditions theory. In *Oikos*, 122, 987–997
- McArthur**, J. V., Aho, J. M., Rader, R. B. *et al.* 1994. Interspecific leaf interactions during decomposition in aquatic and floodplain ecosystems. *J. N. Am. Benthol. Soc.* 13: 57–67
- Novoplansky**, A. (2009): Picking battles wisely: plant behaviour under competition. In *Plant, Cell & Environment*, 32, pp. 726–741
- Ostrofsky**, M. L. (1997): Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. In *J N Am Benthol Soc*, 16, pp. 750–759

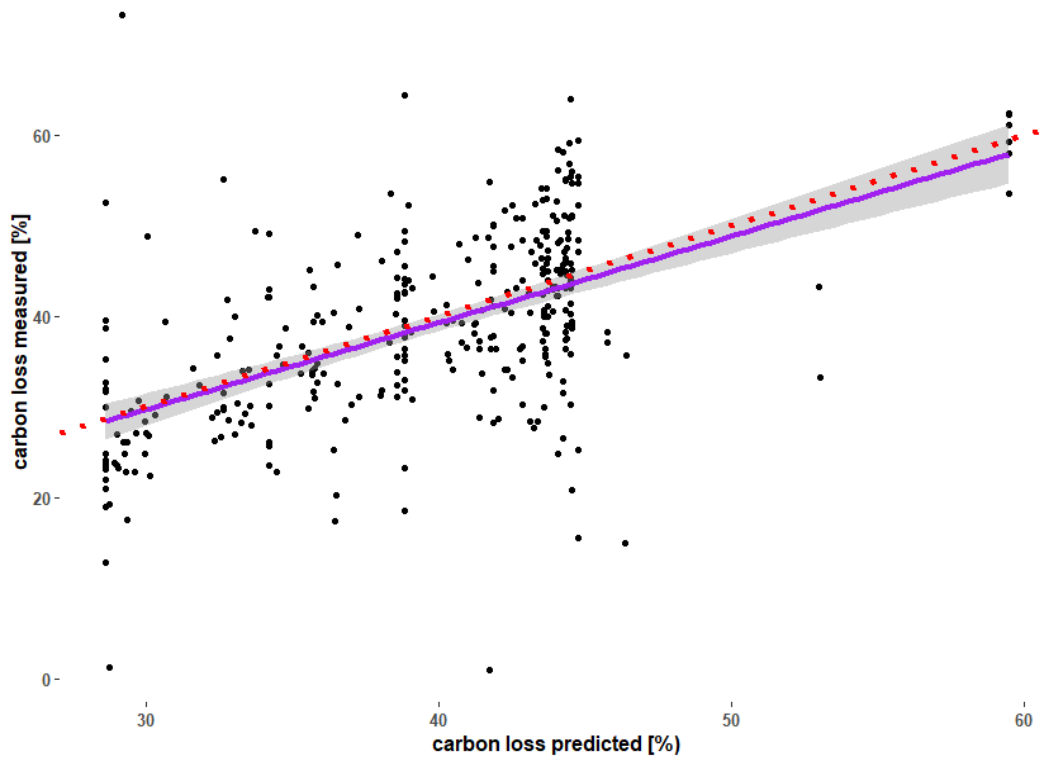
- Pei, Z.,** Leppert, K. N., Eichenberg, D., Bruelheide, H., Niklaus, P. A., Buscot, F., Gutknecht, J. L. M. (2017): Leaf litter diversity alters microbial activity, microbial abundances, and nutrient cycling in a subtropical forest ecosystem. In *Biogeochemistry*, 134, pp. 163-181
- Pérez-Harguindeguy, N., Díaz, S.,** Cornelissen, J.H.C., Vendramini, F., Cabido, M. and Castellanos, A. (2000): Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. In *Plant and Soil*, 218, pp. 21–30
- Pérez-Harguindeguy, N., Diaz, S.,** Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurrich, D. E. *et al.* (2013): New handbook for standardised measurement of plant functional traits worldwide. In *Australian Journal of Botany*, 61, pp. 167–234
- Porre, R. J.,** van der Werf, W., De Dey, G. B., Stomph, T. J. and Hoffland, E. (2020): Is litter decomposition enhanced in species mixtures? A meta-analysis. In *Soil Biology and Biochemistry*, 145
- Quested, H.,** Eriksson, O., Fortunel, C. and Garnier, E. (2007): Plant traits relate to whole-community litter quality and decomposition following land use change, *Functional Ecology*, Volume 21, Issue 6, pp. 1016-1026
- Rees, R.,** Chang, S., Wang, C., Matzner, E. (2006): Release of nutrients dissolved organic carbon during decomposition of *Chamaecyparis obtusa* var. *formosana* leaves in a mountain forest in Taiwan. In *Journal of Plant Nutrition and Soil Science*.
- Ristok, Christian,** Leppert, Katrin N., Franke, Katrin, Scherer-Lorenzen, Michael, Niklaus, Pascal A., Wessjohann, Ludger A., Bruelheide, Helge (2017): Leaf litter diversity positively affects the decomposition of plant polyphenols. In *Plant and Soil* 419 (1-2), pp. 305–317
- David **Sadava,** David Hillis, H. Craig Heller, Sally Hacker (2019): Purves, *Biologie* 10. Auflage. Springer Spektrum, herausgegeben von Jürgen Markl, übersetzt von Andreas Held
- Salamanca, E. F., Kaneko, N.** and Katagiri, S. 1998. Effects of leaf litter mixtures on the decomposition of *Quercus serrata* and *Pinus densiflora* using field and laboratory microcosm methods. *Ecol. Engineering* 10: 53–73
- Santiago, L. S.** (2007): Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. In *Ecology*, 88, pp. 1126–1131



- Santiago**, L.S. (2010): Can growth form classification predict litter nutrient dynamics and decomposition rates in lowland wet forest? In *Biotropica*, 42, pp. 72–79
- Scherer-Lorenzen**, M. *et al.* (2007): Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. In *Oikos*, 116, pp. 2108–2124
- Schleuter**, D., Daufresne, M., Massol, F. and Argillier, C. (2010): A user's guide to functional diversity indices. In *Ecological Monographs*, 80, pp. 469–484
- Sills**, Erin O., Moore, Susan E., Cabbage, Frederick W., McCarter, Kelley D., Holmes, Thomas P., Mercer, D. Evan (2017): Trees At Work: Economic Accounting for Forest Ecosystem Services in the U.S. South. Chapter 4: Forest Ecosystem Services: Carbon and Air Quality (General Technical Report (GTR))
- Skarke**, Felix and Kluge, Corinna (last updated 2019): Modellselektion (AIC, BIC, Pseudo R<sup>2</sup>...). [https://wikis.fu-berlin.de/pages/viewpage.action?pageId=736857812#Modellselektion\(AIC, BIC, PseudoR<sup>2</sup>...\)-AIC\(Akaike-Information-Criterion\)](https://wikis.fu-berlin.de/pages/viewpage.action?pageId=736857812#Modellselektion(AIC,BIC,PseudoR^2...)-AIC(Akaike-Information-Criterion)), last access 08/06/2020
- Speed**, M. P., Fenton, A., Jones, M. G. *et al.* (2015): Coevolution can explain defensive secondary metabolite diversity in plants. In *New Phytologist*
- Swift** MJ, Heal OW, Anderson JM (1979): Decomposition in terrestrial ecosystems. University of California Press, Berkeley
- Tardif**, Antoine, Shipley, Bill, Bloor, Juliette M. G. and Soussana, Jean-Francois (2014): Can the biomass-ratio hypothesis predict mixed-species litter decomposition along a climatic gradient? In *Annals of Botany*, Volume 113, Issue 5, pp. 843-850
- Toledo** Castanho, C. de and **Adalardo** de Oliveira, A. (2008): Relative effect of litter quality, forest type and their interaction on leaf decomposition in southeast Brazilian forests. In *Journal of Tropical Ecology*, 24, pp. 149–156
- Trogisch**, Stefan, He, Jin-Sheng, Hector, Andy, Scherer-Lorenzen, Michael (2015): Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. In *Plant and Soil*, 400, pp. 337-350
- Violle**, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E. (2007): Let the concept of trait be functional! In *Oikos*, 116, pp. 882–892
- Violle**, C., Garnier, E., Lecoœur, J., Roumet, C., Pothier, C., Blanchard, A., Navas, M. L. (2009): Competition, traits and resource depletion in plant communities. In *Oecologia*, 160, pp. 747–755

- Vos, V. C., van Ruijven, J., Berg, M. P., Peeters, E. T. and Berendse, F. (2013):** Leaf litter quality drives litter mixing effects through complementary resource use among detritivores. In *Oecologia*, 173, pp. 269– 280
- Wagai, Rota, Kishimoto-Mo, A.W., Yonemura, S., Shirato, Y., Hiradate, S., Yagasaki, Y. (2012):** Linking temperature sensitivity of soil organic matter decomposition to its molecular structure, accessibility, and microbial physiology. In *Global Change Biology*, Volume 19, Issue 4
- Wardle, D. A., Bardgett, R. D., Klironomos, R. N., Setälä, H., van der Putten, W. H. and Wall, D. (2004):** Ecological linkages between aboveground and belowground biota. In *Science*, 304, pp. 1629–1633
- Xiaoni **Xu** and Eiji **Hirata** (2005): Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: N and P dynamics. In *Plant and Soil* 237, pp. 279-289.
- Yang, Xiaodong, Yang, Zhao, Warren, Matthew W., Chen, Jin (2012):** Mechanical fragmentation enhances the contribution of Collembola to leaf litter decomposition. In *European Journal of Soil Biology* 53, pp. 23–31
- Yang, X. et al. (2013):** Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). In *European Journal of Forest Research*, 132, pp. 593–606





**Figure 11S:** Carbon loss measured against the predicted carbon loss from the monocultures. The violet line shows the linear model fit of the two values. The red dotted line shows predicted equally to the measured decomposition.

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## **Statutory Declaration**

Eidesstattliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit mit dem Titel „Litter quality and tree species richness effects on litter decomposition in subtropical forest“, selbstständig angefertigt habe und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet wurden. Diese Arbeit hat weder in gleicher noch einer ähnlichen Form einer Prüfungskommission vorgelegen.

Ort, Datum

Unterschrift