

# Regeneration & Relations

The effects of plant diversity on plant-based ecosystem  
services for regenerating Neotropical rainforest  
*Research Project for the MSc. Environmental Biology*



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## Abstract

Tropical forests are among the most diverse ecosystems of our planet and provide important ecosystem services (ES) to humanity: benefits enabling life on earth and making it worth living. A third of the tropical forests in the amazon consist of secondary forests, including clear-cut regenerating forests, playing a crucial role in restoring ES and biodiversity. Synergies between diversity and tropical ES —e.g. aboveground carbon (AGC) storage and Non-Timber Forest Product (NTFP) provisioning— would enable simultaneous restoration; targeting ES restoration would automatically entail restoration of diversity. However, it is unclear if diversity and tropical forest ES are linked for regenerating forests. While primary tropical forests exhibit a significant positive relationship between tree species richness and AGC, such a relationship has not yet been robustly established for regenerating forests. In this report, the relationships between species richness and ES, i.e. carbon storage and NTFP provisioning, were studied in a 25-year-old regenerating forest on a former coffee and cacao plantations in Suriname. After 25 years of regeneration, species richness had recovered to primary forest reference levels, although AGC was still markedly lower. The relationship between species richness and carbon storage was found to be insignificant, as well as between species richness and NTFP provisioning. However, evidence of complementarity and selection effects was found; species-rich vegetation contained more individuals with higher wood density (WD). However, significant impacts of complementarity and selection effects on AGC were hindered by the relatively small size (average DBH < 11 cm) of later successional species with a high wood density (WD > 0.6 g cm<sup>-3</sup>). We suggest further investigation into species richness-carbon relationships in regenerating forests, to decipher when complementarity, selection, and insurance effects will start to significantly contribute to an increase in AGC. Policymakers are urged to consider the regeneration of tropical forests to be a long-term project, without immediate apparent positive relationships between plant diversity, carbon storage, and NTFP provisioning.

# 1. Introduction

Tropical forests are among the most diverse ecosystems of our planet, providing more than half of the world's vertebrate and tree species while covering only 7% of the earth's surface (Gatti et al., 2022; Pillay et al., 2022; Primack & Morrison, 2013). This diversity underpins important ecosystem services (ES) tropical forests provide humanity with (Díaz et al., 2005). These services can be described as the benefits provided by an ecosystem to humans, enabling life on earth and making it worth living (Díaz et al., 2005). These benefits can be visible both on a local and a global scale. On a local scale, the provisioning of Non-Timber Forest Products (NTFPs) is important to people living in or close to the forest; food and medicines can be harvested for sustenance and income, facilitating livelihoods and increasing support for forest conservation and forest regeneration (Ros-Tonen & Wiersum, 2005). Locally and globally, carbon storage through the conservation of tropical forests reduces carbon emissions (Houghton & Nassikas, 2017).

Biodiversity and the provisioning of ES by tropical forests are under constant threat; tropical rainforests experience immense anthropogenic pressures, primarily due to deforestation. During the past century, 20% of the forest in the Amazon basin has been lost (Urquhart, 2020). The loss of rainforests often leads to a decline in biodiversity within an area (e.g. Enuoh & Ogogo, 2018; Hayes et al., 2023; Turner, 1996), accompanied by a loss in ES (Intergovernmental Panel On Climate Change, 2023). For instance, clear-cutting of primary forests reduces biodiversity and carbon storage, with the effect size dependent on the type of land use (Bonini et al., 2018). A study in the South-Eastern Amazon basin found clearance of primary forest for soy bean plantations to detail almost a complete loss of aboveground carbon (AGC), while rubber tree plantations resulted in a loss of ~20% of AGC (Bonini et al., 2018).

Former clear-cut areas, although low in diversity and the provisioning of ES, do provide opportunities for the (natural) regeneration of tropical forests, and the occurrence of diversity-ES co-benefits (e.g. Coelho et al., 2022; Matos et al., 2020; Rodrigues et al., 2023). Exemplarily, a 90-year-old regenerating forest on a former coffee plantation in Brazil showed co-benefits of both carbon storage and tree diversity (Rodrigues et al., 2023). The potential contribution of regenerating forests to ES is vast, as 20% of deforested land in Amazonia contains regrowing forests and 33% of all neotropical forests are naturally regenerating forests on former agricultural lands (Chazdon et al., 2009, 2016). These regenerating forests can contribute to restoration of ES and diversity; they are found to act as great biodiversity reservoirs (Chazdon et al., 2009), store a considerable amount of AGC stocks (Chazdon et al., 2016), and prove important areas for NTFP collection (Peters et al., 2023; Ticktin & Nantel, 2004), making them important focal points for safeguarding the earth's biodiversity and ES, next to the conservation of primary forests.

When aiding the regeneration of tropical forests or their conservation, policymakers and ecologists often assume diversity-ES co-benefits: positive relationships between species richness and ES (Díaz et al., 2005). If these assumed positive relationships do occur, win-win situations are possible where targeted regeneration measures can benefit both diversity and ES or where biodiversity and ES are simultaneously conserved, as detailed for instance in REDD+ (reducing emissions from deforestation and forest degradation) objectives (Phelps et al., 2012). The theoretical framework for these positive relationships between plant diversity and plant biomass-derived ES, such as carbon storage and NTFP provisioning, is

based on three main hypotheses: the niche complementarity theory (Tilman, 1999), the insurance hypothesis (Yachi & Loreau, 1999), and the selection effect (Loreau & Hector, 2001). The niche complementarity theory states that a higher species diversity leads to a greater functional diversity and therefore enhanced efficiency of resource utilization in an area, increasing the number of niches occupied and therefore the contained biomass (Tilman, 1999). The insurance hypothesis predicts a system to be more resilient to environmental stressors for a higher diversity, leading to long-term stability of carbon stock (Yachi & Loreau, 1999). The selection effect postulates that for greater diversity, the chance of including a species with the desired traits, e.g. with a high wood density, is greater (Loreau & Hector, 2001). Contrarily, a fourth hypothesis predicts a lack of positive diversity-ES relationships: the mass ratio theory by Grime (1998). This theory details that the identity of the most dominant species of a system predicts its functioning. Therefore, following this theory, aboveground biomass (AGB) is expected to relate to i.e. the community-weighted mean wood density (CWM WD) of the vegetation since the biomass and CWM WD of the vegetation will both be determined by the most dominant species. This theory is assumed applicable to forests with a few highly dominant species (Grime, 1998).

Whether the three positive diversity-biomass hypotheses, and therefore positive diversity-ES relationships, uphold for tropical forests has been the subject of an array of studies (e.g. Poorter et al., 2015; Steur et al., 2020; van der Sande et al., 2017). While positive relationships between diversity and biomass have long been substantiated through experimental studies and observational studies in grasslands (Cardinale et al., 2013; Isbell et al., 2015; Tilman et al., 2001; Yan et al., 2021), this has been more difficult to show for tropical forests, where factors such as plot scale and environmental heterogeneity were found to influence relationships, resulting in insignificant or even negative relationships (Steur et al., 2020, 2022). Nonetheless, when taking plot scale and environmental heterogeneity into account, both a meta-analysis of neotropical primary forests and an empirical study across the Amazon basin found a positive relationship between species richness and carbon storage for primary forests (Steur et al., 2020, 2022). In contrast, the relationship between species richness and NTFP provisioning was found to be insignificant (Steur et al., 2020, 2022). Notably, the studies by Steur et al. (2020, 2021, 2022) are among the few studies on diversity-NTFP relationships, creating a considerable knowledge gap on the relationship between species richness and this ES.

Additionally, studies on tree diversity-carbon relationships for tropical forests have almost exclusively studied primary forests, and it remains unclear if diversity-biomass hypotheses and resulting co-benefits are present in regenerating forests as well (van der Sande et al., 2017). Poorter et al. (2021) compared 77 regenerating tropical forests of different ages across the Neotropics and Africa to reference primary forest plots and found regenerating forests to differ from primary forests in species richness, AGB, and functional characteristics (e.g. community weighted mean wood density (CWM WD)) - key factors in the diversity-AGC and diversity-NTFP relationships (Poorter, Rozendaal, et al., 2021). Regenerating forests started with a lower CWM WD compared to primary forests; CWM WD was found to take an average of 30 years to reach primary rainforest reference values (Poorter, Rozendaal, et al., 2021). This increase in CWM WD through succession is typical for wet neotropical forests, where later successional species are found to have a higher WD as a result of shade tolerance (Rueger et al., 2023). Similarly, species richness, maximum tree

size, and AGB were found to be lower for regenerating forests, taking an average of, respectively, ~35, ~55, and 120 years to reach 90% of reference levels (Poorter, Rozendaal, et al., 2021).

Differences in species richness, CWM WD and AGB could impact the complementarity theory, insurance hypothesis, and selection effect, and weaken positive diversity-ES relationships. For instance, with lower wood density values, the selection effect on AGB will be smaller than in the presence of a species with a higher wood density. Similarly, complementarity and insurance effects can be weaker for forests with lower maximum species richness and/or lower maximum AGB, increasing the difficulty of detecting positive diversity-ES relationships as compared to primary forests, given that the variance of regenerating forest plots is equal to the variance in primary forest plots. Additionally, a lack of later successional species can weaken insurance effects, decreasing recovery after a disturbance and therefore the resilience of the vegetation (Schmitt et al., 2020). Relationships between species richness and ES can therefore be more difficult to detect for regenerating forests than for primary forests; similar positive diversity-ES relationships cannot be a-priori expected. In line with assumed weaker diversity-carbon relationships for regenerating forests, a meta-analysis by Van der Sande et al. (2017) indicated a lower percentage of significant relationships for degraded tropical forests as compared to primary tropical forests. In their research, relationships between grouped taxonomical diversity indicators and carbon stocks were examined for tropical forests and plantations. However, due to a lack of studies on degraded forests, hypothesis testing could not be performed (van der Sande et al., 2017).

It is thus essential to study the relationships between plant diversity and ES, i.e. carbon storage and NTFP provisioning, in regenerating forests to fill current knowledge gaps. Having entered the United Nations decade of ecosystem restoration, increasing emphasis has been placed on the regeneration of ecosystems and their contribution to diversity and ES (Fischer et al., 2021). It is therefore urgent to have clear visions for the purpose of restoration, expected outcomes regarding ES and biodiversity, and strategies for achieving this. Effective and efficient policies for natural regeneration require understanding the ES involved and their potential synergies or trade-offs (Naime et al., 2020). Considering regenerating tropical forests, policymakers need to know whether an increase in biodiversity is related to an increase in carbon storage and NTFP provisioning. When these relationships are present, management and restoration strategies can focus on restoring both biodiversity and ES simultaneously by applying one strategy that fits all. In the absence of positive diversity-ES relationships, trade-offs are presented and policies can be focused on either an increase in diversity or ES.

This study sets out to research the **relationships between tree species richness and ES, i.e. carbon storage and NTFP provisioning, in regenerating tropical forests**. This will be studied as a case study in Peperpot Nature Park (PNP), a Surinamese park consisting of regenerating tropical vegetation. Until 1997, coffee and cacao were cultivated on various former plantations present in the PNP area (Schuttler et al., 2021). See the methods section for a more detailed description. To study the diversity-ES relationships, the heterogeneity of the study area will be taken into account by differentiating between varying vegetation types. Steur et al. (2022) found the relationships between species richness and carbon storage across Amazonia to be significant only after taking the effect of environmental heterogeneity into account. On a smaller scale, these differences could also influence plant diversity-ES relationships when different

vegetation types are present. This could be due to a difference in factors influencing AGC (i.e. CWM WD, stem density, CWM DBH) and their relationship with species richness per type. Furthermore, to place the relationships for the regenerating forest of PNP into context, the history of the vegetation (i.e. former plantation composition), and surrounding vegetation will be taken into account. Thus, this study consists of two parts: 1) research on former and surrounding vegetation types of PNP via a literature study and interviews; 2) research on the vegetation types occurring in PNP anno 2024. Research to the current vegetation of PNP involves a) describing the main vegetation types of PNP; b) studying the relationships between species richness and ES (i.e. carbon storage and the provisioning of NTFPs); c) comparing the vegetational composition and characteristics (e.g. AGC, CWM WD) to primary swamp forest reference values, in order to dive into mechanisms behind possible differences or similarities between diversity-ES relationships found in PNP and positive diversity-carbon relationships and neutral diversity-NTFP relationships found for primary rainforest.

## 2. Methods

### 2.1 Study area and Fieldwork

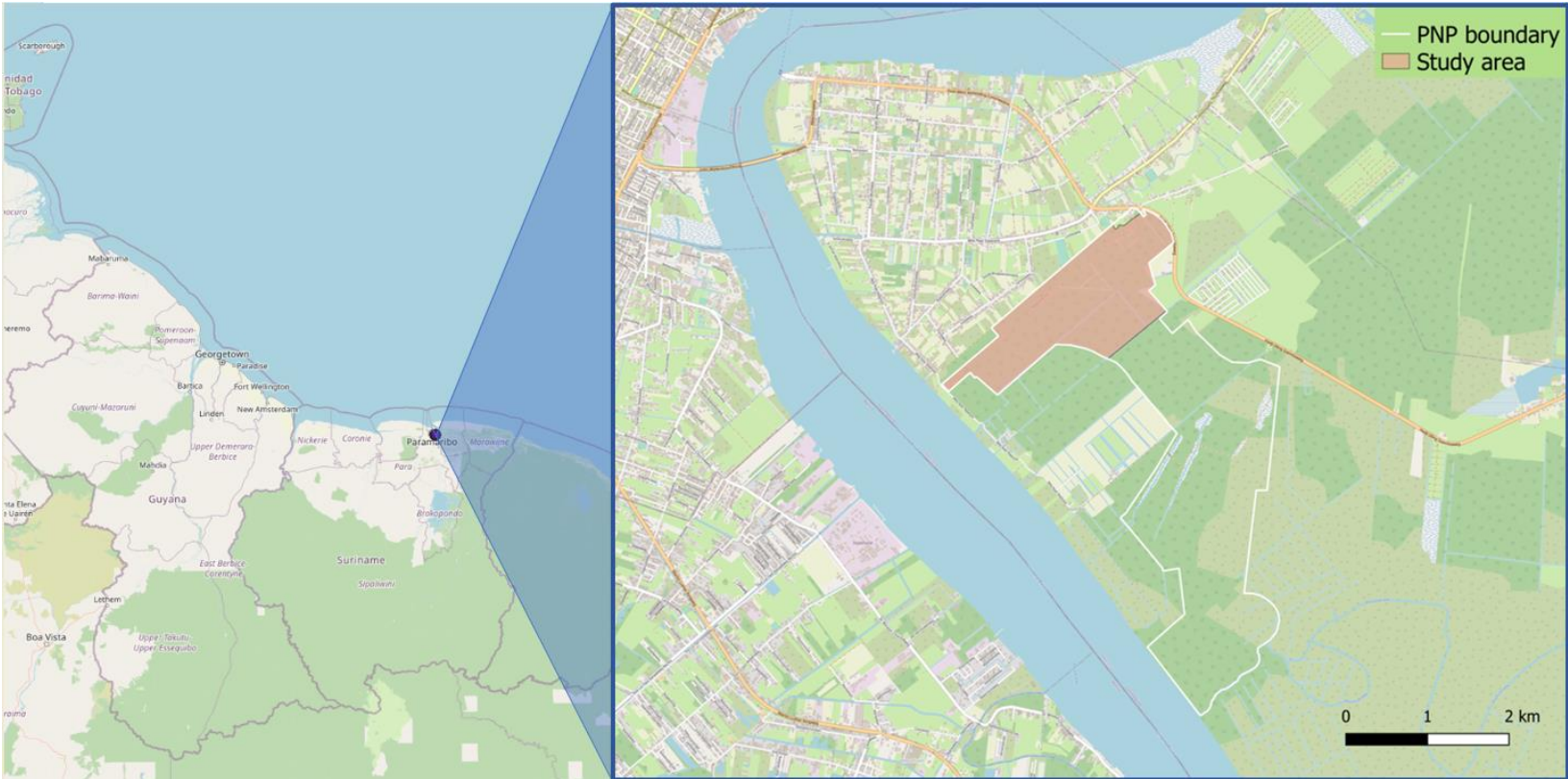
The practical work, including preparation, for this study consisted of four parts: 1) conducting interviews to establish former plantation layout, i.e. which species were planted, in which numbers and their mean diameter at breast height (DBH); 2) Constructing a field key based on a literature study to the surrounding vegetation of PNP with regard to expected vegetation types at PNP anno 2023; 3) Walking transects to establish a map of the main vegetation types of PNP anno 2023; 4) carrying out vegetation surveys in the form of temporary plots. Fieldwork was conducted from November 2023 up until January 2024.

#### 2.1.a Survey area

Spanning 800 hectares, Peperpot Nature Park (PNP) is situated in the Commewijne District of Suriname (5°80'N, 55°12'W, Fig. 2.1). Paramaribo, the capital of Suriname, is separated from Peperpot by the Suriname River. The elevation at PNP is less than 50 m above sea level. The climate is classified Af under the Köppen climate classification (Tropical Rainforest Climate), with an average rainfall of 2225 mm per year and an average temperature of 27.2 °C (Magioli et al., 2023). Peperpot Nature Park comprises five former cacao and coffee plantations. The land has transitioned away from agricultural practices since 1998, leading to the establishment of PNP in 2009 (Moen, personal communication, December 2023; Ramcharan, 2011: local magazine). The completion of the Jules Wijdenbosch bridge across the Suriname river in 2000 facilitated commercial and residential development in the area surrounding Peperpot, particularly within the Commewijne District. The park finds itself surrounded on three sides by areas of intensive land use, with ongoing construction projects. The fourth, southern region contains natural vegetation that remains largely undisturbed (Schuttler et al., 2021). In this section, primary rainforest is connected to PNP through other former plantations (Teunissen, 1978). Peperpot Nature Park attracts tourists throughout the year who utilize a network of trails for recreational activities, e.g. hiking and biking, in a limited section of the Park. Although poaching of wild life is known to occur, seed dispersers such as agoutis, red brocket deer, and tapirs occur in Peperpot (Schuttler et al., 2021). Additionally, locals are known to harvest podosiri, fruits from *Euterpe oleracea* (Moen, personal communication, December 2023). The survey area of this study included the North-Western part of the plantation, including the area open to the public and the area between canal 1 and 2 (Fig. 2.1, Fig. S.2.2).

#### 2.1.b Interviews

To infer the former vegetation structure and carbon storage of PNP, a former plantation worker was interviewed from November 2023 to January 2024. The interviewee had worked at the former plantations in the study area for at least the final 30 years of their operation. Currently (in 2024), the interviewee lives next to PNP and is managing and overseeing park maintenance. Former plantation bed sizes were inferred from the interview and confirmed during the transects by calculating the mean width between small irrigation canals still visible. The average distances between the coffee, cacao, and *Erythrina fusca* individuals on the beds were inferred from the interview, as were estimations of mean DBH. With these numbers, a crude estimation of former carbon stock was performed, see the supplementary methods S.3 for the calculations.



**Figure 2.1. Location of PNP and study area.** The boundary of Peperpot Nature Park (PNP) anno 2024 is indicated with white demarcation. The study area of this research lies within PNP and is indicated in pink.

### 2.1.c Field key

A literature study was conducted on the vegetation in Suriname, mainly PNP and its surroundings, to identify key species for PNP: plant species that can be used to recognize the vegetation types in the field, such as those that occur in high abundance in that vegetation type. To enable a fast workflow, a field key was constructed to recognize the key species during fieldwork. This involved creating an overview of the main vegetation types that were expected to be found in the study area, based on knowledge about the surrounding vegetation types and a species checklist of PNP constructed by Tostain & Leotard (2012). The vegetation types were inferred from the maps of Lindeman & Moolenaar (2011), Teunissen (1978), and the Sarvision map (Quiñones & Hoekman, 2011) (S1, Fig. S.1.1-1.3). The key species of these vegetation types were subsequently based on an overview of tropical vegetation associations (Teunissen, 1980) and supplemented by the species in the vegetation descriptions of Lindeman and Moolenaar (1959). The checklist of Tostain & Leotard (2012) was used to select key species present in PNP. See Supplementary materials 1 for a description of the expected vegetation types, Table S.1 for an overview of these vegetation types, and Table S.2 for an overview of the key species.

### 2.1.d Transects

Across the plantation, 4 transects were walked. The transects ran parallel to the big canals in PNP and ran from the North-Eastern park boundary to the South-Western boundary, see figure S.2.1. During the transects, each 50 m, the most abundant species were noted with a minimum of 5 tree/arborescent palm species. After walking the transects, paths with a right angle to the transects were walked to assess the boundaries of the vegetation types found along the transects. These included walking trails and 'podosiri' paths (Fig. 3.1), paths used by illegal podosiri harvesters. An area was assigned to a main vegetation type according to the abundant presence of key species. During transects, transition zones between vegetation types were followed. Transition zones of the vegetation were marked in the GPS, choosing the middle point



as demarcation point. Afterward, a map of the main vegetation types of PNP was constructed in QGIS using saved GPS coordinates and routes.

### 2.1.e Plots

For each vegetation type, 8 plots of 0.04 ha were established (Fig. S.2.2). Plots were placed following random stratification based on the main vegetation types. Within the plots, of each tree and arborescent palm with a diameter at breast height (DBH) of  $\geq 5$  cm, the individual was identified and the DBH was measured following the Rainfor manual for plot establishment (Phillips et al., 2021). A cut-off of 5 cm was chosen instead of 10 cm since trees  $< 10$  cm DBH represent a large part of taxonomic diversity and can contribute to 5 % of AGC (Ifo et al., 2019; Memiaghe et al., 2016). Additionally, this aligns with the DBH  $\geq 5$  cm cutoff adhered to in the Teunissen dataset of primary forest plots, used as primary forest reference values (see 2.2.d). If an individual could not be identified to species level in the field, pictures were taken and leaf samples collected to enable identification afterward, either at the National Herbarium of Suriname, at Naturalis Biodiversity Center, or by tropical botanists. All individuals were identified at species level. Taxonomic names are according to the World Flora Online (WFO, 2024).

## 2.2 Data analysis

The data analysis concerned 4 components: 1) the calculation and comparison of above-ground carbon (AGC), Non-Timber Forest Product (NTFP) abundance, and species richness for the past and present vegetation of PNP; 2) Comparing AGC, NTFP abundance, species richness, and AGC influencing components between the main vegetation types of PNP anno 2024; 3) Performing regression analyses to assess relationships between species richness and ES, carbon storage and NTFP abundance, and between AGC influencing factors and species richness; 4) Comparing values of species richness, NTFP abundance, AGC and AGC influencing factors to reference values from two primary swamp forest plots sampled by P. Teunissen in 1975. All analyses were conducted in R studio, version 4.0.1 (R Core Team, 2022).

### 2.2.a Calculation of plant diversity and ES

#### Species richness

Species richness was compared between 1970 and 2024, expressed in species per 0.04 ha. For 1970, it was simply the amount of tree species per bed, as this was the same as the number of species per 0.04 ha. Therefore, the standard deviation was zero. For 2024, the mean number of species per vegetation type was estimated and used to calculate a weighted average species richness per 0.04 ha. See S2.1 for the full calculations.

#### NTFP abundance

To determine the NTFP abundance in Peperpot, NTFP species were inferred from the NTFP database composed by Steur et al. (2022). This list consists of currently commercially relevant wild NTFP species in Suriname, combined from multiple Suriname NTFP surveys and their own fieldwork and market surveys carried out during 2017-2018 (Steur, 2022).

### Aboveground carbon

Carbon storage was determined using the moist forest tree diameter allometric equation developed by Chave et al. (2005), calibrated specifically for South American tropical forests and independent of height measurements (Tab. S.1). For palm biomass, the same equation was used, as a comparison by Selaya et al. (2017) indicated that the use of a palm-specific equations does not improve the accuracy of biomass estimates. Wood density was inferred from a database by Ter Steege et al. (in prep.; version 20200401). To convert aboveground biomass to aboveground carbon stock, a conversion factor of 0.474 was applied (IPCC, 2006). See table S.1.

Total AGC was compared between the former plantations present in the study area in 1970 and the current vegetation in 2024. To do so, the total AGC was calculated for the part of PNP comprising the current study area. For 2024, AGC was first calculated per m<sup>2</sup> for each vegetation type and then multiplied by the total number of m<sup>2</sup> of each vegetation type. For the total AGC in 1970, interview data was used to estimate the number of beds containing coffee and cacao in the study area and the number of individuals per bed (Moen, personal communication, December 2023). Average DBH per species was also referred from the interviewee. See the supplementary methods S3 for the calculations. A standard deviation was included for the 2024 estimate, but not for the 1970 estimate as this is a rough estimate based on interview data. Therefore, the comparison was only used to assess if the AGC was roughly in the same ballpark.

### 2.2.b Comparison of the main vegetation types of PNP

For the main vegetation types of PNP anno 2024, AGC, NTFP abundance, species richness, and factors contributing to AGC (i.e. community-weighted mean wood density (CMW WD), CMW DBH, and stem density) were compared. See Table S.2.1 for the formulas of these variables. To compare the variables, either an ANOVA with subsequent Tukey-Kramer post-hoc test was used if the data were normally distributed with equal variance among the groups, or if one or both of these assumptions were not met, a Kruskal-Wallis test with subsequent Dunn's post-hoc test was performed.

Additionally, a principal component analysis (PCA) was used to check the clustering of the vegetation types. Clustering was based on the species identity of the individuals present in the plots (Fig. S.2.4). The matrix was log(y+1) transformed before performing the PCA, as the abundance data was right-skewed. A species richness accumulation curve was plotted per vegetation type and for aggregated plot data to check whether the vegetation (types) were representatively sampled (Fig. S2.5-6). PCA and species accumulation curves were constructed using the Vegan package (Oksanen et al., 2022).

### 2.2.c Regression analyses

Linear regressions were performed to assess whether there are positive, negative, or non-significant relationships between carbon stocks and species richness, and between NTFP abundance and species richness. To study the importance of environmental heterogeneity on the relationships, vegetation types were included in the model as a random effect, with and without interaction. The significance of the interaction was checked, and models without interaction term were run if the interaction was insignificant ( $p < 0.05$ ) unless  $p < 0.1$  and inclusion of the interaction term improved model fit (adjusted  $R^2$ ). Bivariate

models (grouping vegetation types) were run as well to analyze the relationship without taking environmental heterogeneity into account. The amount of variance explained by the inclusion of the variable 'vegetation types' was assessed as well as differences in significance and direction of the slope of the regression curve.

To study mechanisms underlying diversity-AGC relationships, linear regressions between species richness and AGC components (i.e. CWM WD, CWM DBH and mean stem density) were performed. As with the previous analysis, the variable vegetation types was included in models to assess whether these underlying relationships differ between vegetation types or are present for regenerating tropical vegetation in general. Models were tested with and without interaction term. Depending on whether there was a significant interaction between vegetation types and species richness, the model with interaction term or the main effects model was plotted.

Finally, a linear regression between the average DBH of each species and their wood density was performed to assess whether species size decreased for higher wood densities. Since standard errors displayed heteroscedasticity, heteroscedasticity robust standard errors with corresponding t-values were calculated using the sandwich (Zeileis et al., 2020) and lmtest (Zeileis & Hothorn, 2002) packages.

For all regression models, assumptions were checked using QQplots. For the relationship between aboveground carbon (AGC) and species richness, and between AGC and CWM WD, the AGC values were log-transformed since they were right-skewed, inducing outliers and violating assumptions of normality.

#### 2.2.d Comparison with primary forest

To assess the difference in relationships between regenerating and primary forests, and dive into mechanisms behind relationships between woody species richness and carbon storage and NTFP provisioning, the data was compared to two primary forest plots sampled by P. Teunissen in 1975, measuring 0.04 ha. These plots were located in the northern region of Suriname, specifically within the Coastal Plain situated between 4°45' to 6° N. The altitude of the plots was < 100 above sea level, with a tropical forest climate falling in the 'Af' category in the Köppen climate classification, indicating mean temperatures consistently exceeding 18°C and monthly average rainfall consistently exceeding 60 mm. Between 1971-1980, the average annual rainfall in this area ranged from approximately 1500 mm along the coast to about 2500 mm towards the interior. The mean monthly temperature in Suriname fluctuated between 26.2-28.2°C, with an annual temperature amplitude of 2-3°C (SPS et al., 1988). Observations by G. Steur and colleagues from revisiting Teunissen plots in 2018, along with additional floristic fieldwork conducted in Suriname between 2017 and 2019, suggest that the climax vegetation documented in the Teunissen surveys during the 1970s continues to offer an accurate representation of the current climax vegetation in Northern Suriname (Steur et al., 2021), thus enabling a comparison between the regenerating forest of PNP and primary coastal swamp forest. Both plots used for comparison were categorized as coastal swamp forests. Within these plots, all trees and arborescent palms with DBH  $\geq$  5 cm were measured and identified. Mean AGC, NTFP abundance, species richness, CMW WD, CMW DBH, and stem density for PNP were compared to the reference values of the two primary plots of the Teunissen dataset. The comparison was visual, as the sample size was too low for statistical hypothesis testing.

### 3. Results

#### 3.1 Vegetation types, their diversity, and ES

##### 3.1.a Vegetation in 1970

According to a former plantation worker, the layout of the plantations present in 1970 in the current study area consisted of small and wide beds (6 and 7 m wide respectively) separated by small canals of 1 m wide (Fig. S.2.5). The beds were planted with either *Coffea liberica* W. bull or *Theobroma cacao* L. with *Erythrina fusca* Lour. trees in between, providing shade. There was a small area of the plantation dedicated to growing *Coffea arabica* L. (Fig. 3.1.A). A variant of *T. cacao*, locally called ‘Cacao siri’, was grown on a single field. *Coffea spp.* and *T. cacao* were grown in two or three rows per bed, depending on bed width (Fig S.2.5). In the middle row, *E. fusca* was planted. Distance between individuals in a row was 4 or 5 meters, depending on bed width. Taking this lay-out into account, a crude calculation of the aboveground carbon (AGC) shows that in 1970, the total AGC of the 2024 sampled area in PNP was  $\sim 20 \times 10^3$  Mg. Mean woody species richness was 2 species per 0.04 ha, and the mean NTFP abundance was 29 individuals per 0.04 ha.

##### 3.1.b Vegetation in 2024

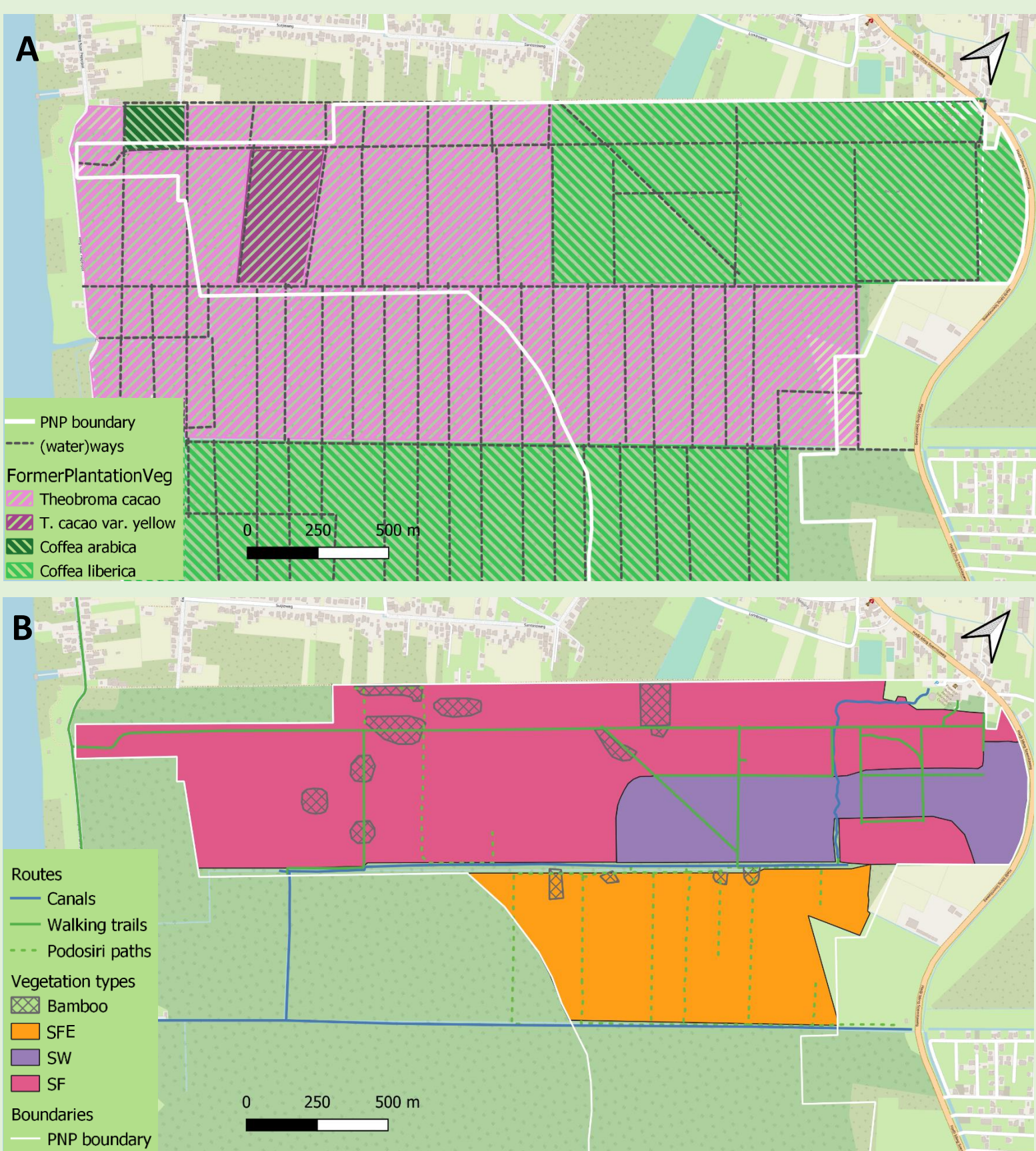
During the 2023-2024 vegetation surveys, a total of 34 tree/arborescent palm species were recorded, spanning 33 genera and 20 families. Predominant families included Moraceae (with four species), Rubiaceae (three species), Fabaceae (three species), and Arecaceae (three species). Species count per plot, for trees/arborescent palms with a diameter at breast height (DBH) of  $\geq 5$  cm, ranged from 8 to 17 species, averaging 10 species per plot. A full list of all trees and arborescent palms, including author names, can be seen in Table S.2.1, and their total abundance in the sampled area in Fig. S.2.6.

Based on the overview of tropical vegetation types by P. Teunissen (1980) and the subsequent key species, the main vegetation types found in PNP were swamp wood (SW) and swamp forest (SF). Swamp wood was characterized by high abundance of *Montrichardia arborescens* (L.) Schott in the understory and *Triplaris weigeltiana* (Rchb.) Kuntze, *Euterpe oleracea* Mart., *Inga ingoides* (Rich.) Willd., *Virola surinamensis* (Roll. Ex Rottb.) Warb. and *Cordia tetrandra* (Aubl.) in the upperstory. See Table 3.1 for the five most abundant tree/arborescent palm species per vegetation type. During the dry season, the soil was still mostly inundated for this vegetation type. The canopy of SW contained big gaps, enabling sunlight to reach the understory for large areas. The vegetation consisted of one tree layer of  $\sim 15$  meters high.

**Table 3.1. Most abundant plant species per vegetation type.** For each vegetation type the top five contributing species to the total number of stems are given, together with their percentage of the total number of stems. Percentages were calculated per plot and averaged per forest type.

Swamp wood (SW)		Swamp forest (SF)		Swamp forest, <i>E. oleracea</i> dominance (SFE)	
<i>Triplaris weigeltiana</i>	(16.7%)	<i>Inga ingoides</i>	(17.4%)	<i>Euterpe oleracea</i>	(55.6%)
<i>Euterpe oleracea</i>	(14.6%)	<i>Guarea guidonia</i>	(16.5%)	<i>Triplaris weigeltiana</i>	(9.9%)
<i>Inga ingoides</i>	(13.0%)	<i>Coffea liberica</i>	(8.9%)	<i>Fareamea occidentalis</i>	(7.2%)
<i>Virola surinamensis</i>	(13.0%)	<i>Euterpe oleracea</i>	(8.8%)	<i>Virola surinamensis</i>	(5.5%)
<i>Cordia tetrandra</i>	(7.0%)	<i>Virola surinamensis</i>	(5.9%)	<i>Inga ingoides</i>	(4.5%)





**Figure 3.1. Main vegetation types of PNP, 1970 vs 2024.** A) During 1970, vegetation on Peperpot consisted of *Theobroma cacao* L., a variant of *T. cacao* with fruits that were considered more yellow, *Coffea arabica* L. and *C. liberica* w. bull. The boundary of Peperpot Nature Park (PNP) anno 2024 is indicated, as well as the former demarcation of plantation areas by walking paths and canals. B) Main vegetation types of PNP in 2024. Swamp forest is indicated in pink (SF), swamp forest with *Euterpe oleracea* Mart. dominance (SFE) in orange, and swamp wood (SW) in purple. Arcated areas: patches where *Bambusa vulgaris* Schrad. Ex J.C. Wendl. is monodominant. The boundary of Peperpot Nature Park (PNP) is indicated, as well as are the large canals and walking paths.

Swamp forest was characterized by a high abundance of *I. ingoides* and *Guarea guidonia* (L. Sleumer), *E. oleracea*, and *V. surinamensis* in the upperstory (~ 20 m), and still contained a high abundance of *C. liberica* in the upper- and understory (Table 3.1). During the dry season, the soil was moist to inundated. The canopy was closed, and the vegetation consisted of a dense shrub layer containing tree saplings (e.g. *I. ingoides*, *G. guidonia*), *Tabernaemontana heterophylla* Vahl, *Heliconia bihai* (L.) L., and *M. arborescens*. An intermediate layer of ~8 m was present containing large shrubs and juvenile trees (*C. liberica*, *G. guidonia*).

A variant of swamp forest dominated by *E. oleracea* was found to contain a distinctly different species composition, being monodominant with more than half of the number of stems belonging to *E. oleracea* (SFE) (table 1). This variant was also differentiated from SF in a PCA analysis (Fig S.2.3). Although the abundance of species differed distinctly from the other swam forest type, there were no abundant unique species distinguishing SFE as a unique vegetation type. However, due to the notable difference in species abundance and forest structure, this variant was analyzed separately from the SF type. Therefore, for ease of communication, SFE will be called a separate vegetation type throughout this paper. The soil of SFE was moist to inundated during the dry season. The vegetation consisted of an open herb layer, containing tree saplings (*Faramea occidentalis* (L.) A.Rich., *E. oleracea*), *Heliconia psittacorum* L.f., *H. bihai*, *Costus Arabicus* L., and *M. arborescens*. An intermediate vegetation layer of ~8 m was present containing juvenile trees (*F. occidentalis*, *Trichilia pallida* Sw.), and an upper layer of ~20 m was present dominated by *E. oleracea*.

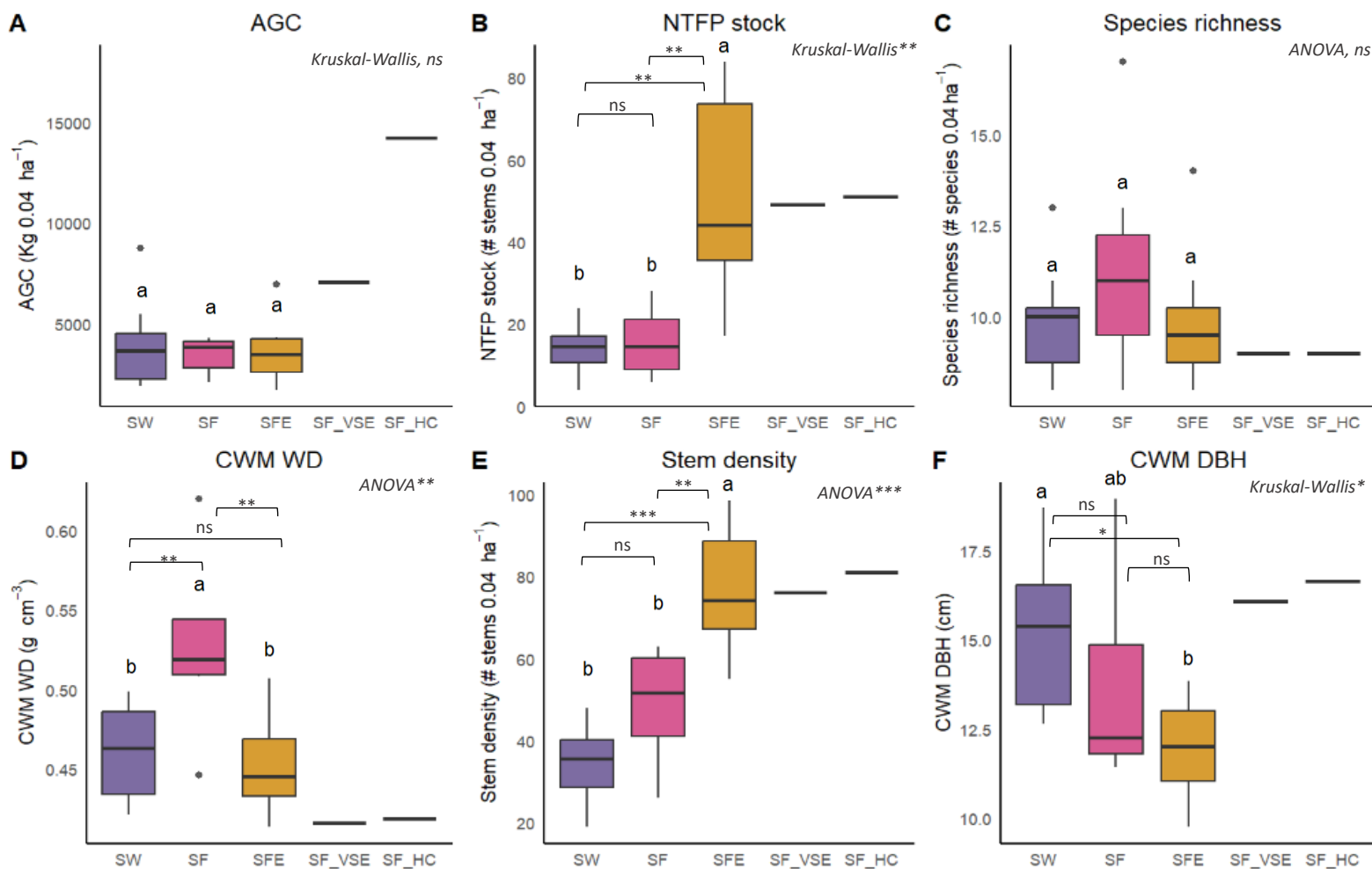
The North-Eastern part of the survey area consisted of SF and SW (Fig. 3.1.B). In the South-Western part of the survey area between canal 1 and 2, the vegetation consisted of SFE. The estimated total AGC of the sampled area was  $2024 \pm 20.87 \times 10^3$  Mg (SD =  $7.45 \times 10^3$ ). Mean tree species richness was 10.7 (SD = 2.5) species per 0.04 ha, and mean NTFP abundance 24.3 (SD = 11.8) individuals per 0.04 ha. See table S.2.3 for mean AGC, NTFP abundance, and species richness per vegetation type.

### 3.1.c Differences in ES and diversity indicators for main vegetation types 2024

There was no significant difference in species richness and AGC between the main vegetation types ( $p > 0.05$ ) (Fig. 3.2). SFE had a higher NTFP stock than SW and SF. Community-weighted mean wood density (CWM WD) was higher for SF than SFE and SW. Stem density was higher for SFE than for SW and SF. The community-weighted mean diameter at breast height (CWM DBH) was higher for SW than for SFE. For mean values and  $p$  scores, see Fig. 3.2 and Table S.2.3 and S.4.1.

Visual comparison to coastal primary swamp forests indicated a lower AGC for all PNP vegetation types. The NTFP abundance appeared similar for SFE to primary swamp forest, but lower for SF and SW (Fig. 3.2). Primary swamp forests appeared equal in species richness to all vegetation types in PNP. All vegetation types in PNP were indicated to have a higher CWM WD than the primary swamp forests. Stem density appeared similar for SFE to the primary swamp forests, but lower for SW and SF. Primary swamp forests were indicated to have an equal CWM DBH as SW, but higher CWM DBH than SF and SFE. Species in the reference primary swamp forests that were not present in PNP were *Hura crepitans* L. (seen once in PNP but not recorded in the plots), *Tabebuia insignis* (Miq.) Sandwith, *Carapa guianensis* Aubl., *Pterocarpus officinalis* Jacq., *Ilex ovalifolia* G. Mey., *Symphonia globulifera* L.f., *Cedrela odorata* L., *Ocotea puberula* Rich. Nees and *Inga bourgoni* (Aubl.) D.C.. The WD of these species ranged from  $0.37 - 0.71$  g cm<sup>-3</sup>, with only 2 species with WD  $> 0.60$  g cm<sup>-3</sup>.



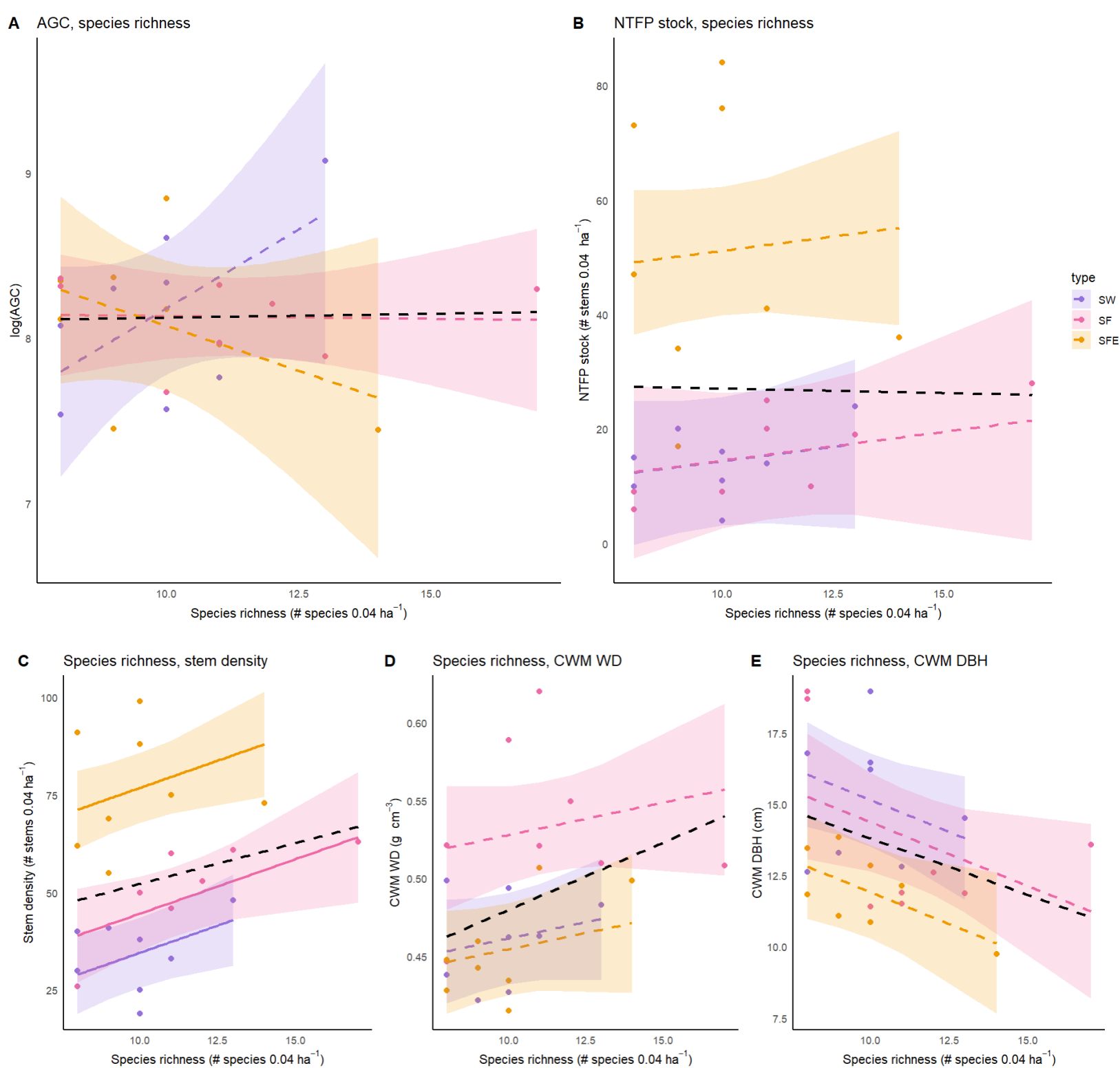


**Figure 3.2. Boxplots of ecosystem services and plant diversity indicators per vegetation type.** Indicators are given for two reference primary swamp forests sampled by P. Teunissen (i.e. swamp forest dominated by *Virola surinamensis*, *Symphonia globulifera* and *Euterpe oleracea* (SF\_VSE, n = 1) and swamp forest dominated by *Hura crepitans* (SF\_HC, n = 1)) and for the main vegetation types of PNP anno 2024 (i.e. swamp wood (SW, n = 8), swamp forest (SF, n = 8) and swamp forest dominated by *Euterpe oleracea* (SFE, n = 8)). A) Aboveground carbon (AGC) per vegetation type. B) Non-Timber Forest product (NTFP) abundance per vegetation type. C) Woody species richness. D) Community-weighted mean wood density (CWM WD). E) Stem density. F) Community-weighted mean diameter at breast height (CWM DBH). ANOVAs with subsequent Tukey-Kramer post-hoc tests were performed for species richness, CWM WD and stem density. For AGC, NTFP abundance and CWM DBH, Kruskal-Wallis tests were performed, with subsequent Dunn's tests. The p-values are indicated; p-value ranks:  $p < 0.001$  (\*\*\*),  $p < 0.01$  (\*\*),  $p < 0.05$  (\*),  $p \geq 0.05$  (ns). Significant differences between the means on the basis of Post-hoc Tukey Kramer test or Dunn's test are indicated by unique letter combinations. Means and 95% confidence intervals are included in Tables S.2.3, test statistics in S.4.1.

## 3.2 Linear relationships for vegetation in PNP

### 3.2.a Relationships ecosystem services and plant diversity PNP

Across and within all three vegetation types, AGC was not significantly related to woody species richness ( $p > 0.05$ ) (Fig. 3). The model with interaction effect explained a higher percentage of the variance than the main effects model and aggregated model (Table S.4.2.1). For SF, there was a positive trend between woody species richness and AGC (Est. = 0.19,  $t = 2.039$ ,  $p < 0.056$ ), but this trend was largely dependent on a mild outlier. After removal of the outlier, the trend disappeared ( $p > 0.05$ ).



**Figure 3. Linear relationships between AGC (components), NTFP abundance and species richness for regenerating forest.** Relationships are plotted between species richness and aboveground carbon (AGC, panel A), Non-Timber Forest Product (NTFP) abundance (panel B), mean stem density (panel C), community weighted mean wood density (CWM WD, panel D), and community weighted mean diameter at breast height (CWM DBH). For panels A and D, models with interaction are plotted against a model with no distinction between vegetation types. For panels B, C, and E, models without interaction term were plotted as interactions were not significant. For models B-E, the variable ‘vegetation type’ was significantly related to the outcome variable. The vegetation types are swamp wood (SW,  $n=8$ ), swamp forest (SF,  $n=8$ ) and swamp forest with *Euterpe oleracea* dominance (SFE). Aggregated relationships are shown in black. Significant relationships are represented by solid lines ( $p < 0.05$ ), trends by dotted lines ( $p < 0.10$ ) and non-significant relationships that are not a trend by dashed lines ( $p \geq 0.10$ ). Model details can be seen in tables S.4.2.1-S.4.2.6.



The abundance of NTFPs was not significantly related to woody species richness across and within all three vegetation types ( $p > 0.05$ ). The main effects model explained a higher percentage of the variance than the model with interaction between woody species richness and vegetation types and than the aggregated model (S.4.2.3). NTFP abundance did show a significant relationship with the variable vegetation types, explaining 55.5% (adj.  $R^2$ ) of the variance ( $p < 0.01$ ).

For all three vegetation types, stem density was positively related to woody species richness; Stem density increased with a mean of 2.80 (se = 1.18) stems per species for SW, SF, and SFE ( $t = 2.37$ ,  $p = 0.028$ , adj.  $R^2 = 69.9\%$ ). The main effects model explained a higher percentage of the variance than the model with interaction between woody species richness and vegetation types and than the aggregated model (S.4.2.6). Stem density was not significantly related to woody species richness when vegetation types were not accounted for in the model ( $p > 0.05$ ).

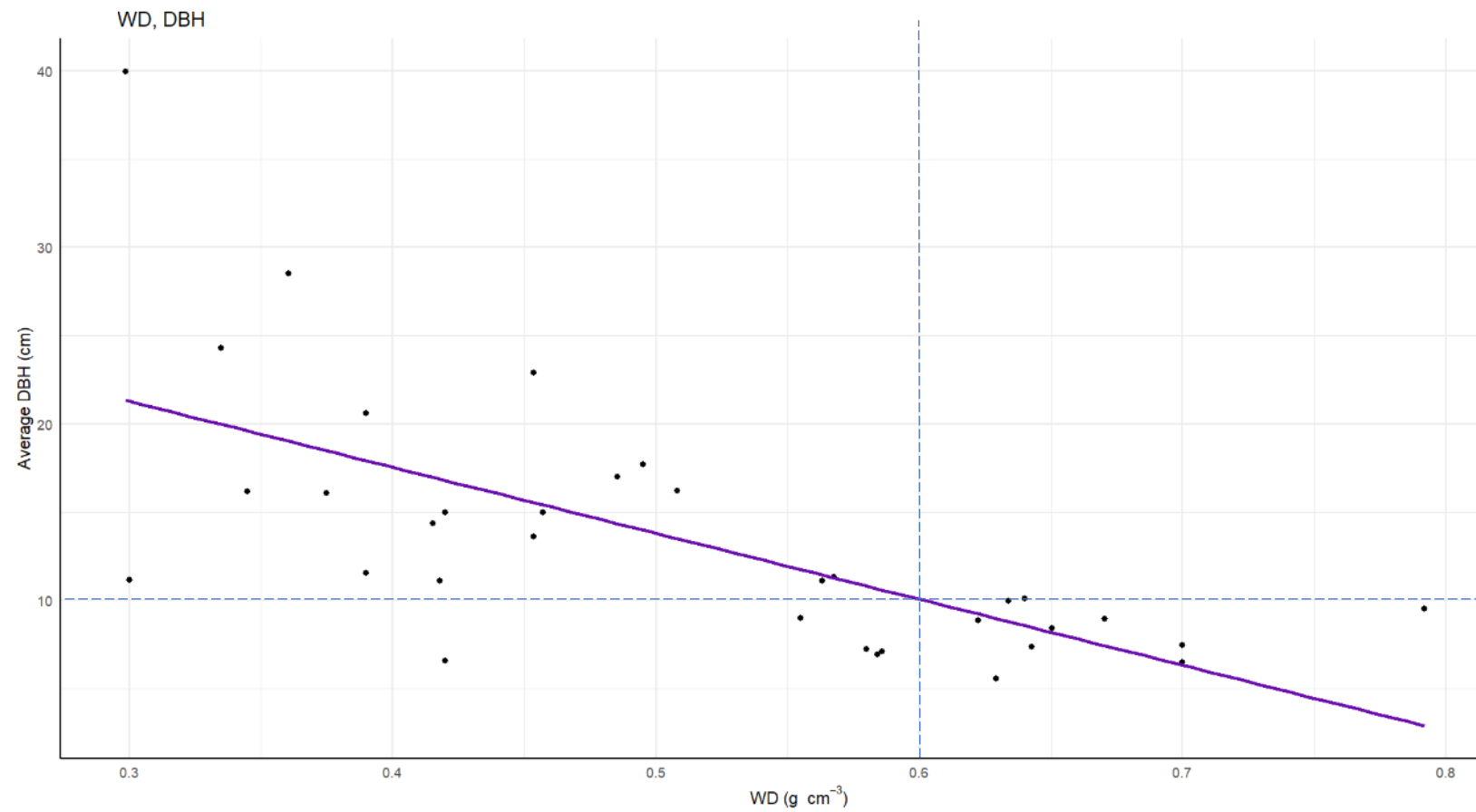
There was a positive trend between CWM WD and woody species richness across all vegetation types; CWM WD showed a mean increase of 8.6 (SE = 4.7)  $\text{mg cm}^{-3}$  per species ( $t = 1.836$ ,  $p = 0.080$ , adjusted  $R^2 = 9.4\%$ ). Within vegetation types, this relationship was not significant ( $p > 0.05$ ). The main effects model explained a higher percentage of the variance than the model with interaction between woody species richness and vegetation types and than the aggregated model (S.4.2.4).

Within all three vegetation types, there was a strong negative trend between CWM DBH and woody species richness, with an estimated effect size of -0.45 (SE = 0.22) cm per species ( $t = -2.075$ ,  $p = 0.051$ , adj.  $R^2 = 30.0\%$ ). The main effects model explained a higher percentage of the variance than the model with interaction between woody species richness and vegetation types and than the aggregated model (S.4.2.5). Woody species richness was not significantly related to stem density when vegetation types were not accounted for in the model ( $p > 0.05$ ).

Across and within all vegetation types, AGC is not significantly related to CWM WD ( $p > 0.05$ , Table S.4.2.2).

### 3.2.b Species wood density and diameter at breast height

The average DBH of trees and arborescent palms in PNP showed a negative relationship with their wood density; DBH decreased with 37.36 (SE = 9.81) cm per  $\text{g cm}^{-3}$  ( $t = 9.81$ ,  $p < 0.01$ ). All species with a WD  $> 0.6 \text{ g cm}^{-3}$  have an average DBH of  $\leq 10$  cm (Fig. 4). With the exception of one species, all species with WD  $< 0.5 \text{ g cm}^{-3}$  have an average DBH of  $> 10$  cm. In the primary swamp forests sampled by P. Teunissen, no significant relationship was found between species wood density and average DBH ( $p > 0.05$ ). For these species, species with WD  $> 0.6 \text{ g cm}^{-3}$  had a WD of  $> 10$  cm. In total, five species had a DBH of  $< 10$  cm for the primary swamp forests, of which three had a WD  $< 0.5$  and two had a WD  $< 0.6$  (Fig. S.2.7).



**Figure 4. Linear relationship between species average diameter at breast height and wood density.** For all species observed in the main vegetation types in PNP anno 2024, average diameter at breast height (DBH) was calculated based on plot data. Average DBH was negatively related to species wood density (WD) with a decrease of 37.36 (SE = 9.81) cm per  $\text{g cm}^{-3}$  ( $t = 9.81$ ,  $p < 0.01$ ). All species with a  $\text{WD} > 0.6 \text{ g cm}^{-3}$  have an average DBH of  $\leq 10$  cm. With the exception of one species, all species with  $\text{WD} < 0.5 \text{ g cm}^{-3}$  have an average DBH of  $> 10$  cm.

## 4. Discussion

This research studied the relationships between tree species richness and ecosystem services (ES), i.e. carbon storage and Non-Timber Forest Product (NTFP) provisioning, for regenerating neotropical vegetation. As a case study, this was examined in Peperpot Nature Park (PNP), a former coffee and cacao plantation in Suriname. Within and across different forest types, no significant relationship was found between species richness and aboveground carbon (AGC), contrasting with demonstrated positive relationships between species richness and AGC in primary (neo)tropical rainforests (Steur et al., 2020, 2022). For regenerating forests, a lack of studies on species richness-carbon storage relationships has prevented clear conclusions on whether this relationship is present in regenerating tropical forests as well (van der Sande et al., 2017). Studies are presenting positive (e.g. Coelho et al., 2022; Rodrigues et al., 2023), neutral (e.g. Pinto et al., 2023), or negative (e.g. Oberleitner et al., 2021) relationships between species richness and AGC. After observing a lack of positive relationships between species richness and AGC in PNP, relationships with the components of AGC (i.e. stem density, community-weighted mean wood density (CWM WD), and community-weighted mean diameter at breast height (CWM DBH)) and species richness were examined. These relationships between diversity and AGC components can be used to examine whether the three hypotheses underlying positive diversity – carbon relationships in primary rainforests are absent in (young) regenerating tropical forests, suggested by an absence of positive diversity – carbon relationships, or whether these hypotheses are present in PNP, yet effecting AGC undetectably.

### 4.1 AGC components

With increasing species richness, stem density increased for all three vegetation types; species-rich vegetation contained a higher amount of individuals compared to species-poor vegetation. Simultaneously, a positive trend between species richness and CWM WD was present across the different vegetation types, with positive but insignificant coefficients for the vegetation types separately. Vegetation with a higher species richness is thus suggested to include species with a higher WD. Relationships between species richness and CWM WD have rarely been studied for (neo)tropical forests but were found positive for African Northern mistbelt forests (Mensah et al., 2016) and Chinese tropical to temperate forests (Wu et al., 2022). For wet neotropical forests, WD increases along succession since late successional species have a higher WD than early successional species due to shade tolerance characteristics (Rueger et al., 2023). Therefore, vegetation stands in PNP exhibiting a high species richness are postulated to contain later successional species characterized by a higher WD compared to species-poor vegetation.

In contrast to stem density and CWM WD, the CWM DBH showed a strong negative trend with species richness within all three forest types in PNP ( $p = 0.051$ ). Together with the positive trend between species richness and CWM WD, this negative diversity - CWM DBH trend points to a relatively smaller size for later successional species compared to early successional species. In PNP, these smaller individuals of late-successional species with a high WD could contribute to an increased species richness, while being too small to significantly increase AGC. For instance, individuals of <10 cm DBH were found to contribute up to 32% of tree species richness, but only < 5% to total AGC in primary tropical forest in Gabon and regenerating tropical forest in Costa Rica (Memiaghe et al., 2016; Oberleitner et al., 2021). To test whether species with a higher WD were indeed (still) smaller than species with a low WD in PNP, linear regression

was performed; a negative relationship between WD and average DBH was observed. All species with a WD of more than  $0.6 \text{ g cm}^{-3}$  were found to have an average DBH of less than 11 cm. In comparison, no significant relationship between species their WD, and average DBH was found for reference primary swamp forest. Thus, later successional species in PNP were significantly smaller than earlier successional species, with a notable contribution to species richness but a scant contribution to AGC. This influences the extent to which all three positive diversity – biomass hypotheses (i.e. the niche complementarity theory, selection effect, and insurance hypothesis) affect the diversity – carbon relationship in PNP.

## 4.2 Niche complementarity

Regarding the niche complementarity hypothesis (Tilman, 1999), stem density increased with species richness, indicating a higher number of individuals and thus occupied niches in species-richer vegetation, supporting the hypothesis. However, the average DBH of late-successional species and the CWM DBH of species-rich vegetation were low, decreasing the contribution of increased niche occupation to AGC, evidenced by the neutral species richness – AGC relationship. Coelho et al. (2022) also observed late successional species to contribute relatively more to species richness than to AGC in young regenerating forests on former eucalyptus tree plantations in the Atlantic rainforest in Brazil. For stands aged 30 years, shade-tolerant species had recovered, on average, 27% of the primary forest reference species richness, but only 3% of the reference carbon stocks. Pioneer species, on the other hand, had recovered 47% of species richness and 40% of carbon stocks (Coelho et al., 2022). Notably, Coelho et. al (2022) stated that only 14% of total carbon stock was recovered, demonstrating the importance of later successional species in total carbon stocks and indicating the relatively small contribution of late-successional species to carbon stocks in early successional stages of tropical forest regeneration. The authors therefore note that shade-tolerant (together with zoochoric) species are shaping carbon stocks in their study area. For PNP, a similar pattern was observed, with pioneer species such as *Erythrina fusca* and *Ceiba pentandra* having an average DBH of respectively 40 cm and 24 cm, while *Andira inermis*, a later successional species, had an average DBH of 7.4 cm. Therefore, a positive effect of niche complementarity on AGC is assumed to increase during succession, when later successional species and thus individuals occupying ‘extra’ niches increase in size. In line with this assumed increasing effect of niche complementarity along succession, an experimental study conducted on subtropical forests in China found niche complementarity effects to increase with stand age (Huang et al., 2018). Thus, for PNP, the niche complementarity effect is deemed present, but with individuals too young to contribute significantly to AGC.

## 4.3 Selection effect

The positive trend between species richness and CWM WD pointed to the inclusion of late-successional species with a higher WD for species-rich vegetation, indicating the inclusion of species with the potential to highly contribute to carbon storage, as postulated by the selection effect (Loreau & Hector, 2001). However, since species with a higher WD ( $> 0.6 \text{ g cm}^{-3}$ ) are still small in PNP (average DBH  $< 11 \text{ cm}$ ), these species do not contribute markedly to the mean AGC of vegetation stands. Therefore, the selection effect seems to be present in PNP, but its effects on AGC cannot be detected yet in this study. In PNP, examples of these late successional species that are (still) small in size are e.g. *Genipa americana*, *Andira inermis*, and *Protium heptaphyllum*. Similarly, a model study simulating the clear-cutting of 75% of a tropical forest



found the selection effect of species richness on AGC to increase over time; over a hundred years passed after clear-cutting before the selection effect had a considerable positive effect on AGC (Schmitt et al., 2020).

#### 4.4 Insurance hypothesis

After the abandonment of the coffee and cacao plantations formerly present in the study area, natural regeneration has run its course for ~25 years. This is a short time frame for insurance effects to become evident since it encompasses a brief period for: 1) a regenerating forest to have diverged in species richness and for major disturbances to subsequently occur (other than the initial clear-cutting of the area); and 2) the recovery of (resilient) vegetation from a disturbance and the differentiation of recovery rates for varying degrees of species richness. For instance, in the simulated tropical forest study by Schmitt et al. (2020), AGC took ~20 years to rebound from a 75% clear-cutting disturbance. Additionally, since insurance effects on AGC stability are dependent on species diversity through complementarity and selection effects (Schmitt et al., 2020), the relatively weaker effects of niche complementarity and selection effects in early successional forests compared to later successional forests (e.g. Huang et al., 2018; Schmitt et al., 2020) also point to a lower contribution of insurance effects to AGC stability in regenerating forests than in primary forests. Furthermore, Schmitt et al. (2020) noted that vegetation containing early successional species would have an impeded recovery compared to vegetation containing later successional species, corroborated by a study on regenerating tropical forests in Sabah Malaysia (Qie et al., 2019). Concluding, it is unlikely that species-rich vegetation in PNP can display a higher AGC as a consequence of insurance effects, due to a short timespan since the start of regeneration and a lack of adult individuals of later successional species.

#### 4.5 Alternative explanatory factors

The absence of a positive relationship between species richness and carbon storage in regenerating forests has also been observed in Costa Rican and Andean regenerating tropical forests (Oberleitner et al., 2021; Pinto et al., 2023). Pinto et al. (2023) found no significant relationship in secondary 30-35-year-old logged or burned Andean forests. Other factors were found to be explanatory instead, such as CWM leaf thickness and temperature. In PNP, AGC might be shaped by environmental factors (e.g. hydrological and edaphic constraints) and functional traits (e.g. specific leaf area) as well, rather than species richness.

A negative relationship between species richness and aboveground biomass was found for regenerating Costa Rican clear-cut and logged tropical forests (Oberleitner et al., 2021). The authors suggest this negative relationship to be the effect of monodominance by *Virola ferruginea*, which has a high growth rate and contributes vastly to carbon stocks. For PNP, a similar monodominance is observed for *Euterpe oleracea* in swamp forest dominated by *E. oleracea* (SFE, >50 % of stems in this vegetation type, sensu the monodominance definition of ter Steege et al. (2019)). The inclusion of extra species in a plot might thus contribute little to total carbon stocks if they are largely dominated by *E. oleracea*. This points to the mass ratio theory of Grime (1998), which details that the identity of the most dominant species of a system predicts its functioning, assumed applicable to forests with a few highly dominant species (Grime, 1998). However, the mass ratio theory was found non-explanatory for mean AGC values in PNP, as there was no significant relationship between AGC and CWM WD across and within different vegetation types. The mass

ratio theory can be expected to affect AGC when different plots with varying monodominant species are included in the analysis. However, *E. oleracea* was the only monodominant species and monodominance occurred in only one of the three vegetation types. Thus, due to the absence of different highly dominant species, AGC was not related to CWM WD values, and the mass ratio theory can be assumed non-explanatory for AGC differences within and between vegetation types in PNP.

#### 4.6 NTFP provisioning

Within and across different forest types, no significant relationship was found between species richness and NTFP abundance. The lack of positive diversity – NTFP relationships is in line with the absence of these relationships in primary tropical rainforests (e.g. Steur, 2022; Steur et al., 2020, 2021). This absence suggests that species richness is not the driving mechanism behind NTFP provisioning, which might instead be species identity, vegetation type, and floristic composition (Steur et al., 2021). The provisioning of NTFPs is therefore not linked to diversity in PNP but is heavily dependent on forest type and the presence of abundant NTFP species. For instance, PNP has a high occurrence of *E. oleracea*, especially in SFE. The abundance of NTFP stems is therefore heavily dependent on vegetation type in PNP and seems to be determined mainly by one species. Similarly, Steur et al. (2021) found NTFP abundance to be mainly determined by a few dominant species, so-called NTFP oligarchs. For PNP, *E. oleracea* could therefore be called an NTFP oligarch. Although biodiversity generally underpins ES and is assumed to positively affect biomass-derived ES (Díaz et al., 2005; Steur, 2022: PhD thesis), this alignment does not appear to hold for NTFP provisioning.

#### 4.7 Caveats and suggestions

An alternative explanation for the lack of significant positive relationships between AGC and species could be that since the relationship is weak for primary forests (Steur et al., 2020), it might be statistically difficult to detect for regenerating (swamp) forest with lower max AGC and species richness values, if this resulted in a lower effect size (Guan et al., 2023). This means a large sample size is required, while the current study only included 24 plots. Furthermore, this study has a small plot size of 0.04 ha, while 1 ha is the standard plot size used in tropical forest inventories for determining AGC (see e.g. RAINFOR and AFRITRON protocols). The minimum plot size for performing reliable carbon stock measurements in tropical forests was found to be  $\geq 0.2$  for tropical lowland forests in Papua New Guinea and  $\geq 0.06$  ha for tropical forests in Brazil (Grussu et al., 2016; L. O. R. Pinto et al., 2021). With smaller plot sizes, sampling issues occur, for example, due to in- or excluding large trees by chance (Grussu et al., 2016; L. O. R. Pinto et al., 2021). The fieldwork team noted that during fieldwork, sometimes a large tree (DBH  $>40$  cm) was just outside the plot and would have led to a much higher mean AGC for these plots. Therefore, relationships might have been impacted by sampling bias, for example, while excluding a large tree in a diverse vegetation or including a large tree in a species poorer vegetation. Thus, larger plots would seem a more representative sample of the carbon stock of PNP. Furthermore, a cut-off of 5 cm DBH might make a relationship between species richness and AGC more difficult to detect, because individuals with a DBH under 10 cm contribute significantly to species richness, but only up to 5% to the total biomass of vegetation (Ifo et al., 2019; Memiaghe et al., 2016). It is therefore suggested to repeat the analysis with different cut-offs, (e.g. 10 or

20 cm) and compare it to the results of the analysis with a cut-off of DBH  $\geq$  5 cm. Future research is therefore also suggested to study the effects of measurement cut-offs on diversity – carbon relationships.

Furthermore, research solely focusing on the richness effect is recommended, thus compensating for stem density, to compare plots with the same number of large trees but many of the same species versus the same number of large trees but different species. Perhaps the relationship would be stronger for Shannon diversity when considering the distribution of vegetation. Using this indicator, more diverse systems both include more species (i.e., more stems) and have a higher evenness. Evenness was discovered to be significant for productivity-diversity relationships; highly rich, even communities tend to be more productive, according to a synthesis study across the globe (Hordijk et al., 2023). Another way to compensate for increasing stem density with species richness is by opting for rarefied species richness, i.e. a certain number of species per a certain number of stems. Additionally, conducting research that incorporates total plant diversity might be interesting, to see whether carbon-diversity co-benefits include total plant-diversity, or whether this relationship only holds for tree species richness. Future research is also suggested to include functional traits, e.g. leaf thickness, SLA, and tree category (e.g. evergreen/deciduous, pioneer/late-successional species, wind-dispersed/zoochoric); In two studies on Brazilian regenerating forests, diversity – carbon relationships were found to differ between species groups differing in functional characteristics, explaining a considerable amount of variance (Coelho et al., 2022; Matos et al., 2019).

Meta-analysis and modeling studies studying the effect of the age of regenerating tropical forests on the strength of complementarity, selection, and insurance effects are suggested to study when positive diversity carbon effects start to occur. While doing so, the land-use history of the vegetation should be taken into account. For PNP, former plantation species were still present in reasonable abundance, i.e. *Coffea liberica* and *Erythrina fusca*, influencing species composition. *C. liberica* was even in the top 5 most abundant species for one of the vegetation types, although with a low average DBH (<10 cm). *E. fusca* was not present in the top 5 most abundant species for any of the vegetation types, but had a large average DBH of 40 cm, influencing carbon stocks when present. *E. fusca* is a native pioneer species in Suriname with a low wood density. In PNP, this species therefore acts as a pioneer species, posing no probable deviations from expected succession trajectories.

## 4.8 implications

The findings of this study offer insights into the relationships between species richness and ES, i.e. carbon storage and NTFP provisioning, within regenerating tropical forests. Despite the absence of significant relationships between species richness and AGC in PNP, signs of diversity mechanisms that can eventually contribute to increased AGC are emerging: the niche complementarity theory and the selection effect. Although these mechanisms are not contributing significantly to an increased AGC yet, due to a low average DBH of late-successional species, their effect on AGC is likely to increase during the coming years. Furthermore, after 25 years of natural regeneration, species richness in PNP has reached levels comparable to primary forests, showing promising progress in biodiversity recovery compared to former plantation lands. This biodiversity recovery is in line with other studies on neotropical regenerating forests, e.g. a mean recovery of 77% in 20 years (Poorter, Craven, et al., 2021), and a variance in recovery from 46 – 99

% after 20 years (Rozendaal et al., 2019). While AGC in PNP forests remains lower than in primary swamp forests, the slower recovery of biomass than species richness is in line with a mean biomass recovery of 34% found across (neo)tropical forests (Poorter, Craven, et al. 2021), although lower than the >80% recovery found in other neotropical forest sites (Poorter et al., 2016). Nonetheless, the trajectory for biomass recovery appears promising, with the potential for significant gains in AGC over time. Following the mean recovery trajectory of Poorter et al. (2021), AGC could increase a further 20% in the coming 20 years. Given the variability in vegetation legacy (e.g. land-use history) and species composition across different forests, caution is warranted when extrapolating the findings of this study to other regenerating forests. Concluding, a long-term vision for restoration efforts in regenerating forests is imperative, recognizing the time needed for the recovery of both plant-diversity and carbon storage, and the possible absence of relationships between plant diversity and plant-based ES, i.e. carbon storage and NTFP provisioning, in young regenerating forests. This stresses the need for adaptive management strategies with a clear long-term vision regarding diversity, AGC, and NTFP provisioning outcomes, including continued monitoring efforts, to facilitate the regeneration of ecosystems, ES, and biodiversity.

## 5. Conclusion

After 25 years of natural regeneration, Peperpot Nature Park, a neotropical rainforest regenerating on former coffee and cacao plantations, exhibits a species richness comparable to reference primary swamp forests, showcasing substantial progress in biodiversity recovery. Contrarily, the total aboveground carbon stock remains similar to the former plantation carbon stock and is lower than in primary swamp forests, suggesting that the trajectory for biomass recovery is slower than that of species richness. Although AGC is not yet related to woody species richness, signs of diversity effects contributing to increased AGC are emerging, particularly the niche complementarity and selection effects. While these mechanisms may not yet significantly impact AGC in young regenerating forests, their influence is expected to increase over time. It is thus crucial to recognize that these relationships may emerge with a longer time horizon beyond 25 years of natural regeneration. Hence, the restoration of tropical forests should be viewed as a marathon rather than a sprint, emphasizing the importance of long-term vision and adaptive management strategies. While regenerating forests may currently have a decreased carbon storage relative to primary forests, they play a crucial role as corridors and biodiversity reservoirs and may provide valuable NTFPs. Regeneration of tropical forests and their conservation is thus essential to facilitate ecosystem restoration, enhance ecosystem services, and increase biodiversity.

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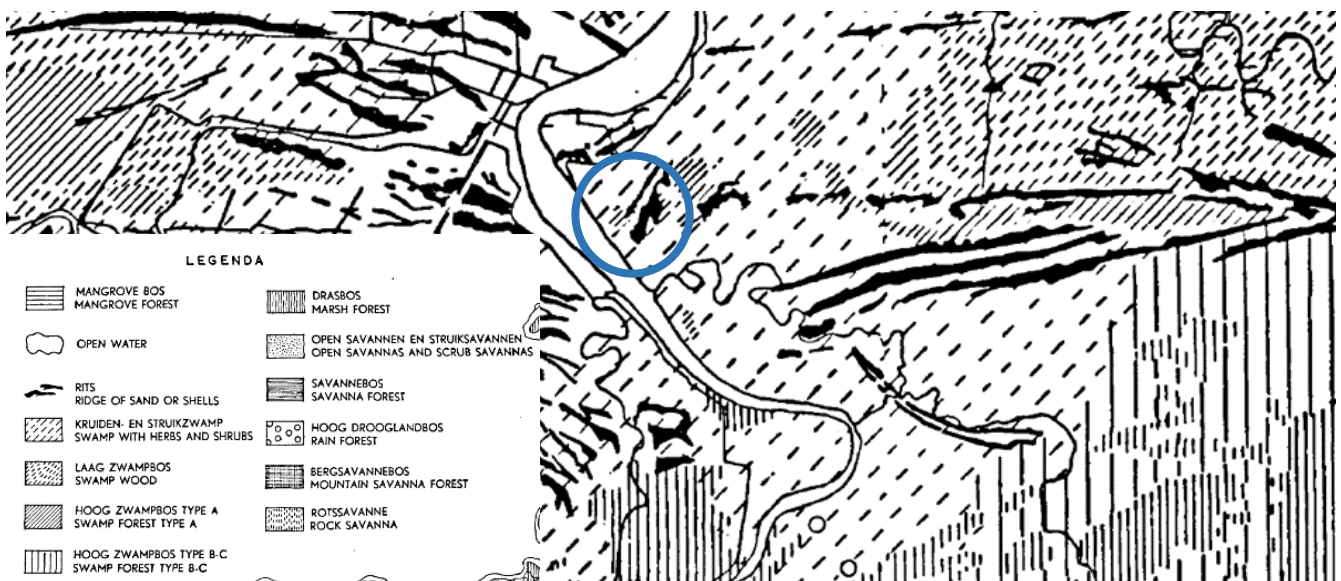
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# Supplementary materials 1

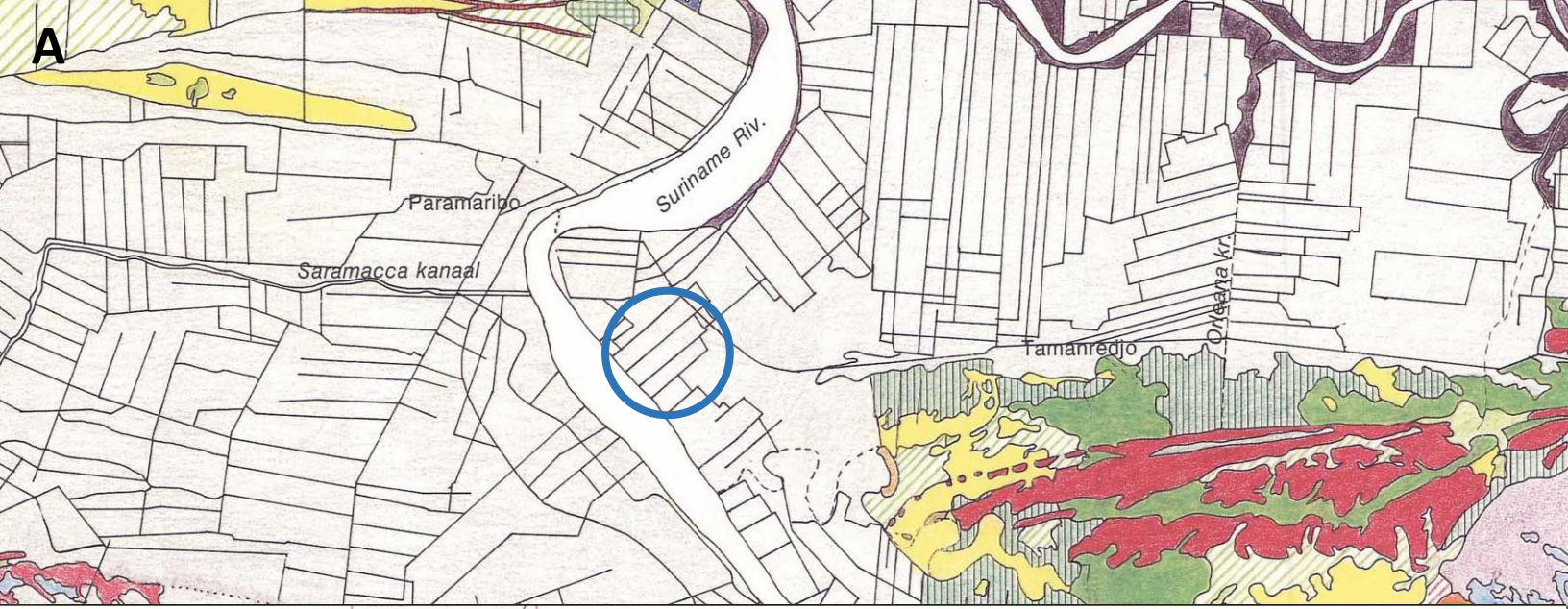
## S1 Expected main vegetation types surrounding PNP

The expected main vegetation types are inferred from vegetation maps of the study area, constructed by Lindeman & Moolenaar (1959, Fig. S.1.1), Teunissen (1978, Fig. S.1.2), and Quiñones & Hoekman (2011, Fig. S.1.3). According to these maps, the main vegetation types covering and surrounding Peperpot are cultivated vegetation of old fields, grass swamps, swamp woods, swamp forests, marsh forests, and dryland forests (Lindeman & Molenaar, 1959; Quiñones & Hoekman, 2011; P. A. Teunissen, 1978). The vegetation types can be further divided into subtypes. Lindeman & Molenaar recognize the following subtypes for the area of Peperpot Nature Park (PNP): swamp with herbs and shrubs, swamp forest type A (with *Triplaris weigeltiana*), swamp forest type B (with a high abundance of *Symphonia globulifera* and *Virola surinamensis*), swamp forest type C (with a high abundance of *Eschweilera sp.* and *Cynometra bostmanniana*), marsh forest, and swamp wood. Teunissen has mapped the vegetation of Peperpot as former agricultural fields (P. A. Teunissen, 1978). On the Southern edge of Peperpot, Teunissen describes a more variegated composition of vegetation types. These types consist of tall grass swamps, ombrogenous peat swamps, scattered watrabebe bushes in tall grass swamps, hydrophytic swamp forests dominated by *V. surinamensis*, *S. globulifera* and *Euterpe Oleracea*, hydrophytic swamp forests dominated by *Triplaris weigeltiana*, and mixed mesophytic dryland forest and marsh forest. It is expected that during the 25 years after the construction of the Teunissen map, the vegetation types bordering the southern part of PNP have spread further North, given abiotic conditions are similar. After abandonment, former agricultural land is subject to succession of bordering vegetation types. If these vegetation types consist of tropical forests, the vegetation on the former plantation will transition to secondary tropical forests, as described by a review of tropical forest regeneration by Jakovac et al. (2021). Therefore, it is expected that former agricultural fields have been subject to the immigration of species outside the former plantation. Thus, vegetation types depicted by Teunissen on the outside of PNP are expected to currently occur on the more southern side PNP. Expected vegetation types can be seen in Tables S.1.1.



**Figure S.1.1.** Map of vegetation types northern Suriname, adapted from Lindeman & Molenaar (1959).





**B**

**ECOSYSTEMEN VAN DE KUSTVLAKTE / ECOSYSTEMS OF THE COASTAL PLAIN**

**ECOSYSTEMEN VAN ZOUT- TOT BRAKWATERGEBIEDEN / ECOSYSTEMS OF SALT TO BRACKISH-WATER AREAS**

**ECOSYSTEMEN VAN STRANDEN EN JONGE RITSEN / ECOSYSTEMS OF BEACHES AND YOUNG RIDGES**

Strandvegetatie: kruidenvegetatie met geleenheid en zaai, verspreide maai-struikgroepen en pinna-koestergroepen / Beach vegetation: herb vegetation with *Pomarea pas-caprae* and *Canevalia maritima*, scattered fibrous *Silene*-scrub and *Avicennia germinans*-forest fragments

Savannes van het Galibi-type (droge en drasse strand-savannes); grassavennes met verspreide struikgroepen en kruipelbosjes / Savannes of Galibi type (dry and marshy beach savannes); short grass savannes with scattered scrub and gnarled treelets

Gemengd kust-savannebos, in O.Suriname rijk aan zulfucassen / Mixed xerophytic coastal wood and forest, in E.Suriname rich in cactuses (*Cereus hexagonus*)

**ECOSYSTEMEN VAN MODDERBANKEN EN JONGE ZWAMPEN / ECOSYSTEMS OF MUDFLATS AND YOUNG SWAMPS**

Modderbanken / Coastal mudflats

Sarasasgras-vegetatie op modderbanken en jong paraweb / Coastal mudflat vegetation (*Spartina brasiliensis*) and mangrove (*Avicennia germinans*) wood

Volwassen paraweb / Mature mangrove forest, dominated by *Avicennia germinans*

Alstervend paraweb / Dying mangrove forest (*Avicennia germinans*)

Diepe lagunes en brakwater-pannen / Salt water ponds with *Ruppia maritima* and brackish ponds and lakes with *Ruppia maritima* and *Hymenapha ampia*

Ondiepe lagunes met halofyten-kruidenvegetatie / Shallow salt water swamps with halophytic herb vegetation, dominated by *Sesuvium portulacastrum*, *Batis maritima*, or *Sporobolus virginicus*

**ECOSYSTEMEN VAN BRAK- TOT ZOETWATERGEBIEDEN / ECOSYSTEMS OF BRACKISH TO FRESH-WATER AREAS**

**ECOSYSTEMEN VAN JONGE RITSEN / ECOSYSTEMS OF YOUNG RIDGES**

Gemengd kust-savannebos tot gemengd hoog drooglandbos en hoog drasbos, plaatselijk possentri-drasbos / Mixed xero-mesophytic dryland- and marsh forest, locally *Hura crepitans* marsh forest

Pruiamen-zuurzak-bos / Hydrophytic swamp wood, with *Chrysobalanus icaco* and *Annona glabra*

country: Suriname  
subject: Thema (ecol)  
scale: 1:200.000  
map ref.: Sur. 2.8

**LEGENDA / LEGEND**

**ECOSYSTEMEN VAN JONGE ZWAMPEN / ECOSYSTEMS OF YOUNG SWAMPS**

**ECOSYSTEMEN VAN BRAKKE RIVIEROEVERS / ECOSYSTEMS OF ESTUARY FLOODPLAINS**

Brak- tot zoetwater graszwampen / Brackish to fresh-water swamp scrub, dominated by *Typha angustifolia*

Bramimaka-struikgewas / Brackish to fresh-water swamp scrub, dominated by *Machaerium lunatum*

Kotnama-bos / Brackish to fresh-water swamp wood, dominated by *Erythrina glauca*

Brak- tot zoetwater mangrovebos met prasaara-palmen / Brackish to fresh-water mangrove forest with *Euterpe oleracea*-palms

Mango-bos / Brackish to fresh-water mangrove forest, dominated by *Rhizophora mangle*

Overwegend gemengd hoog drooglandbos en hoog drasbos, plaatselijk hoog savannebos, drasbos in W.Suriname rijk aan krapa / Predominantly mixed mesophytic dryland- and marsh forest, marsh forest in W.Suriname rich in *Carapa procera*

Possentri-drasbos / Mesophytic marsh forest, dominated by *Hura crepitans*

Possentri-zwampbos / Hydrophytic swamp forest, dominated by *Hura crepitans*

Mierenhout-bos / Hydrophytic swamp forest, dominated by *Triplaris surinamensis*

Watrabebos / Hydrophytic swamp wood, dominated by *Pterocarpus officinalis*

Verspreide watrabebosjes in graszwampen / Scattered *Pterocarpus*-bushes in tall grass swamps

Verspreide pruimen-zuurzak-bosjes in gras- en veenzwampen / Scattered *Chrysobalanus-Annona*-bushes in tall grass and fern swamps

Verspreide mauri-palmen in gras- en veenzwampen / Scattered *Mauritia flexuosa*-palms in tall grass and fern swamps

Verspreide mauri-palmen in watrabebos- of pruimen-zuurzak-bos / Scattered *Mauritia flexuosa*-palms in *Pterocarpus*- or *Chrysobalanus-Annona*-wood

Gesloten mauri-bos / Closed xerophytic palm swamp forest, dominated by *Mauritia flexuosa*

Graszwampen, overwegend gemengd, plaatselijk gedomineerd door leng-gras, grasro-gras o.a.; ook veenzwampen / Tall grass swamps, predominantly mixed, locally dominated by *Typha angustifolia*, *Cyperus giganteus*, or *Rhynchospora corymbosa*; also fern swamps, dominated by *Blechnum indicum*

Drijvende waterplanten-vegetatie / Floating aquatic vegetations

Overwegend gemengd hoog drooglandbos en hoog drasbos, drasbos in W.Suriname rijk aan krapa / Predominantly mixed mesophytic dryland- and marsh forest, marsh forest in W.Suriname rich in *Carapa procera*

Mora-bos / Mesophytic marsh forest, dominated by *Mora excelsa*

Gemengd hoog drooglandbos en hoog drasbos / Mixed mesophytic dryland- and marsh forest

Foengon-bos / Mesophytic marsh forest, rich in *Parinari campestris*

Overwegend gemengd hoog en laag droogland- en dras savannebos, plaatselijk gedomineerd door walaba / Predominantly mixed xerophytic dryland- and marsh forest and wood, locally dominated by *Eperua falcata*

Bakaberibos / Xerophytic marsh forest, dominated by *Humiria balsamifera* var. *balsamifera*

Drasse witzand-savannes van het Watamaleo-type; grassavennes met verspreide struikgroepen en mauri(palm)-baten / Marshy white sand savannas of Watamaleo type; short grass savannas with scattered scrub and *Mauritia flexuosa*-palm galleries

Gemengd hoog drooglandbos en hoog drasbos / Mixed mesophytic dryland- and marsh forest

**ECOSYSTEMEN VAN JOUNGERE OEVERWALLEN / ECOSYSTEMS OF YOUNGER RIVER BANKS**

Watrabebos / Hydrophytic swamp wood, dominated by *Pterocarpus officinalis*

Verspreide watrabebosjes in gras- en veenzwampen / Scattered *Pterocarpus*-bushes in grass and fern swamps

Watrabili-watrapa-bos / Xerophytic swamp forest and wood, with *Crucie glaberrima* and *Macrobium acaciifolium*

Verspreide watrabili-watrapa-bosjes en struikgewas in graszwampen / Scattered *Crucie-Macrobium*-bushes and *Galearia glauca*-scrub in grass swamps

Verspreide mauri-palmen in watrabebos- of watrabili-watrapa-bos of in graszwampen / Scattered *Mauritia flexuosa*-palms in *Pterocarpus*, *Crucie*, *Macrobium*-scrub or grass swamps

**ECOSYSTEMEN VAN SCHOLLEN / ECOSYSTEMS OF OLD FLATS**

Gemengd hoog drooglandbos en hoog drasbos / Mixed mesophytic dryland- and marsh forest

Gemengd laag droogland- en drasbos / Mixed meso-xerophytic dryland- and marshland wood

Drasse klei-savannes van het Wanekreek-type; grassavennes met verspreide struikgroepen en mauri(palm)-baten / Marshy clay savannas of Wanekreek type; short grass savannas with scattered scrub and *Mauritia flexuosa*-palm galleries

Drasse klei-savannes van het Welgelegen-type; grassavennes met verspreide struikgroepen en mauri(palm)-baten / Marshy clay savannas of Welgelegen type; short grass savannas with scattered scrub and *Mauritia flexuosa*-palm galleries

Droge savannes van het Welgelegen-type (klei-savannes); grassavennes met verspreide kruipelbosjes en bosjes / Dry savannas of Welgelegen type (clay savannes); short grass savannas with scattered gnarled treelets and bushes

**ECOSYSTEMEN VAN OUDE ZWAMPEN / ECOSYSTEMS OF OLD SWAMPS**

Baboen-mataki-(grasra)-zwampbos / Hydrophytic swamp forest with *Viola surinamensis*, *Symphonia globulifera* (and *Euterpe oleracea*)

Overwegend gemengd hoog droogland- en dras savannebos, plaatselijk gedomineerd door walaba, dakama of savanne-ijzerhart / Predominantly mixed xerophytic dry- and marshland forest, locally dominated by *Dimorphandra conjugata* or *Swartzia bannia*

Dakama-bos / Xerophytic dryland forest, dominated by *Dimorphandra conjugata*

Laag droogland- en dras savannebos; plaatselijk gedomineerd door dakama, savanne-ijzerhart, savanne-mango o.a. / Xerophytic dryland- and marshland wood, locally dominated by *Dimorphandra conjugata*, *Swartzia bannia*, *Clusia foetida* o.o.

Droge witzand-savannes van het Cassipora-type; grassavennes met verspreide struikgroepen en bosjes / Dry white sand savannas of Cassipora type; short grass savannas with scattered scrub and bushes

Drasse witzand-savannes van het Zanderi-type; grassavennes met verspreide struikgroepen en mauri(palm)-baten / Marshy white sand savannas of Zanderi type; short grass savannas with scattered scrub and *Mauritia flexuosa*-palm galleries

**ECOSYSTEMEN VAN KREEKDALLEN / ECOSYSTEMS OF CREEK VALLEYS**

Baboen-mataki-(grasra)-kreekbos / Hydrophytic swamp forest with *Viola surinamensis*, *Symphonia globulifera* and *Euterpe oleracea*

**ECOSYSTEMEN VAN DE SAVANNEGORDEL / ECOSYSTEMS OF THE SAVANNA BELT**

**ECOSYSTEMEN VAN PLATEAUS EN HELLINGEN / ECOSYSTEMS OF PLATEAUS AND SLOPES**

Overwegend gemengd hoog drooglandbos, in W.Suriname plaatselijk gedomineerd door zwet-parelhout, moriboskies of demerara-groenhart / Predominantly mixed mesophytic dryland forest, in W.Suriname locally dominated by *Aspidosperma excelsum*, *Mora gongrijp* or *Clusia rodiaei*

Gemengd laag drooglandbos / Mixed meso-xerophytic dryland wood

Droge bruinzand-savannes van het Coeswijpe-type; grassavennes met verspreide kruipelbosjes en bosjes / Dry brown sand savannas of Coeswijpe type; short grass savannas with scattered gnarled treelets and bushes

Drasse bruinzand-savannes van het Coeswijpe-type; grassavennes met verspreide struikgroepen en mauri(palm)-baten / Marshy brown sand savannas of Coeswijpe type; short grass savannas with scattered scrub and *Mauritia flexuosa*-palm galleries

Overwegend gemengd hoog droogland- en dras savannebos, plaatselijk gedomineerd door walaba, dakama of savanne-ijzerhart / Predominantly mixed xerophytic dry- and marshland forest, locally dominated by *Eperua falcata*, *Dimorphandra conjugata* or *Swartzia bannia*

Dakama-bos / Xerophytic dryland forest, dominated by *Dimorphandra conjugata*

Laag droogland- en dras savannebos; plaatselijk gedomineerd door dakama, savanne-ijzerhart, savanne-mango o.a. / Xerophytic dryland- and marshland wood, locally dominated by *Dimorphandra conjugata*, *Swartzia bannia*, *Clusia foetida* o.o.

**ECOSYSTEMEN VAN KREEKDALLEN / ECOSYSTEMS OF CREEK VALLEYS**

Baboen-mataki-(grasra)-kreekbos / Hydrophytic swamp forest with *Viola surinamensis*, *Symphonia globulifera* and *Euterpe oleracea*

**OVERIGE LAAGLAND ECOSYSTEMEN / OTHER LOWLAND ECOSYSTEMS**

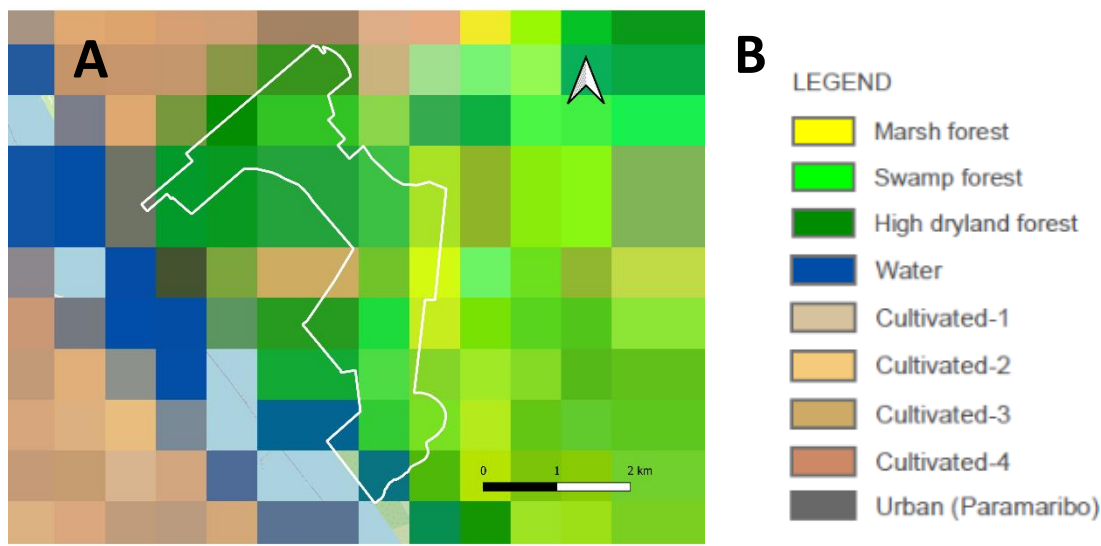
**ECOSYSTEMEN VAN RESIDUAIRE HEUVELS IN LAAGLAND GEBIED / ECOSYSTEMS OF RESIDUAL HILLS IN LOWLAND AREA**

Overwegend gemengd hoog drooglandbos en hoog savannebos / Predominantly mesophytic and xerophytic dryland forest

**ISM - WAGENINGEN**  
country: ;  
subject: ;  
scale: ;  
map ref.: 504 2.8  
libr. ref.:

**Figure S.1.2.** A) Map of the vegetation types of Peperpot Nature Park (PNP) and surrounding areas in 1978, adapted from Teunissen (1978). The location of PNP is indicated with a blue circle. B) The legend accompanying Figure I.2.A.





**Figure S.1.3.** A) Sarvision map of the vegetation types of Peperpot Nature Park (PNP), adapted from Quiñones & Hoekman (2011). White outline shows PNP boundaries. B) legend accompanying Figure I.3.A.

**Table S.1.1.** Overview of expected vegetation types in Peperpot based on Teunissen (1980)

Vegetation type Teunissen: code	Vegetation type Teunissen: Ecology	Vegetation type Teunissen: description	Vegetation type Blok
L30	Ecosystems of fresh-water areas; ecosystems of young swamps	Grass swamps, predominantly mixed, locally dominated by <i>Typha angustifolia</i> , <i>Cyperus giganteus</i> , <i>Leersia hexandra</i> or <i>Rhynchospora corymbosa</i>	Grass swamp
L12	Ecosystems of brackish to fresh-water areas; ecosystems of young ridges	Mixed xero mesophytic dryland- and marsh forest, locally <i>Hura crepitans</i> marsh forest	Dryland/marsh forest
L18a	Ecosystems of fresh-water areas; ecosystems of young ridges	Predominantly mixed mesophytic dryland and marsh forest; marsh forest in W. Suriname rich in <i>Carapa procera</i>	Dryland/marsh forest
L32	Ecosystems of fresh-water areas; ecosystems of young river banks	Predominantly mixed mesophytic dryland and marsh forest; marsh forest in W. Suriname rich in <i>Carapa procera</i>	Dryland/marsh forest
L20	Ecosystems of fresh-water areas; ecosystems of young swamps	Hydrophytic swamps forest with <i>Virola surinamensis</i> , <i>Symphonia globulifera</i> and <i>Euterpe oleracea</i>	Swamp forest
L22	Ecosystems of fresh-water areas; ecosystems of young swamps	Hydrophytic swamp forest, dominated by <i>Triplaris weigeltiana</i>	Swamp forest
L15	Ecosystems of brackish to fresh-water areas; ecosystems of young swamps	Brackish to fresh water swamp wood, dominated by <i>Erythrina fusca</i>	Swamp wood
L23	Ecosystems of fresh-water areas; ecosystems of young swamps	Hydrophytic swampwood, dominated by <i>Pterocarpus officinalis</i>	Swamp wood
L25	Ecosystems of fresh-water areas; ecosystems of young swamps	Hydrophytic swamp wood, with <i>Chrysobalanus icaco</i> and <i>Annona glabra</i>	Swamp wood
L66	Other lowland ecosystems	Ecosystems of urban areas, farmland, livestock meadows, forest plantations, mining areas and old fields	Vegetation of old fields

**Table S.1.2.** Alphabetic register of key species indicating habitat types. Based on the overview of expected vegetation types in PNP referred from Teunissen (1980), see Table S.1.1.

<b>Species</b>	<b>Family</b>	<b>Vegetation type</b>
<i>Acrostichum aureum</i>	Pteridaceae	Grass swamp, Swamp wood
<i>Acrostichum danaeifolium</i>	Pteridaceae	Grass swamp
<i>Andira inermis</i>	Leguminosae	Dryland/marsh forest
<i>Annona glabra</i>	Annonaceae	Grass swamp, Swamp wood
<i>Annona montana</i>	Annonaceae	Dryland/marsh forest
<i>Attalea maripa</i>	Arecaceae	Dryland/marsh forest
<i>Bambusa vulgaris</i>	Poaceae	Vegetation of old fields
<i>Calathea elliptica</i>	Marantaceae	Dryland/marsh forest
<i>Carapa guianensis</i>	Meliaceae	Dryland/marsh forest
<i>Ceiba pentandra</i>	Malvaceae	Swamp wood
<i>Chrysobalanus icaco</i>	Chrysobalanaceae	Swamp wood
<i>Cocos nucifera</i>	Arecaceae	Vegetation of old fields
<i>Coffea arabica</i>	Rubiaceae	Vegetation of old fields
<i>Coffea liberica</i>	Rubiaceae	Vegetation of old fields
<i>Copaifera guyanensis</i>	Leguminosae	Dryland/marsh forest
<i>Cordia tetrandra</i>	Boraginaceae	Swamp forest
<i>Costus scaber</i>	Costaceae	Dryland/marsh forest
<i>Cupania scrobiculata</i>	Sapindaceae	Dryland/marsh forest
<i>Diospyros guianensis</i>	Ebenaceae	Dryland/marsh forest
<i>Elaeis guineensis</i>	Arecaceae	Vegetation of old fields
<i>Erythrina fusca</i>	Leguminosae	Swamp wood
<i>Eschweilera subglandulosa</i>	Lecythidaceae	Dryland/marsh forest
<i>Euterpe oleracea</i>	Arecaceae	Dryland/marsh forest, Swamp forest, Swamp wood
<i>Ficus crocata</i>	Moraceae	Swamp wood
<i>Ficus maxima</i>	Moraceae	Grass swamp
<i>Ficus pertusa</i>	Moraceae	Swamp wood
<i>Fuirena umbellata</i>	Cyperaceae	Grass swamp
<i>Heliconia psittacorum</i>	Heliconiaceae	Swamp wood
<i>Ilex guianensis</i>	Aquifoliaceae	Swamp wood
<i>Inga bourgonii</i>	Leguminosae	Dryland/marsh forest, Swamp forest
<i>Inga leptingoides</i>	Leguminosae	Dryland/marsh forest
<i>Ipomoea tiliacea</i>	Convolvulaceae	Grass swamp
<i>Ischnosiphon arouma</i>	Marantaceae	Dryland/marsh forest
<i>Macroptilium gracile</i>	Leguminosae	Grass swamp
<i>Manilkara bidentata</i>	Sapotaceae	Dryland/marsh forest
<i>Mikania micrantha</i>	Compositae	Grass swamp
<i>Montrichardia arborescens</i>	Araceae	Grass swamp, Swamp wood
<i>Oenocarpus bacaba</i>	Arecaceae	Dryland/marsh forest
<i>Paullinia pinnata</i>	Sapindaceae	Swamp forest, Swamp wood
<i>Pterocarpus officinalis</i>	Leguminosae	Swamp forest, Swamp wood
<i>Siparuna cuspidata</i>	Siparunaceae	Dryland/marsh forest
<i>Spondias mombin</i>	Anacardiaceae	Dryland/marsh forest, Swamp forest
<i>Symphonia globulifera</i>	Clusiaceae	Swamp forest
<i>Tabebuia insignis</i>	Bignoniaceae	Swamp wood
<i>Tabernaemontana siphilitica</i>	Apocynaceae	Swamp forest
<i>Talisia sylvatica</i>	Sapindaceae	Dryland/marsh forest
<i>Telmatoblechnum serrulatum</i>	Blechnaceae	Grass swamp
<i>Theobroma cacao</i>	Malvaceae	Vegetation of old fields
<i>Trichilia quadrijugata</i>	Meliaceae	Dryland/marsh forest
<i>Triplaris weigeltiana</i>	Polygonaceae	Swamp forest, Swamp wood

<i>Typha angustifolia</i>	Typhaceae	Grass swamp
<i>Varronia curassavica</i>	Boraginaceae	Grass swamp
<i>Virola surinamensis</i>	Myristicaceae	Dryland/marsh forest, Swamp forest
<i>Vitex compressa</i>	Lamiaceae	Dryland/marsh forest



## Supplementary materials 2

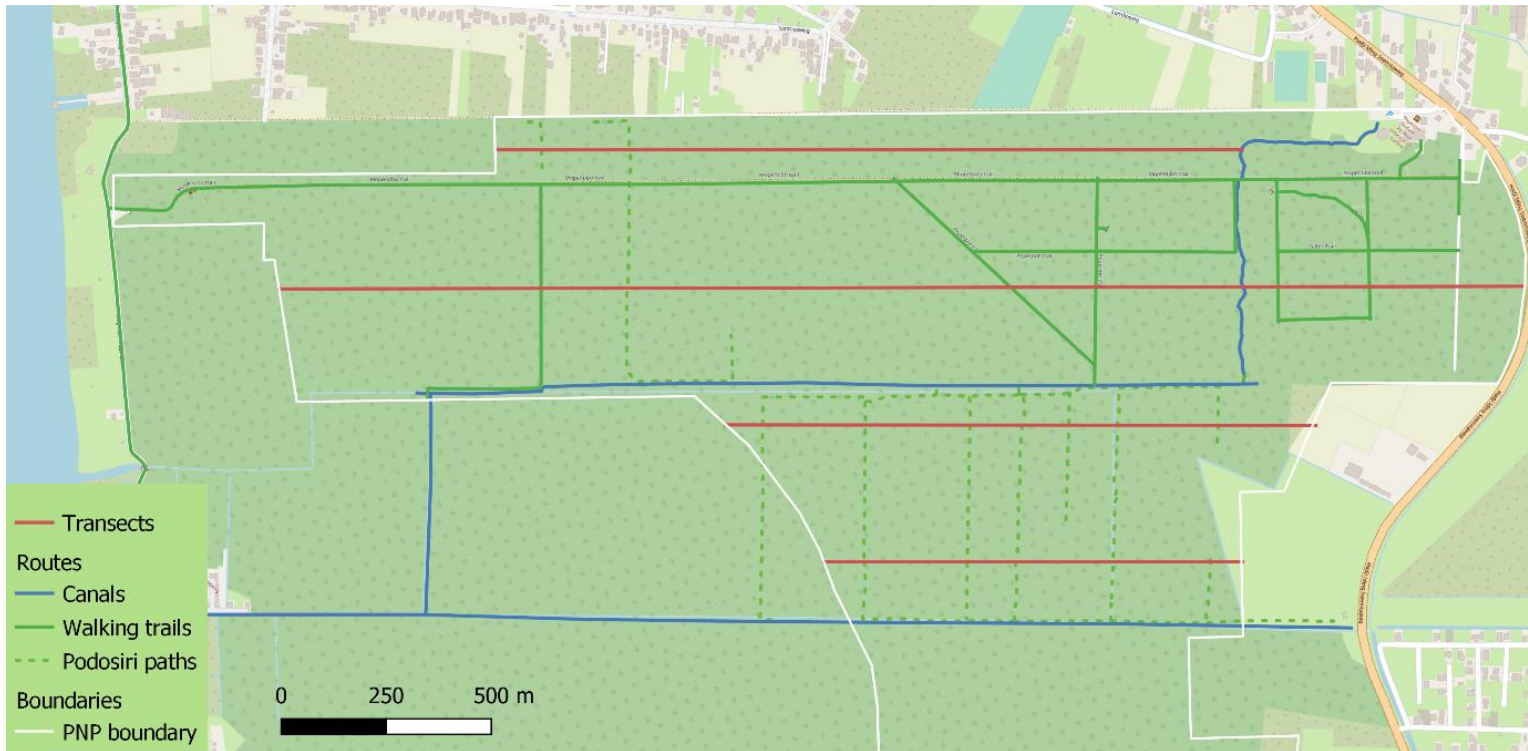


Figure S.2.1. Transects in PNP. Transects walked in PNP during November 2023.

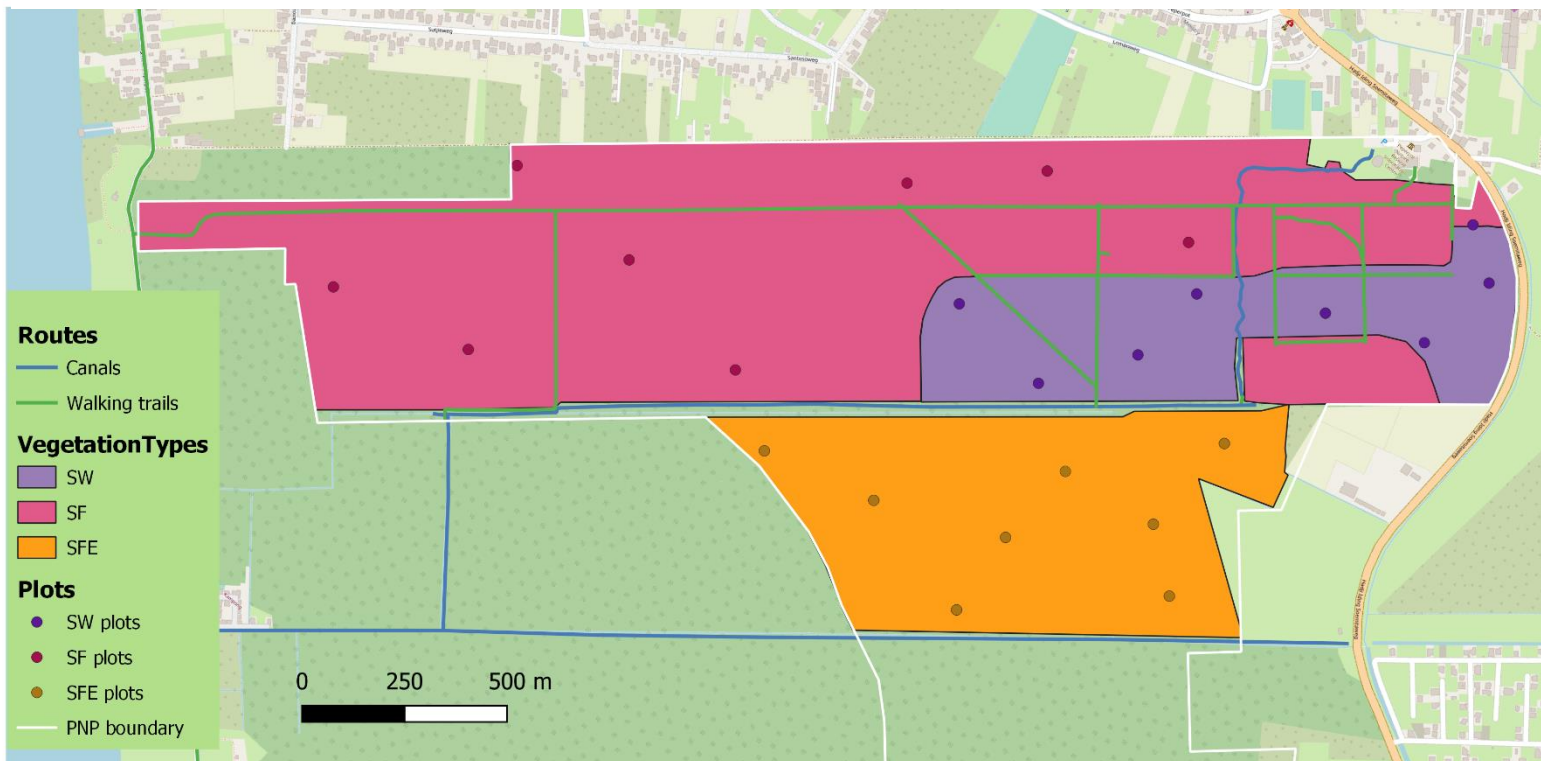
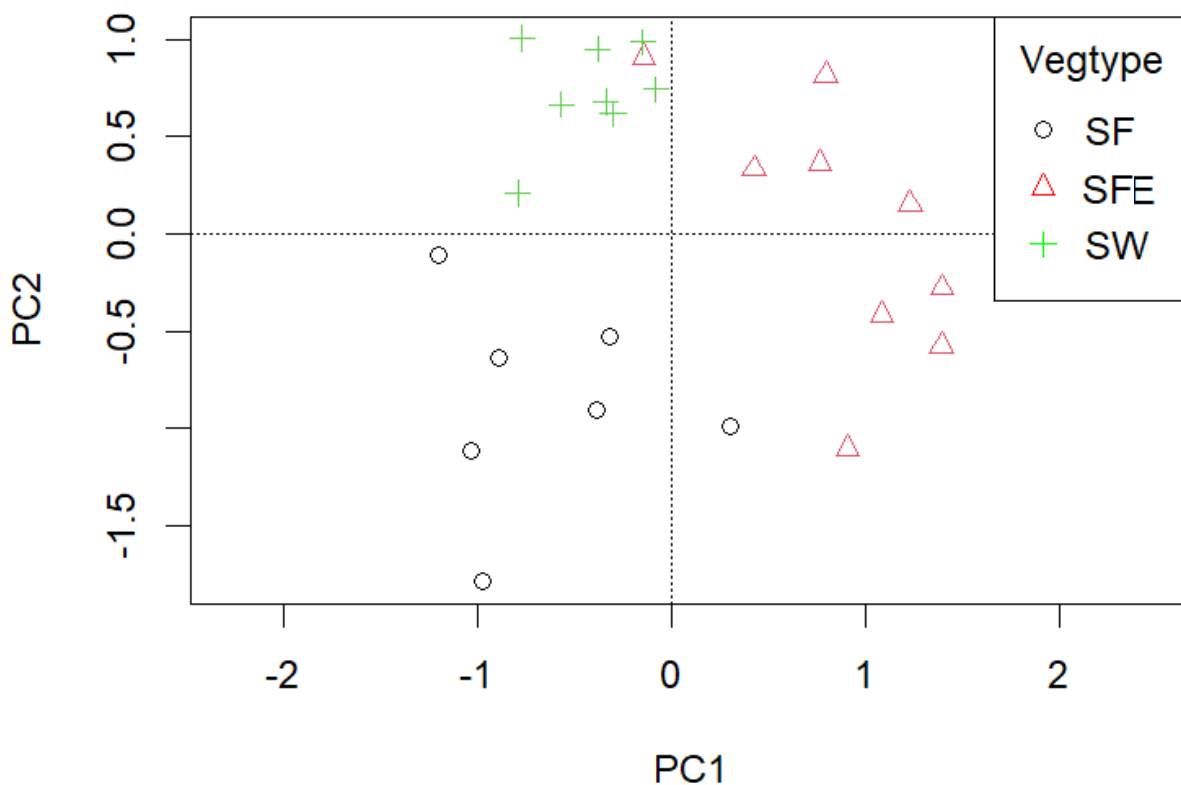


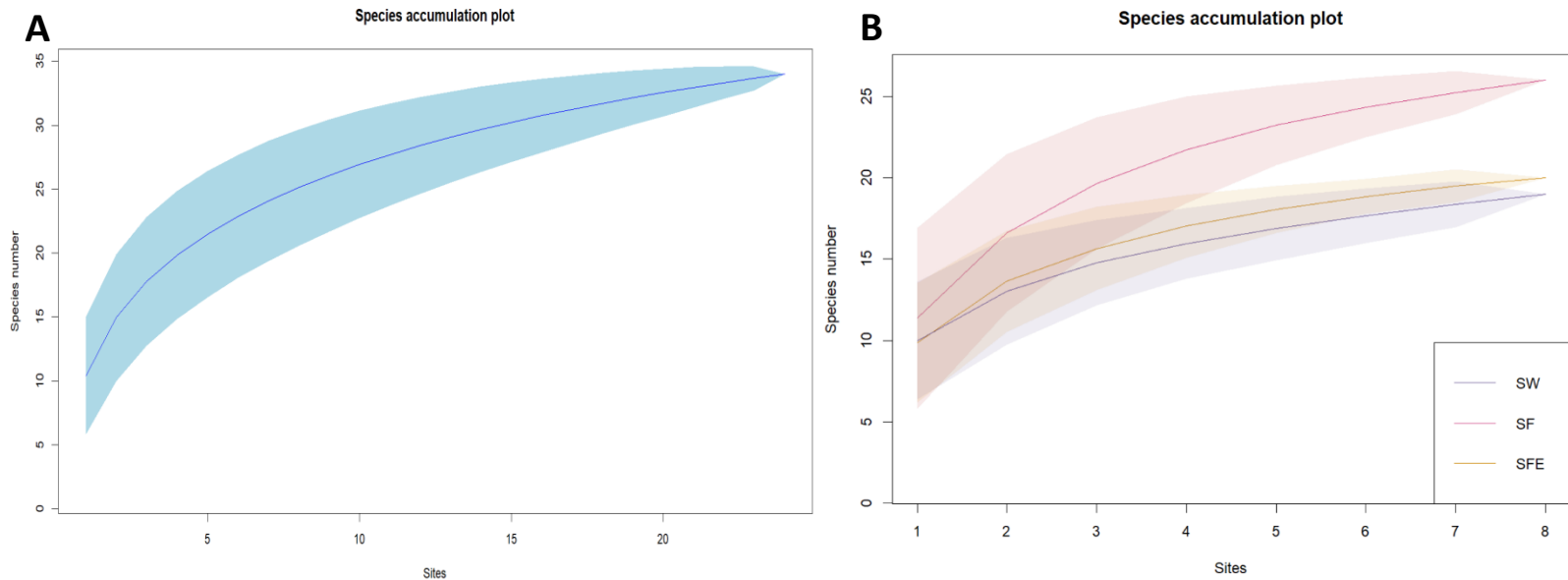
Figure S.2.2. Distribution of plots. Plots follow random stratification, with 8 plots per vegetation type (SW = swampwood; SF = swamp forest; SFE = swamp forest dominated by *Euterpe oleracea*).

**Table S.2.1. Indicators used in statistical analyses.** For each indicator, the formula and the definition of the variables is given, as well as a reference to the corresponding paper.

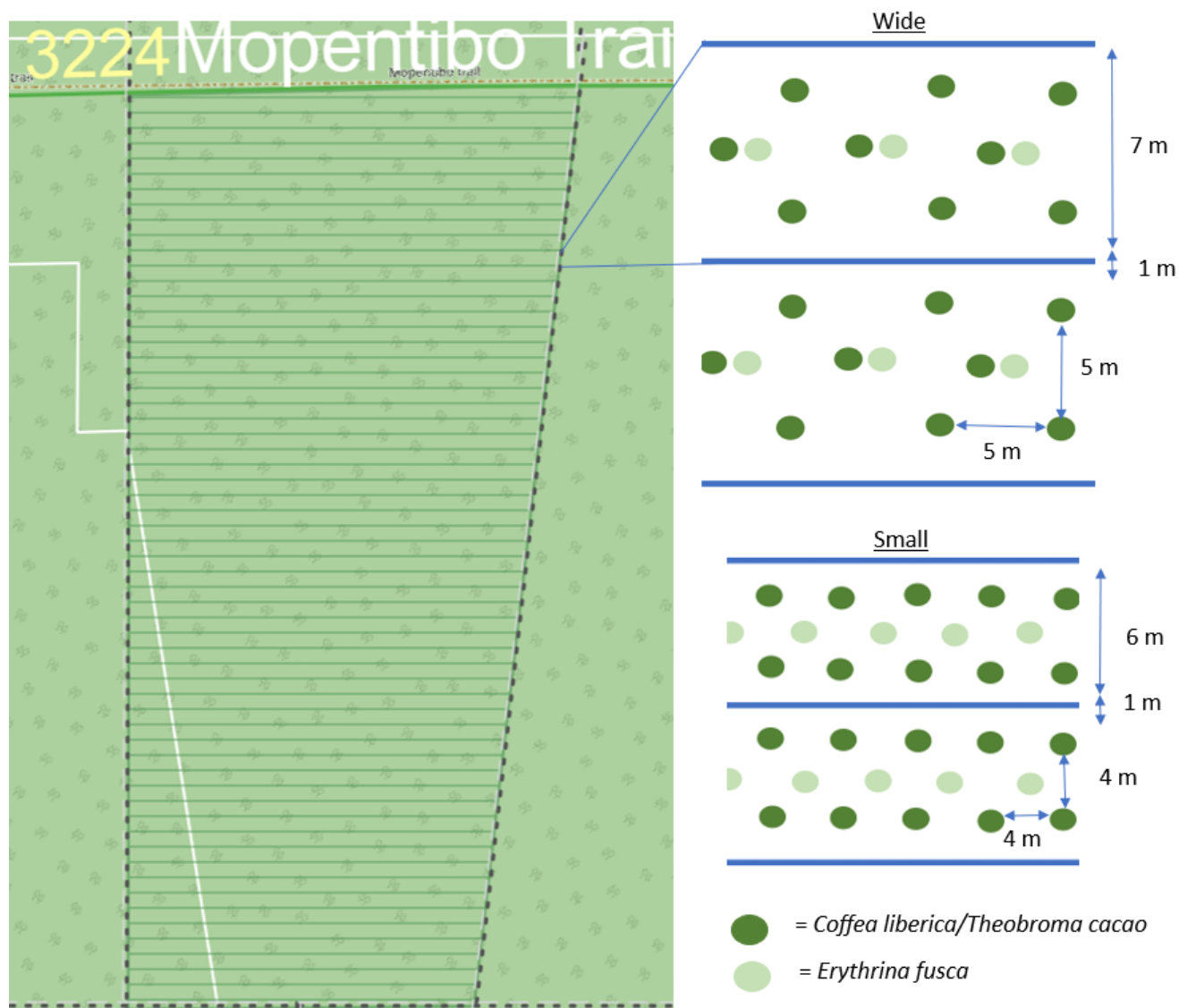
Indicator	Formula	Variables	Reference
Above ground carbon (AGC)	$AGC = AGB * 0.474$ $AGB = \sum \rho_i * \exp(-1.499 + 2.148 * \log(DBH_i) + 0.207 * (\log(DBH_i)^2) - 0.0281 * (\log(DBH_i)^3))$	AGB = aboveground biomass $\rho_i$ = wood density of the $i$ th individual DBH $_i$ = diameter at breast height of the $i$ th individual	Chave et al., 2005
Species richness	$S = I_s + M_s$	$I_s$ = the number of uniquely identified species $M_s$ = number of distinct morpho species	Sullivan et al., 2017
Non-timber forest product (NTFP) stock	$NTFP = \sum \#stems\_NTFP_i$	$stems\_NTFP_i$ = number of stems of the $i$ th NTFP species	Steur et al., 2021
Community-weighted mean wood density (CWM WD)	Mean $\rho = \sum \rho_i / \#stems$	$\rho_i$ = wood density of the $i$ th individual $\#stems$ = total number of stems (DBH $\geq$ 5 cm)	Duncan et al., 2015
Mean stem density	Mean stem density = $\#stems / 0.04 \text{ ha}$	$\#stems$ = total number of stems (DBH $\geq$ 5 cm)	Van der Sande et al., 2017
CWM DBH	Mean DBH = $\sum DBH_i / \#stems$	DBH = diameter at breast height	This study



**Figure S.2.3.** PCA of vegetation plots with log transformed abundances. The vegetation types (swamp forest (SF), swamp forest dominated by *Euterpe oleracea* (SFE) and swamp wood (SW) are indicated.



**Figure S.2.4 Species accumulation curves for PNP.** The species accumulation curves illustrate the anticipated count of observed species relative to sampling effort. Confidence intervals are depicted through polygons, derived via a randomized subsampling method without replacement. A) Species accumulation curve for aggregated data. B) Species accumulation curves per vegetation type (i.e. swamp wood (SW), swamp forest (SF), and swamp forest dominated by *Euterpe oleracea* (SFE)).



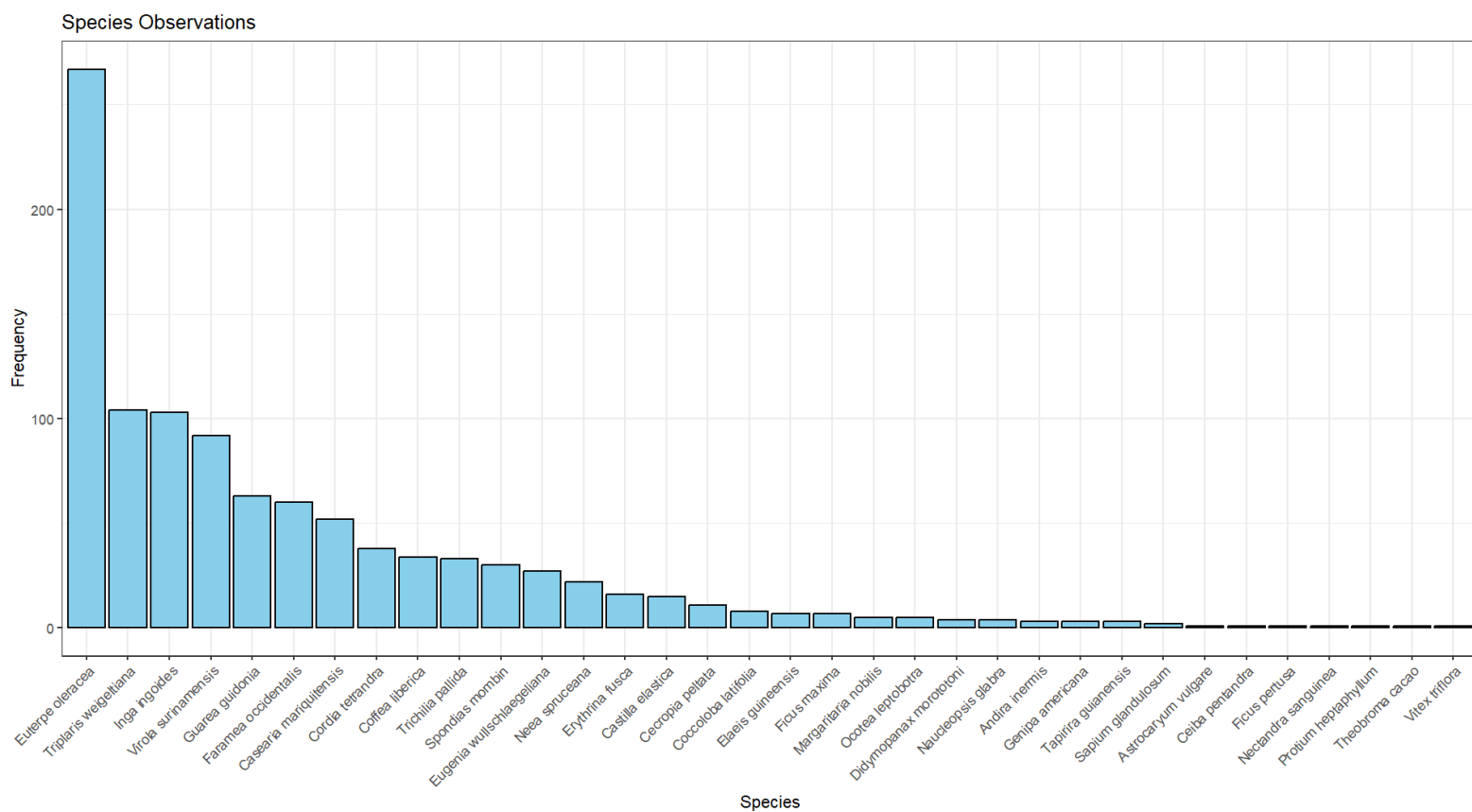
**Figure S.2.5. Layout of plantation beds in 1970.** During 1970, vegetation in the study area consisted of *Theobroma cacao*, *Coffea liberica* and *Erythrina fusca* planted in between for shade.

**Table S.2.2** Alphabetic species register trees and arborescent palms

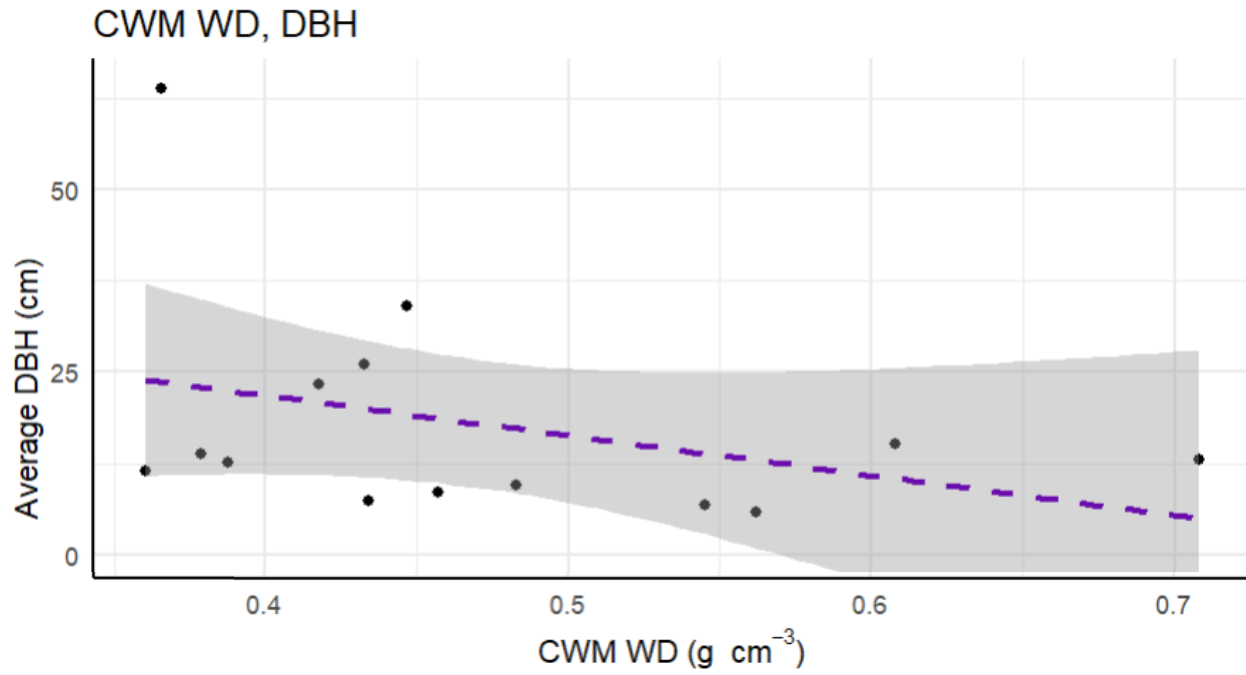
<b>Scientific name</b>	<b>Family</b>
<i>Andira inermis</i> (W. Wright) Kunth ex DC.	Fabaceae
<i>Astrocaryum vulgare</i> Mart.	Arecaceae
<i>Casearia mariquitensis</i> Kunth	Salicaceae
<i>Castilla elastica</i> Cerv.	Moraceae
<i>Cecropia peltate</i> L.	Urticaceae
<i>Ceiba pentandra</i> (L.) Gaertn.	Malvaceae
<i>Coccoloba latifolia</i> Poir.	Polygonaceae
<i>Coffea liberica</i> W. bull	Rubiaceae
<i>Cordia tetrandra</i> Aubl.	Boraginaceae
<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	Araliaceae
<i>Elaeis guineensis</i> Jacq.	Arecaceae
<i>Erythrina fusca</i> Lour.	Fabaceae
<i>Eugenia wulfschlaegeliana</i> Amshoff	Myrtaceae
<i>Euterpe oleracea</i> Mart.	Arecaceae
<i>Faramea occidentalis</i> (L.) A.Rich.	Rubiaceae
<i>Ficus maxima</i> (Mill.)	Moraceae
<i>Ficus pertusa</i> L.f.	Moraceae
<i>Genipa americana</i> L.	Rubiaceae
<i>Guarea guidonia</i> (L.) Sleumer	Meliaceae
<i>Inga ingoides</i> (Rich.) Willd.	Fabaceae
<i>Margaritaria nobilis</i> L.f.	Phyllanthaceae
<i>Naucleopsis glabra</i> Spruce ex Pittier	Moraceae
<i>Neea Spruceana</i> Heimertl	Nyctaginaceae
<i>Nectandra sanguinea</i> Rol.	Lauraceae
<i>Ocotea leptobotra</i> (Ruiz & Pav.) Mez	Lauraceae
<i>Protium heptaphyllum</i> (Aubl.) Marchand	Burseraceae
<i>Sapium glandulosum</i> (L.) Morong	Euphorbiaceae
<i>Spondias mombin</i> L.	Anacardiaceae
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae
<i>Theobroma cacao</i> L.	Malvaceae
<i>Trichilia pallida</i> Sw.	Meliaceae
<i>Triplaris weigeltiana</i> (Rchb.) Kuntze	Polygonaceae
<i>Virola surinamensis</i> (Roll. ex Rottb.) Warb.	Myristicaceae
<i>Vitex triflora</i> Vahl	Lamiaceae

**Table S.2.3. Mean values for plant-based ecosystem services, their components and species richness per vegetation type.** For the three mean vegetation types in PNP, i.e. swamp wood (SW, n = 8), swamp forest (SF, n = 8) and swamp forest dominated by *Euterpe oleracea* (SFE, n = 8), the following variables are given: Richness = species richness per 0.04 ha; AGC\_plot = aboveground carbon (Kg per 0.04 ha); NTFP\_density = number of stems belonging to individuals producing non-timber forest products per 0.04 ha; CMW\_WD\_n = community-weighted mean wood density (g cm<sup>-3</sup>); dbh\_avg = community-weighted mean diameter at breast height (cm). For these values, mean, standard deviation, width of the 95% confidence interval and its lower and upper boundaries, minimum and maximum observed values are given.

type	variable	mean	sd	ci	lwr	upr	min	max
SW	Richness	9.875	1.642	1.373	8.502	11.248	8	13
SF	Richness	11.25	2.915	2.437	8.813	13.687	8	17
SFE	Richness	9.875	1.959	1.638	8.237	11.513	8	14
SW	AGC_plot	3975.174	2286.973	1911.957	2063.217	5887.131	1879.48	8729.028
SF	AGC_plot	3484.477	799.474	668.377	2816.1	4152.854	2148.427	4271.73
SFE	AGC_plot	3585.595	1680.622	1405.035	2180.56	4990.63	1711.437	6944.884
SW	NTFP_density	14.25	6.159	5.149	9.101	19.399	4	24
SF	NTFP_density	15.75	8.311	6.948	8.802	22.698	6	28
SFE	NTFP_density	51	23.857	19.945	31.055	70.945	17	84
SW	Stem_density	34.25	9.407	7.865	26.385	42.115	19	48
SF	Stem_density	48.125	14.827	12.396	35.729	60.521	26	63
SFE	Stem_density	76.5	15.081	12.608	63.892	89.108	55	99
SW	CMW_WD_n	0.461	0.03	0.025	0.436	0.486	0.422	0.499
SF	CMW_WD_n	0.533	0.053	0.045	0.488	0.578	0.446	0.62
SFE	CMW_WD_n	0.454	0.033	0.027	0.427	0.481	0.415	0.507
SW	dbh_avg	15.218	2.259	1.888	13.33	17.106	12.64	18.964
SF	dbh_avg	13.823	3.175	2.654	11.169	16.477	11.418	18.973
SFE	dbh_avg	11.981	1.391	1.163	10.818	13.144	9.742	13.854



**Figure S.2.6. Total abundance of trees and arborescent palms in PNP for sampled area.** The total number of stems summed over all plots in PNP for each tree or arborescent palm.



**Figure S.2.7. Linear relationship between species average diameter at breast height and wood density for Primary swamp forest.** For two primary swamp forest reference plots, for all species observed the average diameter at breast height (DBH) was calculated based on plot data. Average DBH was not related to species wood density (WD) ( $p > 0.05$ ).



## Supplementary materials 3

### S.3 Supplementary R script for AGC calculation (1970 vs 2024)

Below, the R script is given for the calculation of the total AGC, species richness per 0.04 ha and NTFP abundance (# stems per 0.04 ha) for PNP anno 1970 and anno 2024. To do so, the number of small & wide beds containing coffee and the number of small and wide beds containing cacao are calculated for the survey area. This is done by selecting the area of the main vegetation types in the survey area, and calculating the number of small and wide beds (coffee or cacao) for this area. Then, the number of *Coffea liberica*/*Coffea arabica*/*Theobroma cacao* trees and the number of *Erythrina fusca* individuals is estimated per bed and subsequently for the whole area. Then, AGC is calculated by taking the average DBH of these species and wood density as input for the moist tropical forest equation by Chave (2005). The NTFP abundance is calculated per 0.04 ha, taking the average number of coffee/cacao trees on 0.04 ha. Woody species richness per 0.04 ha was simply the amount of species on a bed, which is two (*E. fusca* and either *C. liberica*/*C. arabica* or *T. cacao*).

For 2024, mean AGC and sd is calculated as well. For each vegetation type, the mean AGC per plot is calculated, converted to mean AGC  $m^{-2}$  and then multiplied by the area of the vegetation type. Finally the three different AGC estimates are added. For 2024, mean species richness is calculated as well. For each vegetation type, mean species richness is calculated per plot. Then, a weighted average of species richness is taken, with the area of the vegetation types as weights. In the same way, mean NTFP abundance is calculated per vegetation type, and used in a weighted average to calculate total NTFP abundance.

```
#-----AGC 1970-----  
  
# The plantation was divided into small and wide beds. For the area which we sampled:  
# The area of the small beds encompasses 346365 (SF) + 582019 (SFE) = 928384 m^2  
# The area of the wide beds encompasses 389313 (SW) + 1015689 (SF) = 1405002 m^2  
  
# ----- small beds -----  
  
# SFE forest all cacao, small beds  
# SFE_area = 582019  
# Small bed = 7 m x 120 m = 840 m^2 # this includes the canal in between  
  
# n beds = 582019/840 = 692  
#   n T. cacao per bed = 2*(120/4)= 60 trees # 2 rows with 4 m in between trees  
#   n E. fusca per bed = (120/4)-1 = 29 # 1 row in between T. Cacao rows  
#   SFE_cacao = n T.cacao per bed * n beds = 60*692 = 41520  
#   SFE_fusca = n E. Fusca per bed * n beds = 29*692 = 20068  
  
# SF forest contains both cacao and coffee beds, wide and small  
# SF_small_cacao area = 138055  
# amount of beds = 138055/840 = 164  
# SF_cacao_small = 164*60 = 9840  
# SF_fusca_small = 164*29 = 4756 #n erythrina fusca for small beds with cacao  
  
# SF forest small coffee
```

```
# SF small coffee area = 212065 + 870 = 212935
# n beds = 212935/840 = 253
# SF_coffee_small = 253*60 = 15180
# SF_coffusca_small = 253*29 = 7337 #n erythrina fusca for small beds with coffee
```

```
#----- wide beds -----
```

```
# SF wide beds cacao
# SF_wide_cacao area = 607599
# Wide bed = 8 m x 120 m = 960 m^2
# n beds = 607599/960 = 632
# amount of cacao trees in a row = 120/5 = 24
# amount of cacao trees on the bed = 2*24+23 = 71 #three rows of T. cacao per bed
# amount of E. fusca on the bed = 23 # one row of E. fusca in the middle
# SF_cacao_wide = 632*71 = 44872
# SF_fusca_wide = 632*23 = 14536
```

```
# SF & SW wide beds coffee
# SF_wide_coffee area = 790336
# SF_wide_coffee beds = 790336/960 = 823
# SF_coffee_wide = 823*71 = 58433
# SF_coffusca_wide = 823*23 = 18929
```

```
#-----
```

```
# so in total n coffee trees = SF_coffee_wide + SF_coffee_small = 73613
# n cacao trees = SFE_cacao + SF_cacao_small + SF_cacao_wide = 96232
# n fusca trees = SFE_fusca + SF_fusca_small + SF_coffusca_small + SF_fusca_wide + SF_coffusca_wide =
65626
```

```
n_coffea = 73613 #
n_cacao = 96232
n_fusca = 65626
```

```
# carbon for peperpot ~ 1970
WoodDensity <- function(df){
  df$AGB <- df$WD * exp(
    -1.499+2.148 * log(df$DBH)+0.207* (log(df$DBH)^2) -0.0281 * (log(df$DBH)^3)
  )
  df$AGC <- df$AGB*0.474
  return(df)
}
```

```
df_peperpot <- data.frame(
  N_species = c(n_coffea, n_cacao, n_fusca),
  specs_identity = c("Coffea liberica", "Theobroma cacao", "Erythrina fusca"),
  DBH = c(15, 15, 30.0),
```

```

WD = c(0.7, 0.420, 0.298465))

# calculate AGB and AGC for the specs then multiply by amount of specs
df_peperpot <- WoodDensity(df_peperpot)

df_peperpot$total_AGC = df_peperpot$N_species*df_peperpot$AGC

# so the total carbon for peperpot
AGC_1970 <- sum(df_peperpot$total_AGC)

#----- Carbon storage current situation Peperpot -----

# mean AGC per plot * area type
# mean AGC per type
AGC_SFE = mean(Plot_summary$AGC_plot[Plot_summary$type == "SFE"])/400 # / 20 m x20 m, so AGC *
m^-2
AGC_SF = mean(Plot_summary$AGC_plot[Plot_summary$type == "SF"])/400
AGC_SW = mean(Plot_summary$AGC_plot[Plot_summary$type == "SW"])/400

AGC_SFE_sd = sd(Plot_summary$AGC_plot[Plot_summary$type == "SFE"])/400
AGC_SF_sd = sd(Plot_summary$AGC_plot[Plot_summary$type == "SF"])/400
AGC_SW_sd = sd(Plot_summary$AGC_plot[Plot_summary$type == "SW"])/400

# areas of vegtypes (m^2)
Area_SFE = 582019
Area_SF = 1362054
Area_SW = 389313 #m^2

# AGC per type
AGC_total_SFE = AGC_ES*Area_SFE
AGC_total_SF = AGC_SF*Area_SF
AGC_total_SW = AGC_MM*Area_SW

AGC_2024 = sum(AGC_total_SFE, AGC_total_SF, AGC_total_SW)

#total sd
AGC_2024_sd = sum(Area_SFE*AGC_SFE_sd + Area_SF*AGC_SF_sd + Area_SW*AGC_SW_sd)

#----- calculate mean species richness of PNP anno 2024-----

# mean species richness per type
SR_SFE = mean(Plot_summary$Richness[Plot_summary$type == "SFE"])
SR_SF = mean(Plot_summary$Richness[Plot_summary$type == "SF"])
SR_SW = mean(Plot_summary$Richness[Plot_summary$type == "SW"])

SR_SFE_sd = sd(Plot_summary$Richness[Plot_summary$type == "SFE"])

```

```

SR_SF_sd = sd(Plot_summary$Richness[Plot_summary$type == "SF"])
SR_SW_sd = sd(Plot_summary$Richness[Plot_summary$type == "SW"])

# areas of vegtypes (m^2)
Area_SFE = 582019
Area_SF = 1362054
Area_SW = 389313 #m^2

Total_Area = Area_SFE+Area_SW+Area_SF

# total mean sr per 0.04 ha
# give vegetation types weight of the area
SR_total = SR_SFE * (Area_SFE/Total_Area) + SR_SF * (Area_SF/Total_Area) + SR_SW *
(Area_SW/Total_Area)

# total sd
SR_sd_total = SR_SFE_sd * (Area_SFE/Total_Area) + SR_SF_sd * (Area_SF/Total_Area) + SR_SW_sd *
(Area_SW/Total_Area)

#----- mean NTFP abundance per 0.04 ha anno 2024-----
NTFP_SFE = mean(Plot_summary$NTFP_density[Plot_summary$type == "SFE"]) # / 20 m x20 m, so AGC *
m^-2
NTFP_SF = mean(Plot_summary$NTFP_density[Plot_summary$type == "SF"])
NTFP_SW = mean(Plot_summary$NTFP_density[Plot_summary$type == "SW"])

NTFP_SFE_sd = sd(Plot_summary$NTFP_density[Plot_summary$type == "SFE"])
NTFP_SF_sd = sd(Plot_summary$NTFP_density[Plot_summary$type == "SF"])
NTFP_SW_sd = sd(Plot_summary$NTFP_density[Plot_summary$type == "SW"])

# areas of vegtypes (m^2)
Area_SFE = 582019
Area_SF = 1362054
Area_SW = 389313 #m^2

Total_Area = Area_SFE+Area_SW+Area_SF

# total mean sr per 0.04 ha

```

# give vegetation types weight of the area

$$\text{NTPF\_total} = \text{NTPF\_SFE} * (\text{Area\_SFE}/\text{Total\_Area}) + \text{NTPF\_SF} * (\text{Area\_SF}/\text{Total\_Area}) + \text{NTPF\_SW} * (\text{Area\_SW}/\text{Total\_Area})$$

# total sd

$$\text{SR\_sd\_total} = \text{NTPF\_SFE\_sd} * (\text{Area\_SFE}/\text{Total\_Area}) + \text{NTPF\_SF\_sd} * (\text{Area\_SF}/\text{Total\_Area}) + \text{NTPF\_SFE\_sd} * (\text{Area\_SFE}/\text{Total\_Area})$$

## Supplementary materials 4

### S.4 Test statistics and QQplots

#### S.4.1 test statistics Fig. 3.2.

**Table S.4.1.1.** Output Kruskal-Wallis test AGC ~ vegetation\_types.

	<b>n</b>	<b>statistic</b>	<b>df</b>	<b>p</b>	<b>method</b>
AGC_plot	24	0.0350	2	0.983	Kruskal-Wallis

**Table S.4.1.2.** Output ANOVA CWM WD ~ vegetation\_types.

	<b>Df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F value</b>	<b>Pr(&gt;F)</b>
Type	2	0.03068	0.015342	9.561	0.00112 **
Residuals	21	0.03370	0.001605		

**Table S.4.1.3.** Output Tukey Kramer post-hoc test CWM WD ~ vegetation\_types.

<b>Comparison</b>	<b>diff</b>	<b>lwr</b>	<b>upr</b>	<b>p adj</b>
SF-SW	0.072144420	0.02165960	0.12262924	0.0045742
SFE-SW	-0.006935488	-0.05742031	0.04354934	0.9362426
SFE-SF	-0.079079909	-0.12956473	-0.02859508	0.0020362

**Table S.4.1.4.** Output ANOVA stem density ~ vegetation\_types.

	<b>Df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F value</b>	<b>Pr(&gt;F)</b>
type	2	7421	3710	20.78	1.05e-05 ***
Residuals	21	3750	179		



**Table S.4.1.5.** Output Tukey Kramer post-hoc test stem density ~ vegetation\_types.

Comparison	diff	lwr	upr	p adj
SF-SW	13.875	-2.96711	30.71711	0.1190791
SFE-SW	42.250	25.40789	59.09211	0.0000083
SFE-SF	28.375	11.53289	45.21711	0.0010078

**Table S.4.1.6.** Output Kruskal-Wallis test CWM DBH ~ vegetation\_types.

	n	statistic	df	p	method
dbh_avg	24	6.54	2	0.038	Kruskal-Wallis

**Table S.4.1.7.** Output Dunn's post-hoc test CWM DBH ~ vegetation\_types.

	group1	group2	n1	n2	statistic	p	p.adj	p.adj.signif
1 dbh_avg	SW	SF	8	8	-1.48	0.138	0.413	ns
2 dbh_avg	SW	SFE	8	8	-2.55	0.0109	0.0327	*
3 dbh_avg	SF	SFE	8	8	-1.06	0.289	0.867	ns

**Table S.4.1.8.** Output Kruskal-Wallis test NTFP ~ vegetation\_types.

	n	statistic	df	p	method
NTFP_density	24	12.7	2	0.00179	Kruskal-Wallis

**Table S.4.1.9.** Output Dunn's post-hoc test NTFP ~ vegetation\_types.

	group1	group2	n1	n2	statistic	p	p.adj	p.adj.signif
1 NTFP_density	SW	SF	8	8	0.142	0.887	1	ns
2 NTFP_density	SW	SFE	8	8	3.15	0.00164	0.00492	**
3 NTFP_density	SF	SFE	8	8	3.01	0.00264	0.00791	**

**Table S.4.1.10** Output ANOVA Species richness ~ vegetation\_types.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
type	2	10.08	5.042	1.006	0.383
Residuals	21	105.25	5.012		

## S.4.2 test statistics linear regressions

**Table S.4.2.1** Output linear models with  $\ln(\text{AGC})$  (= logAGC) and species richness (Richness).

Model	Adj_R_Squared	Predictors	Estimates	Std_Errors	T_Values	P_Values
<i>logAGC ~ Richness * type</i>	0.0492	Richness	0.191273	0.09379	2.039383	0.05637
		typeSF	1.896571	1.11914	1.694668	0.107369
		typeSFE	2.891921	1.225462	2.359863	0.029775
		Richness:typeSF	-0.19455	0.107643	-1.80735	0.087451
		RichnesstypeSFE	-0.29991	0.12237	-2.45086	0.0247
<i>logAGC ~ Richness + type</i>	-0.1437	Richness	0.00471	0.043563	0.108118	0.914979
		typeSF	-0.03557	0.231346	-0.15377	0.879334
		typeSFE	-0.06971	0.223457	-0.31196	0.758298
<i>logAGC ~ Richness</i>	-0.0448	Richness	0.004664	0.039775	0.117267	0.907713

**Table S.4.2.2** Output linear models with  $\ln(\text{AGC})$  (= logAGC) and CWM WD (WD).

Model	Adj_R_Square	Predictor	Estimate	Std_Error	T_Value	P_Values
	d	s	s	s	s	
<i>logAGC ~ WD * type</i>	-0.032	WD	5.305	5.385	0.985	0.337648
		SF	3.036	2.963	1.025	0.31901
		SFE	6.258	3.335	1.876	0.07692
		WD:SF	-6.467	6.167	-1.049	0.308225
		WD:SFE	-13.854	7.269	-1.906	0.072756
<i>logAGC ~ WD + type</i>	-0.119	WD	-1.627	2.408	-0.676	0.506978
		SF	0.088	0.281	0.314	0.756739
		SFE	-0.081	0.222	-0.365	0.71863
<i>logAGC ~ WD</i>	-0.035	WD	-0.785	1.676	-0.469	0.643843

**Table S.4.2.3** Output linear models with NTFP and species richness (Richness).

Model	Adj_R_Squared	Predictors	Estimates	Std_Errors	T_Values	P_Values
<i>NTFP ~ Richness*Vegetation_types</i>	0.53	Richness	1.603	3.552	0.451	0.657207
		SF	-7.348	42.38	-0.173	0.864281
		SFE	72.785	46.406	1.568	0.134191
		Richness:SF	0.591	4.076	0.145	0.886405
		Richness:SFE	-3.649	4.634	-0.787	0.441249
<i>NTFP ~ Richness+Vegetation_types</i>	0.543	Richness	1.005	1.483	0.678	0.505718
		SF	0.118	7.873	0.015	0.988144
		SFE	36.75	7.605	4.832	0.000101
<i>NTFP ~ Richness</i>	-0.045	Richness	-0.156	2.143	-0.073	0.942598

**Table S.4.2.4** Output linear models with CWM DBH and species richness (Richness).

Model	Adj_R_Squared	Predictors	Estimates	Std_Errors	T_Values	P_Values
<i>CWM_DBH ~ Richness*Vegetation_types</i>	0.256	Richness	-0.032	0.527	-0.061	0.952204
		SF	4.762	6.288	0.757	0.458645
		SFE	1.011	6.885	0.147	0.884927
		Richness:SF	-0.543	0.605	-0.899	0.380762
		Richness:SFE	-0.43	0.688	-0.626	0.539325
<i>CWM_DBH ~ Richness+Vegetation_types</i>	0.3	Richness	-0.449	0.216	-2.075	0.051079
		SF	-0.778	1.149	-0.677	0.506189
		SFE	-3.238	1.11	-2.917	0.008528
<i>CWM_DBH ~ Richness</i>	0.071	Richness	-0.396	0.238	-1.661	0.110909

**Table S.4.2.5** Output linear models with CWM WD and species richness (Richness).

Model	Predictors	Estimates	Std_Errors	T_Values	P_Values	Adj_R2
<i>CWM WD ~ Richness*Vegetation_types</i>	Richness	0.004	0.009	0.439	0.665834	0.406
	SF	0.102	0.112	0.907	0.376399	
	SFE	-0.077	0.123	-0.628	0.537816	
	Richness:SF	-0.003	0.011	-0.29	0.775369	
	Richness:SFE	0.007	0.012	0.58	0.569346	
<i>CWM WD ~ Richness+Vegetation_types</i>	Richness	0.004	0.004	1.072	0.296631	0.431
	SF	0.066	0.021	3.214	0.004355	
	SFE	-0.007	0.02	-0.347	0.731852	
<i>CWM WD ~ Richness</i>	Richness	0.009	0.005	1.836	0.07988	0.093

**Table S.4.2.6** Output linear models with stem density and species richness (Richness).

Model	Adj_R_Squared	Predictors	Estimates	Std_Errors	T_Values	P_Values
<i>Stem_density ~ Richness*Vegetation_types</i>	0.698	Richness	1.603	2.787	0.575	0.572338
		SF	-17.71	33.252	-0.533	0.600835
		SFE	53.116	36.411	1.459	0.161857
		Richness:SF	2.612	3.198	0.817	0.42485
		Richness:SFE	-1.1	3.636	-0.303	0.765642
<i>Stem_density ~ Richness+Vegetation_types</i>	0.699	Richness	2.798	1.179	2.373	0.027771
		SF	10.028	6.262	1.601	0.124955
		SFE	42.25	6.048	6.986	8.86E-07
<i>Stem_density ~ Richness</i>	0.002	Richness	2.092	2.05	1.021	0.318542

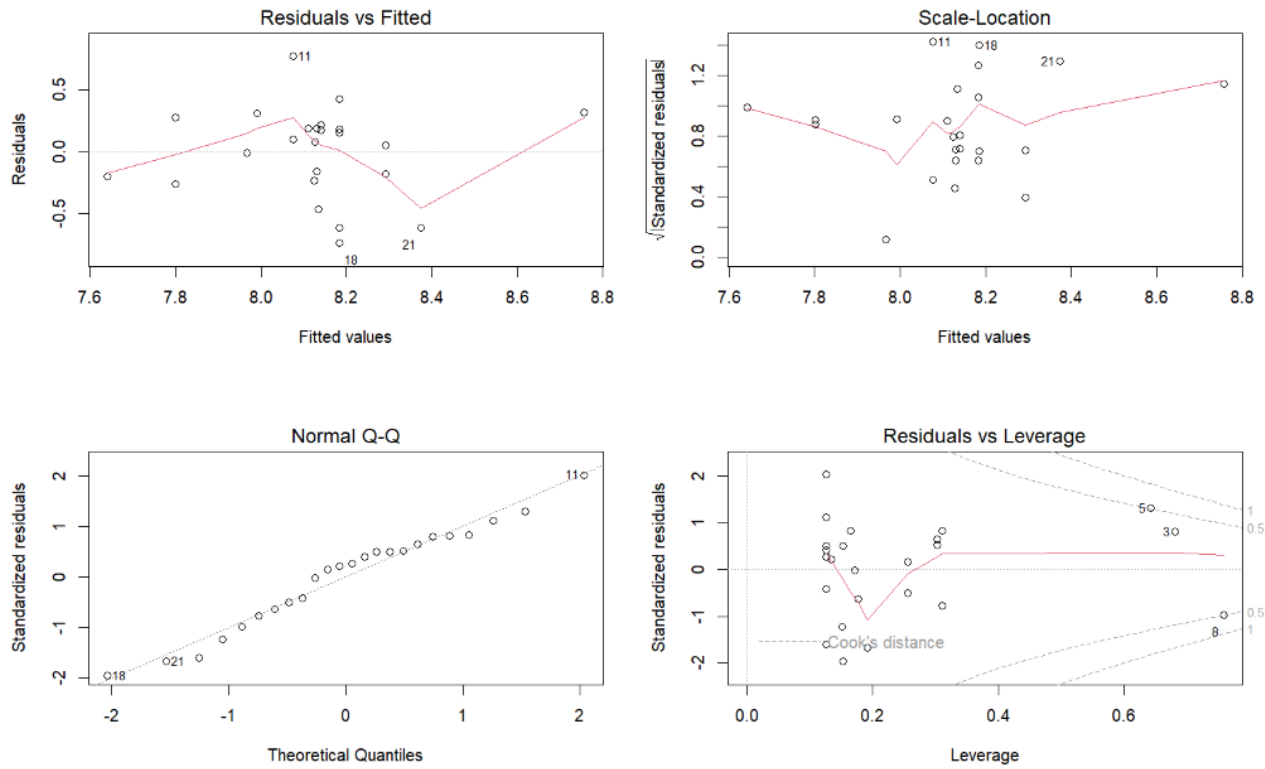


Figure S.4.2.1.a QQplots  $\ln(\text{AGC}) \sim \text{species richness} * \text{vegetation\_types}$

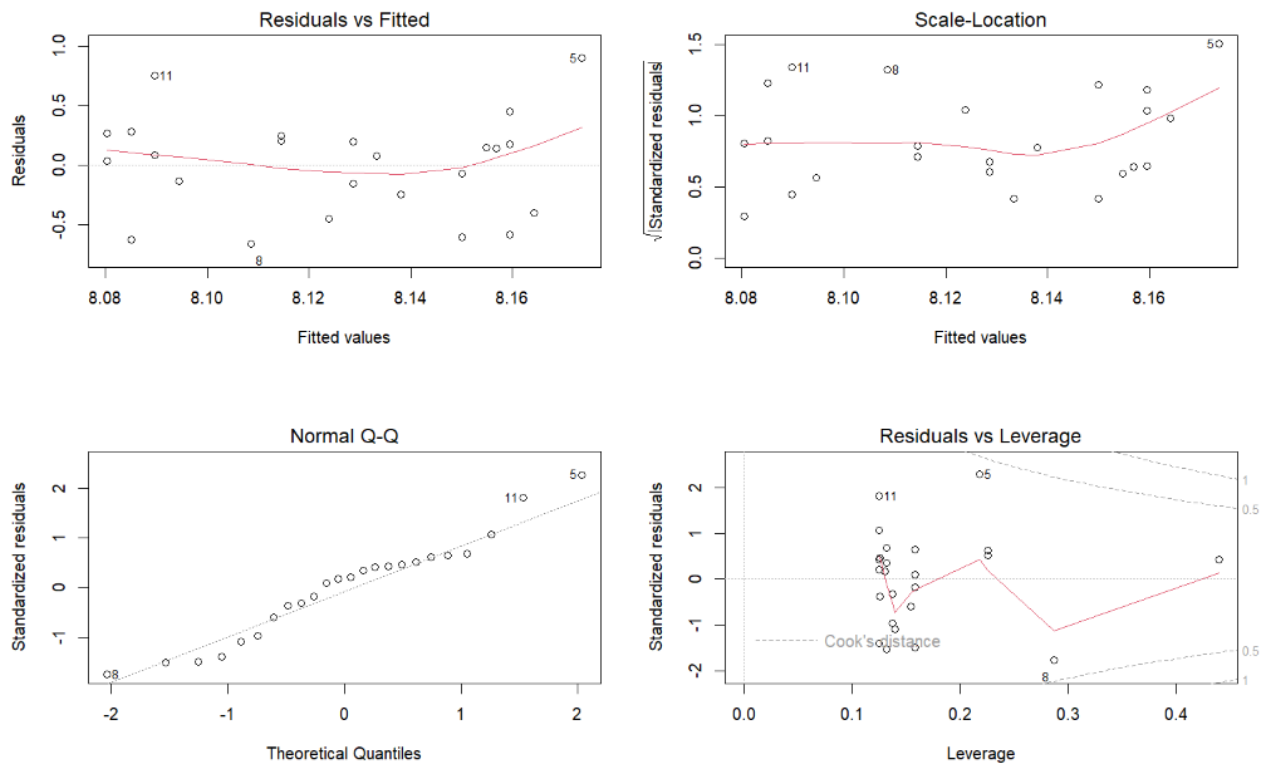


Figure S.4.2.1.b QQplots  $\ln(\text{AGC}) \sim \text{species richness} + \text{vegetation\_types}$



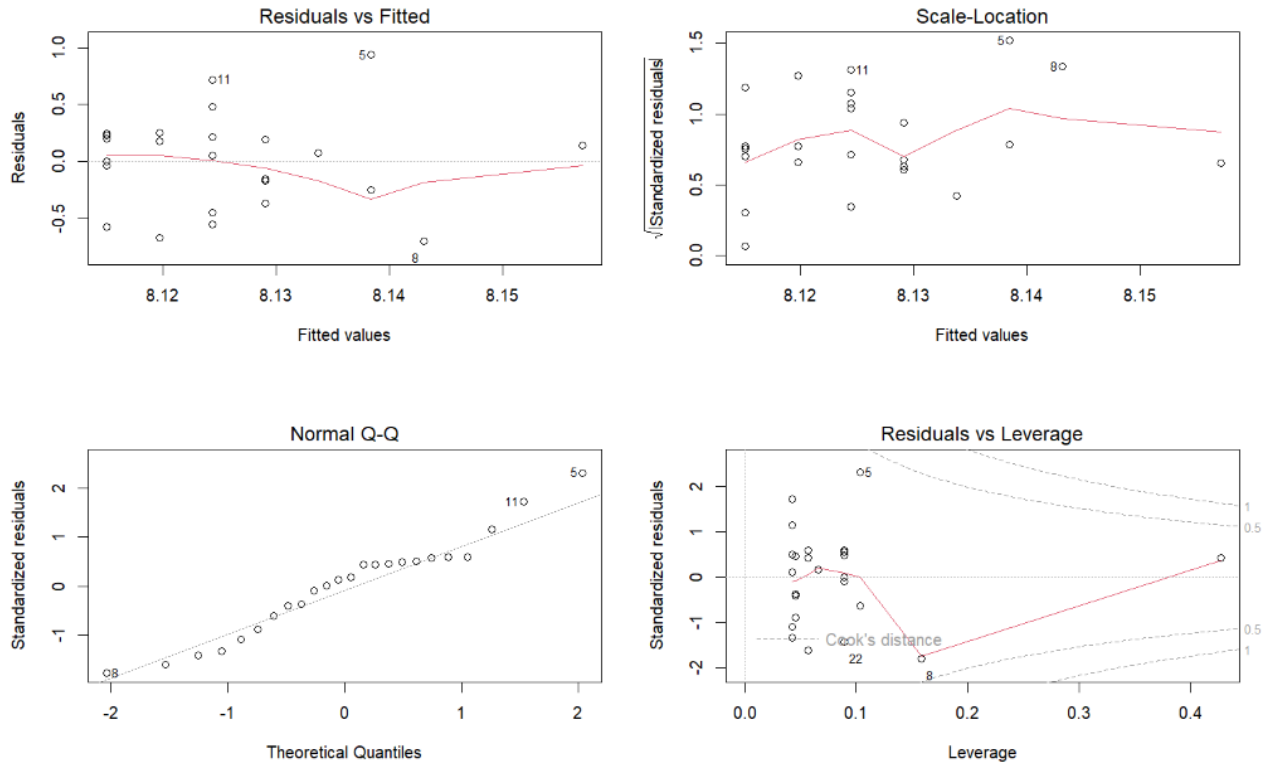


Figure S.4.2.1.c QQplots  $\ln(\text{AGC}) \sim \text{species richness}$

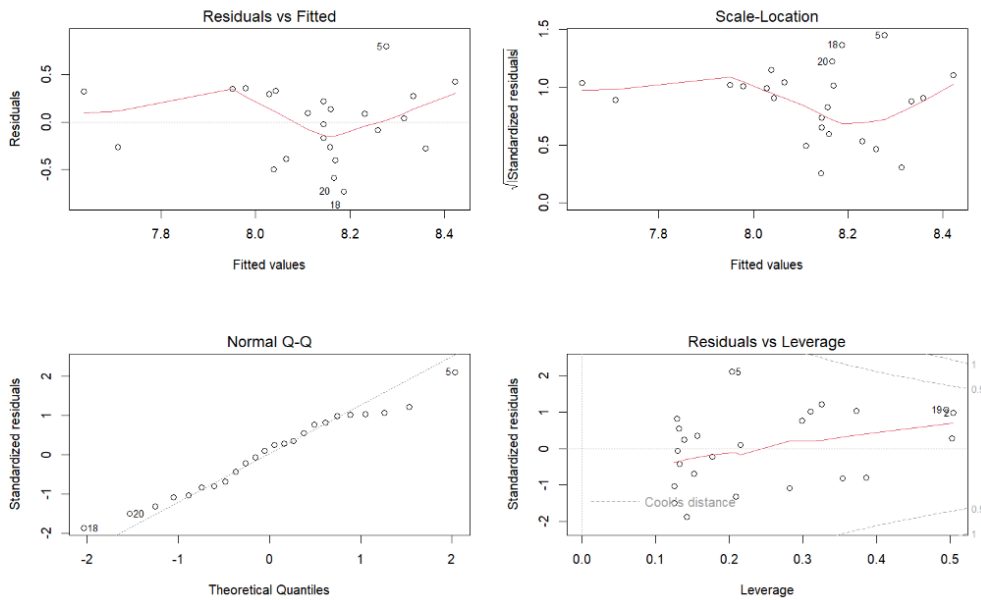
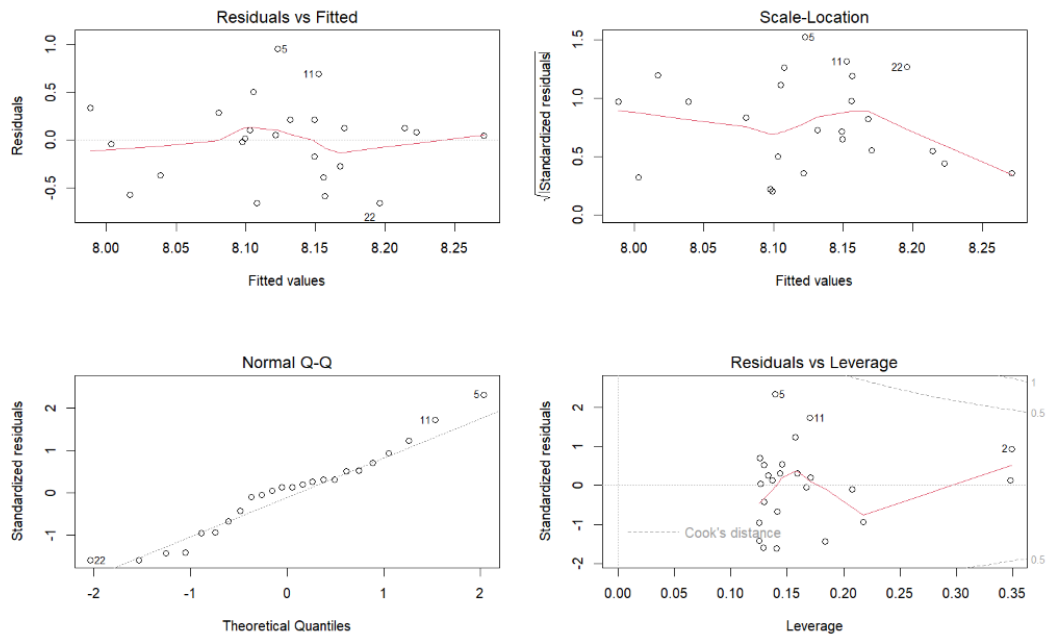
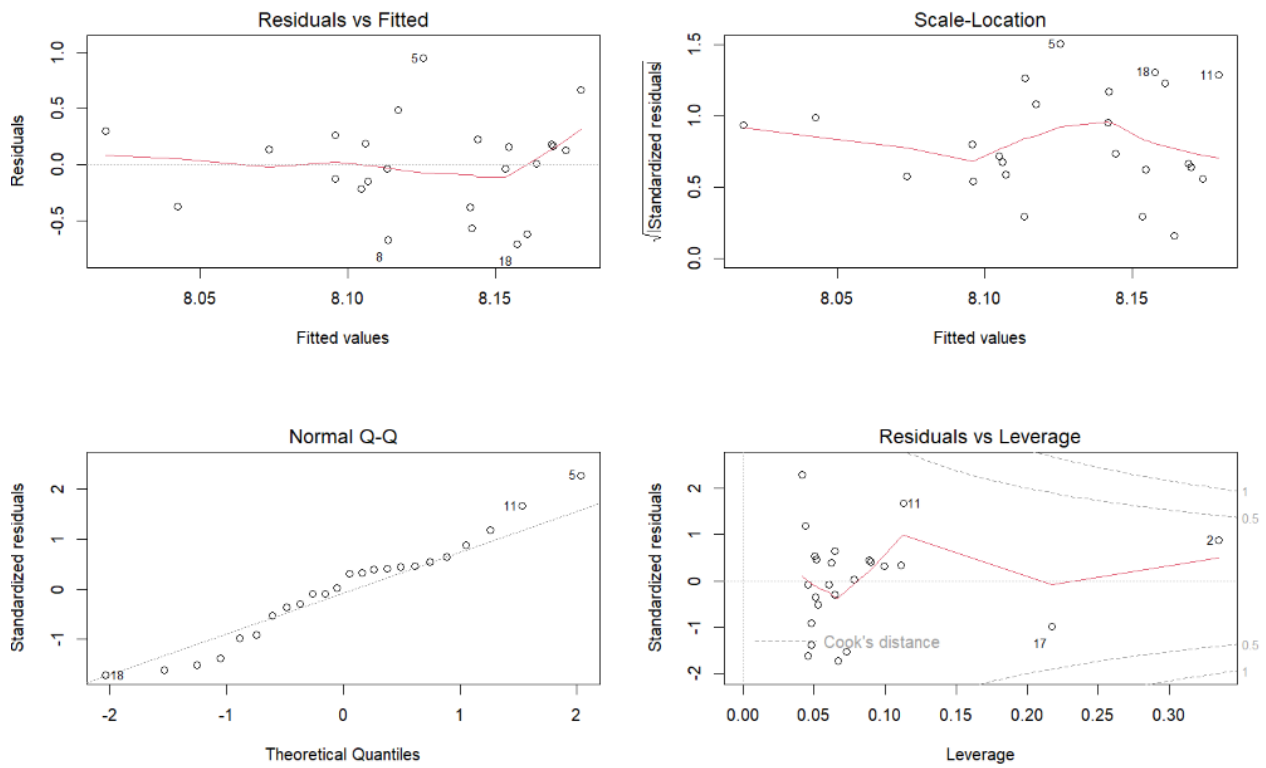


Figure S.4.2.2.a QQplots  $\ln(\text{AGC}) \sim \text{CWM WD} * \text{vegetation\_types}$



**Figure S.4.2.2.b** QQplots  $\ln(\text{AGC}) \sim \text{CWM WD} + \text{vegetation\_types}$



**Figure S.4.2.2.c** QQplots  $\ln(\text{AGC}) \sim \text{CWM WD}$

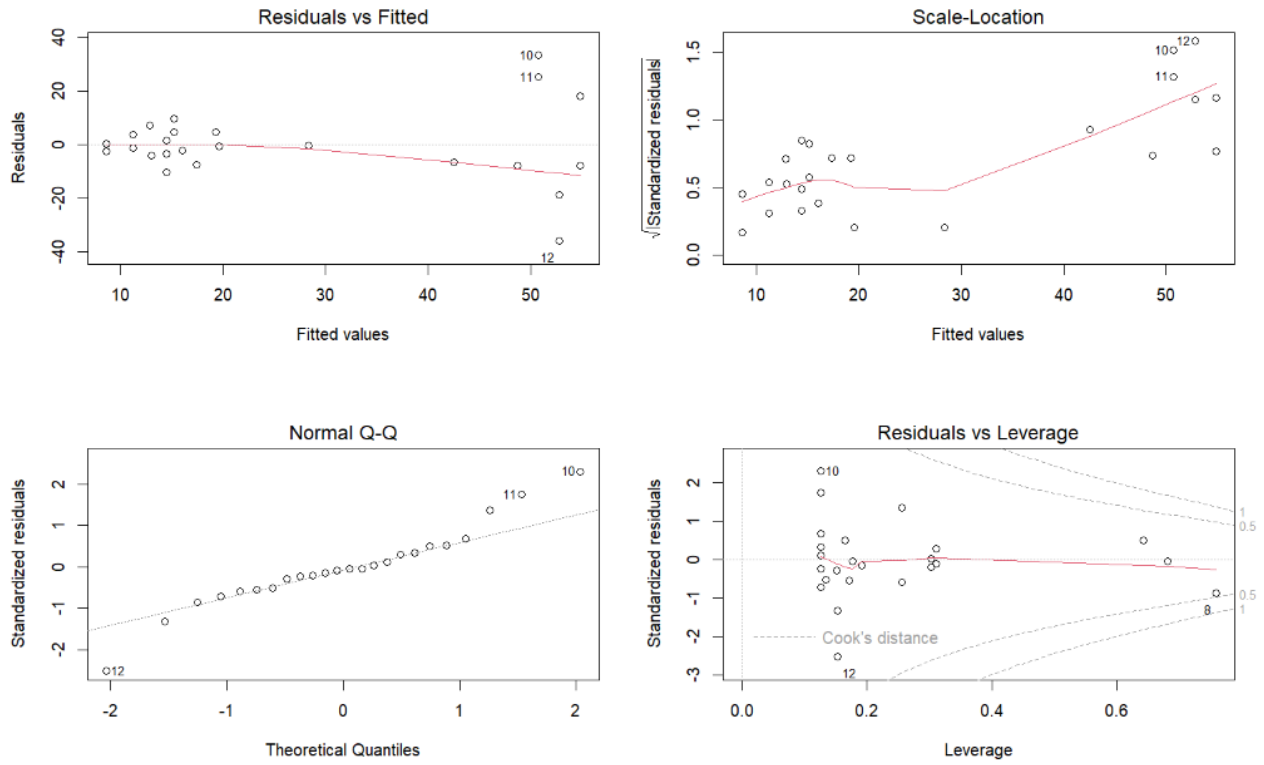


Figure S.4.2.3.a QQplots  $NTFP \sim \text{species richness} * \text{vegetation\_types}$

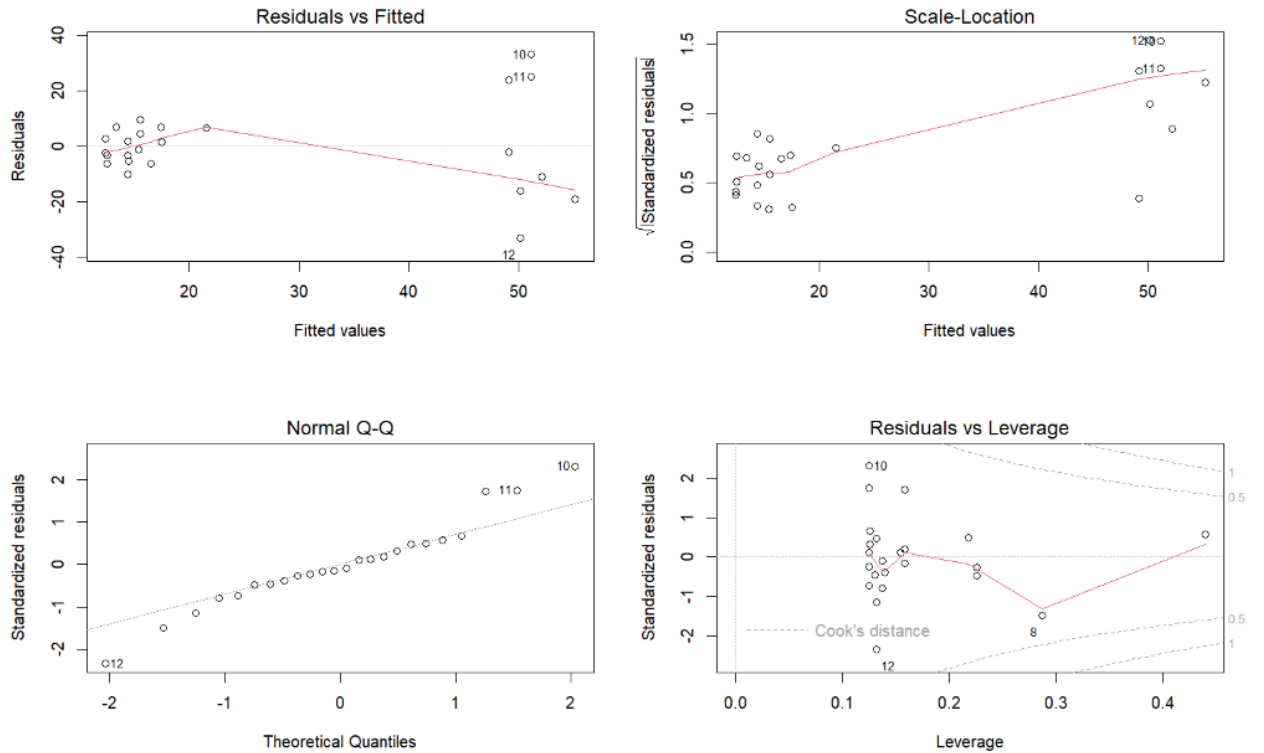


Figure S.4.2.3.b QQplots  $NTFP \sim \text{species richness} + \text{vegetation\_types}$

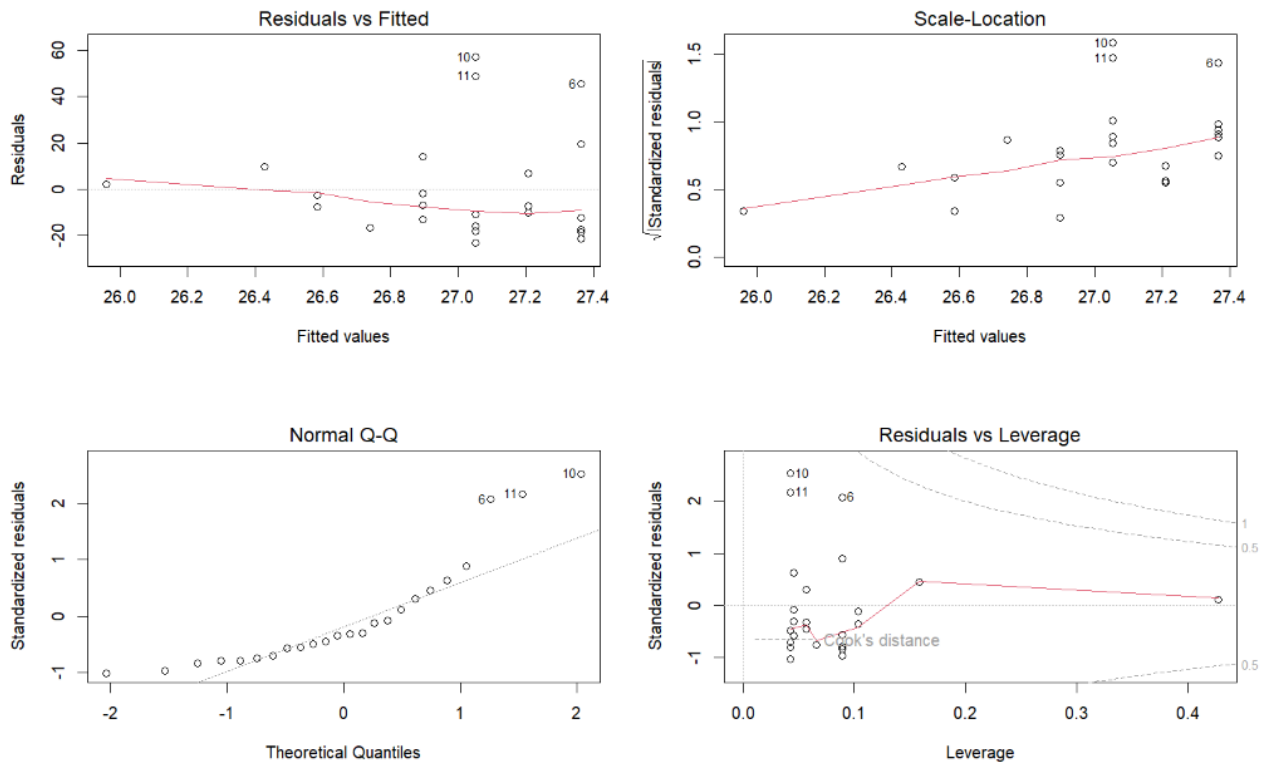


Figure S.4.2.3.c QQplots  $NTFP \sim \text{species richness}$

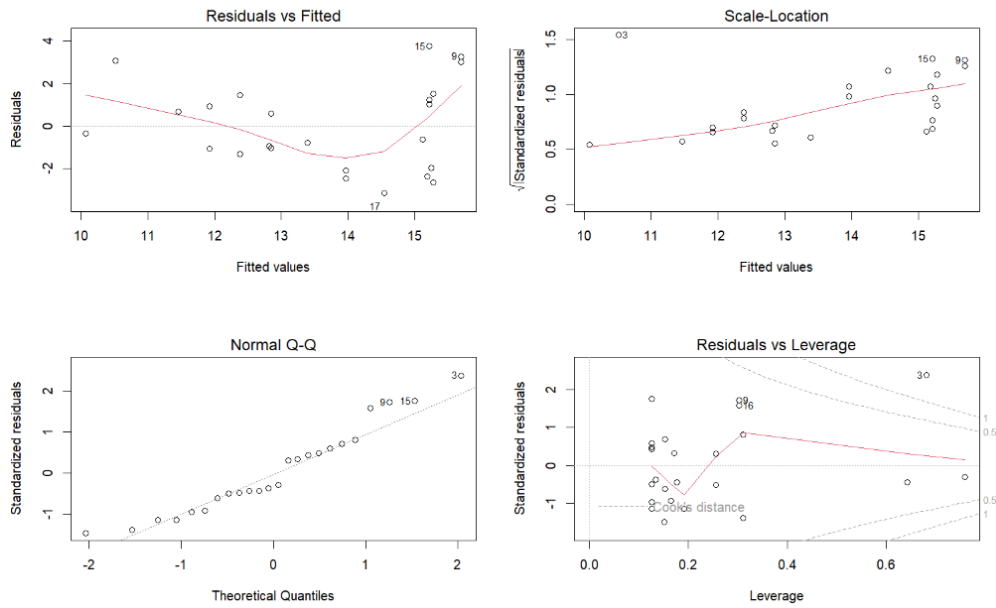
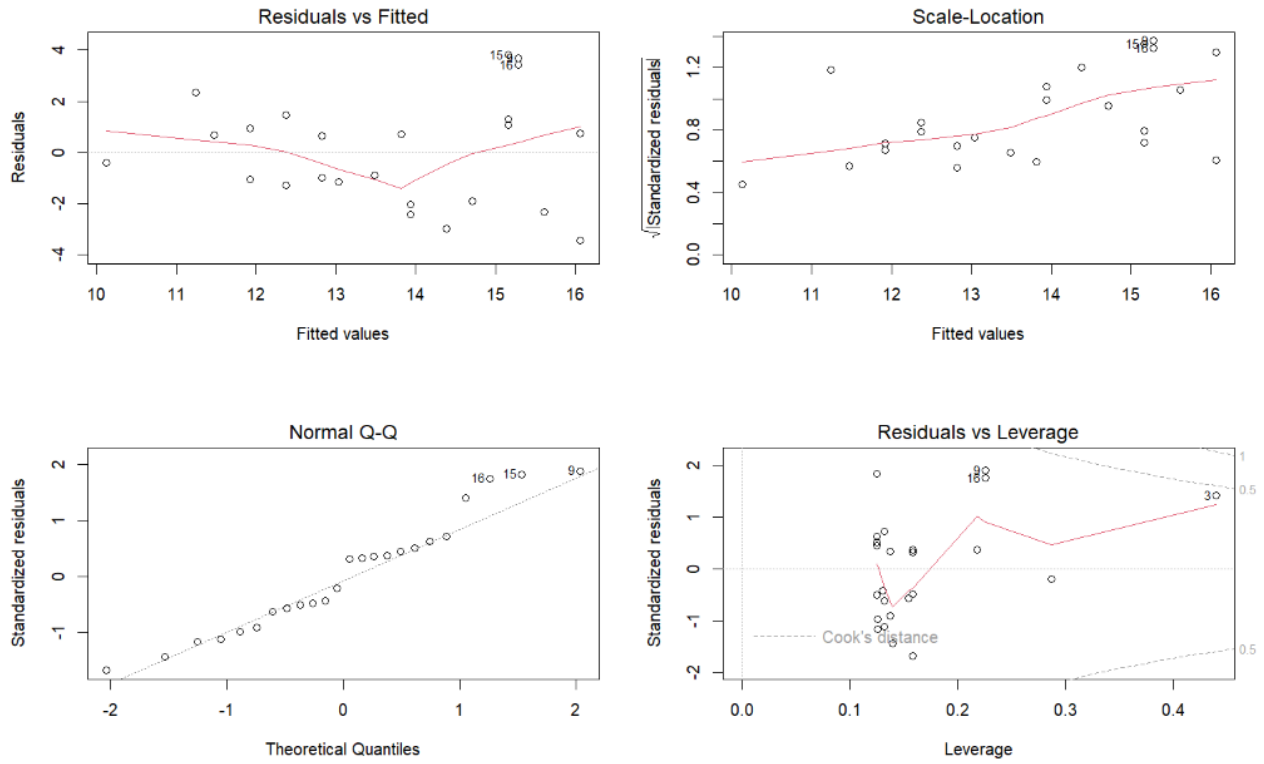
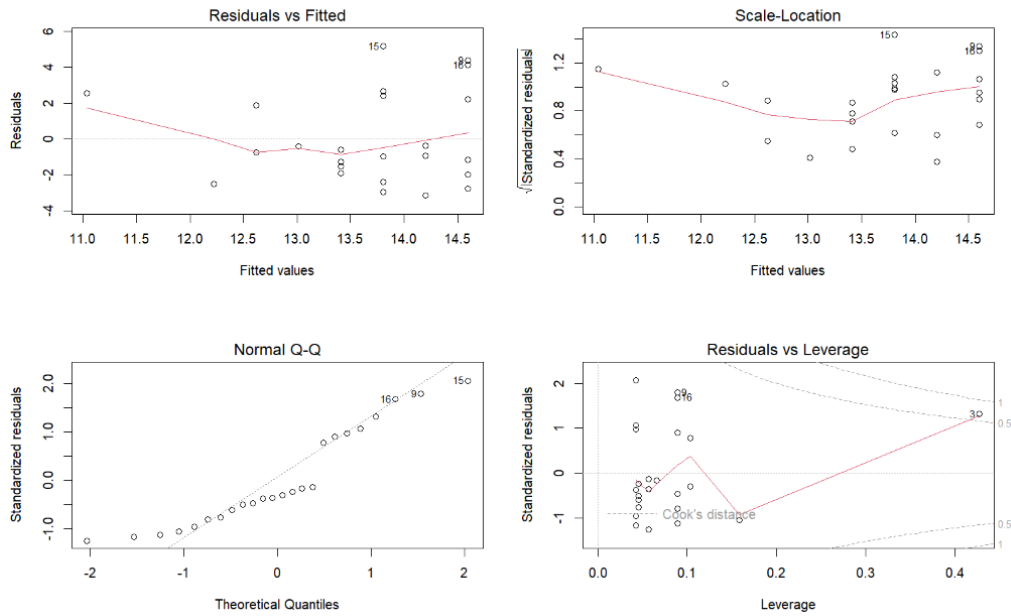


Figure S.4.2.4.a QQplots  $CWM\ DBH \sim \text{species richness} * \text{vegetation\_types}$



**Figure S.4.2.4.b** QQplots CWM DBH  $\sim$  species richness+vegetation\_types



**Figure S.4.2.4.c** QQplots CWM DBH  $\sim$  species richness

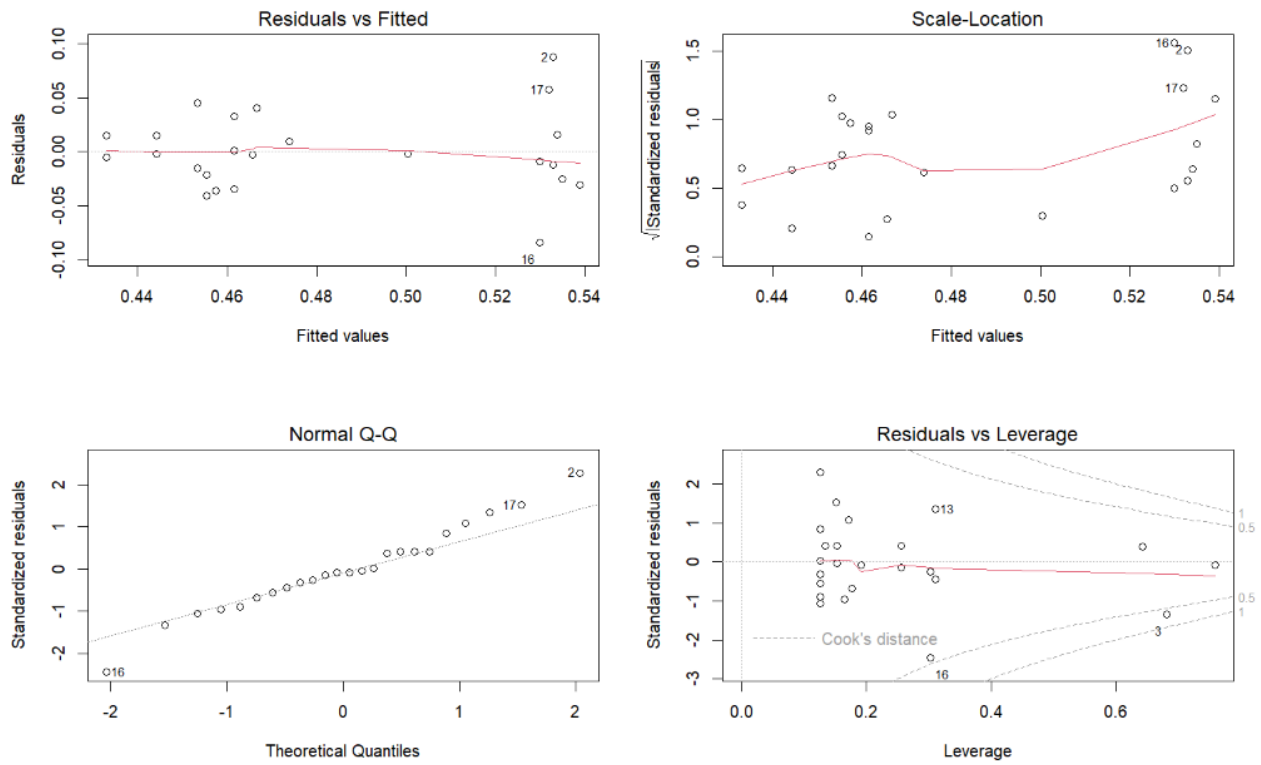


Figure S.4.2.5.a QQplots CWM WD ~ species richness\*vegetation\_types

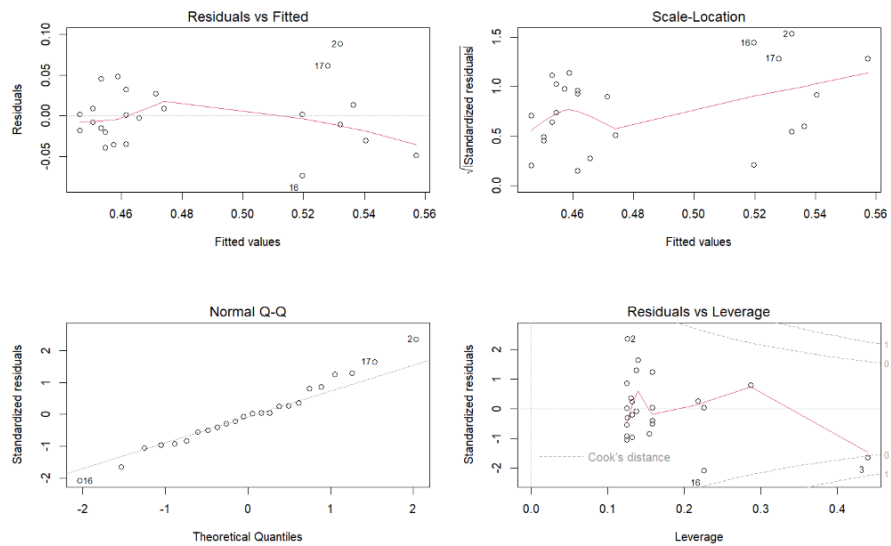


Figure S.4.2.5.b QQplots CWM WD ~ species richness+vegetation\_types



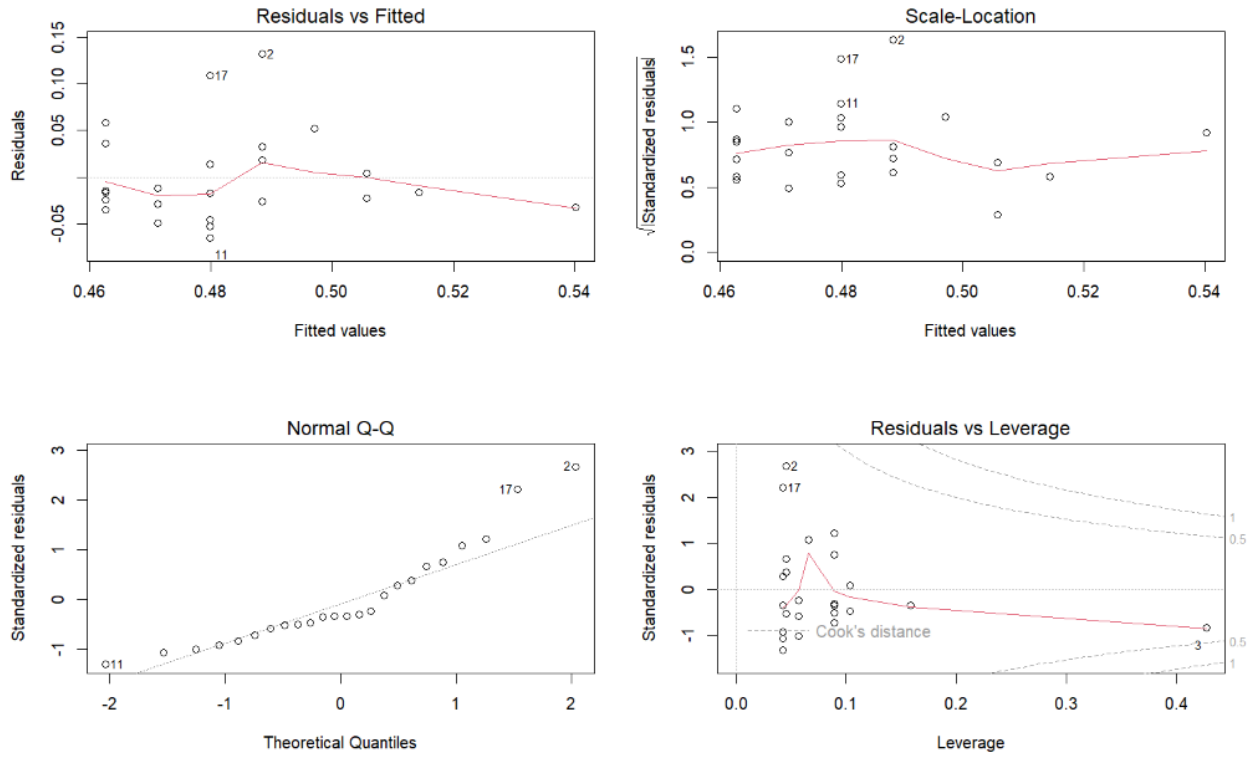


Figure S.4.2.5.c QQplots CWM WD ~ species richness

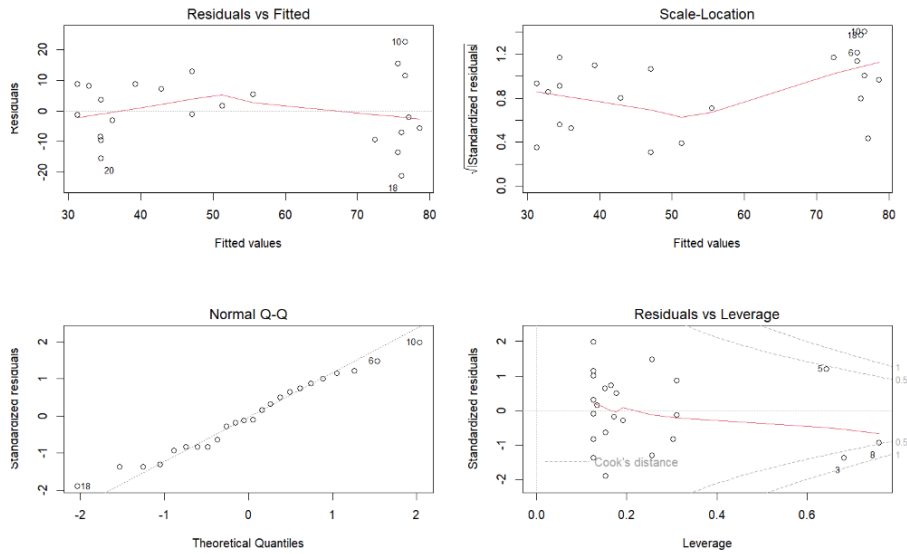


Figure S.4.2.6.a QQplots stem density ~ species richness\*vegetation types

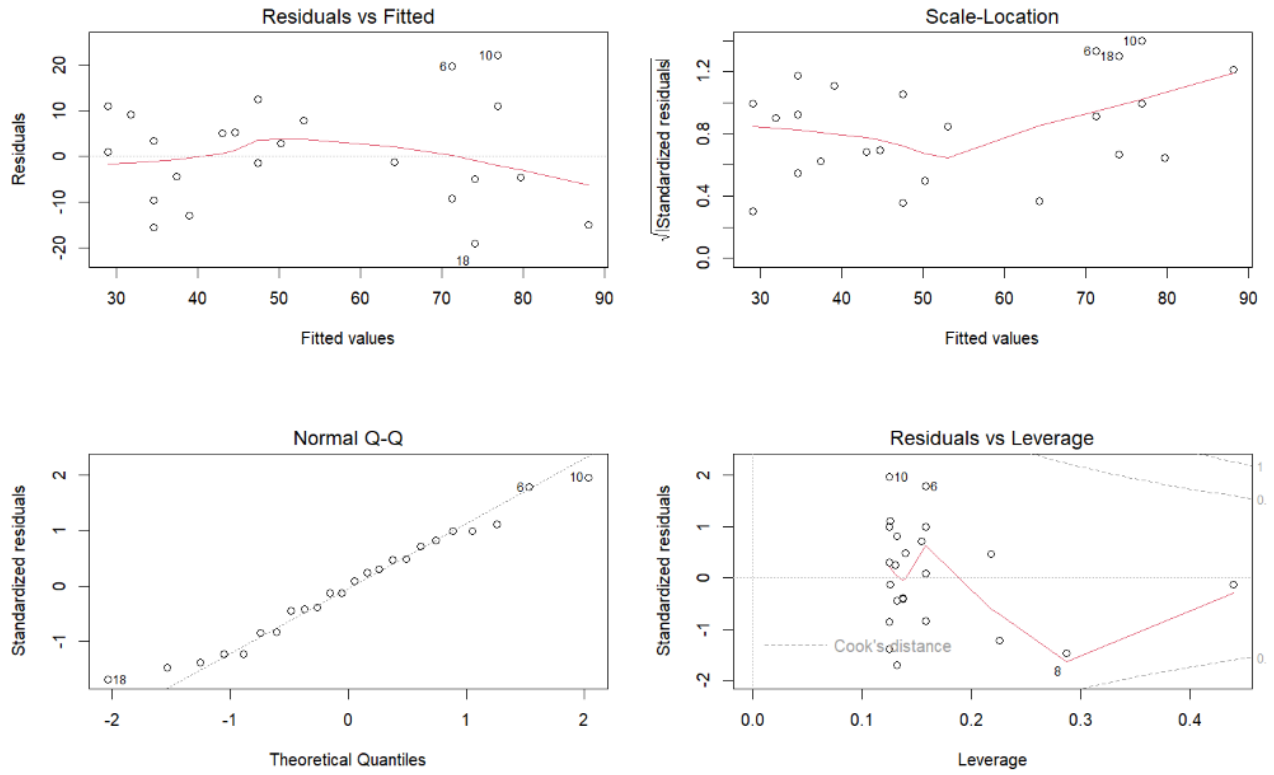


Figure S.4.2.6.b QQplots stem density ~ species richness+vegetation types

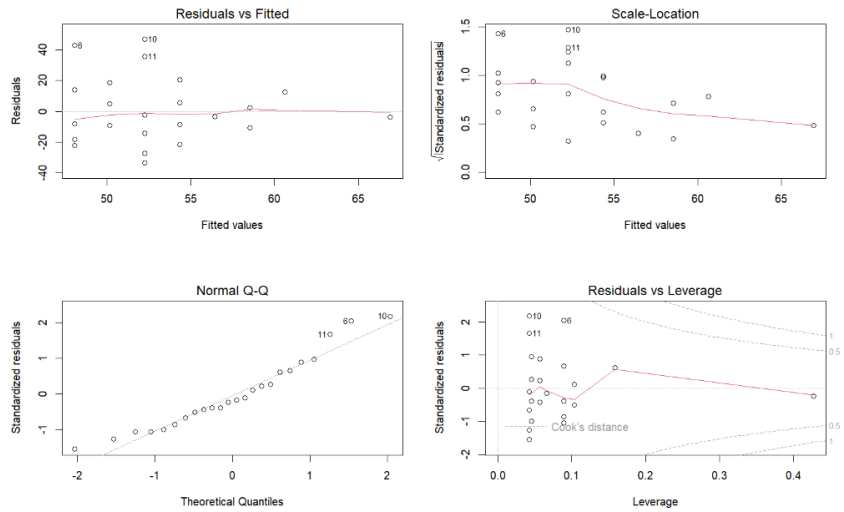
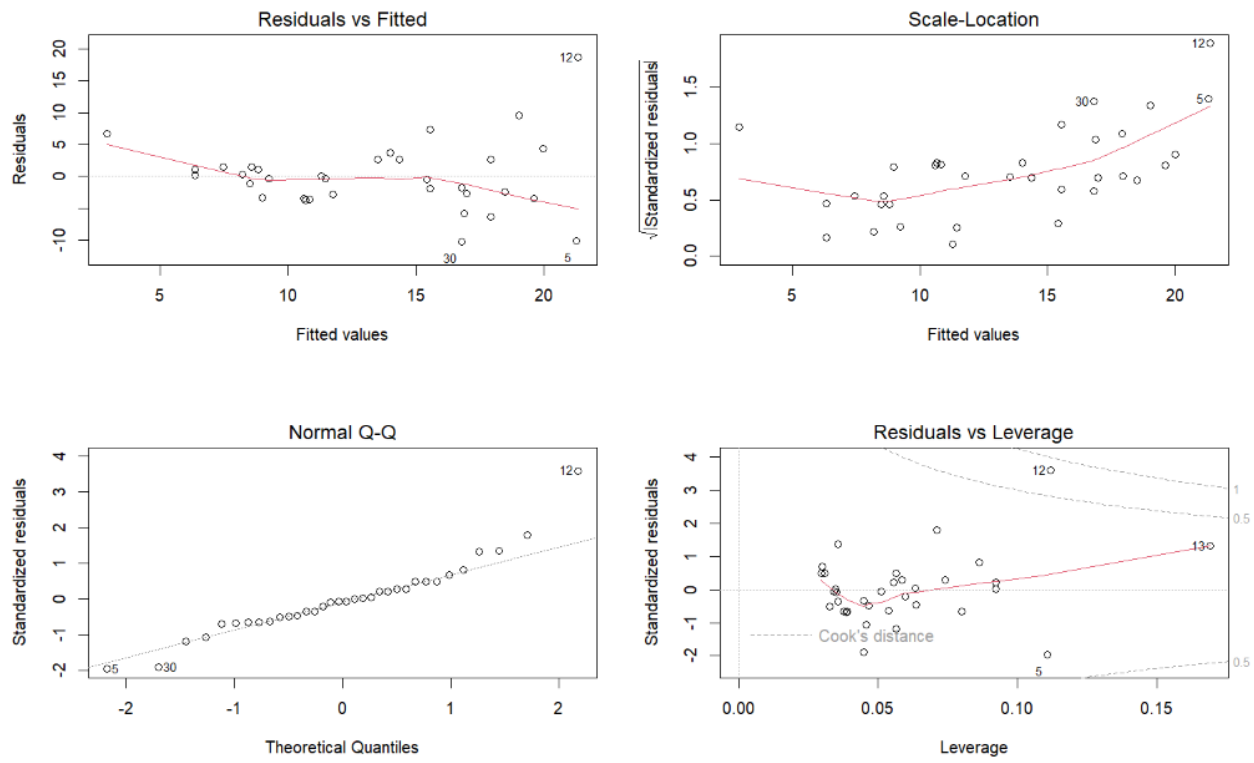


Figure S.4.2.6.b QQplots stem density ~ species richness



**Figure S.4.2.7** QQplots average DBH ~ WD