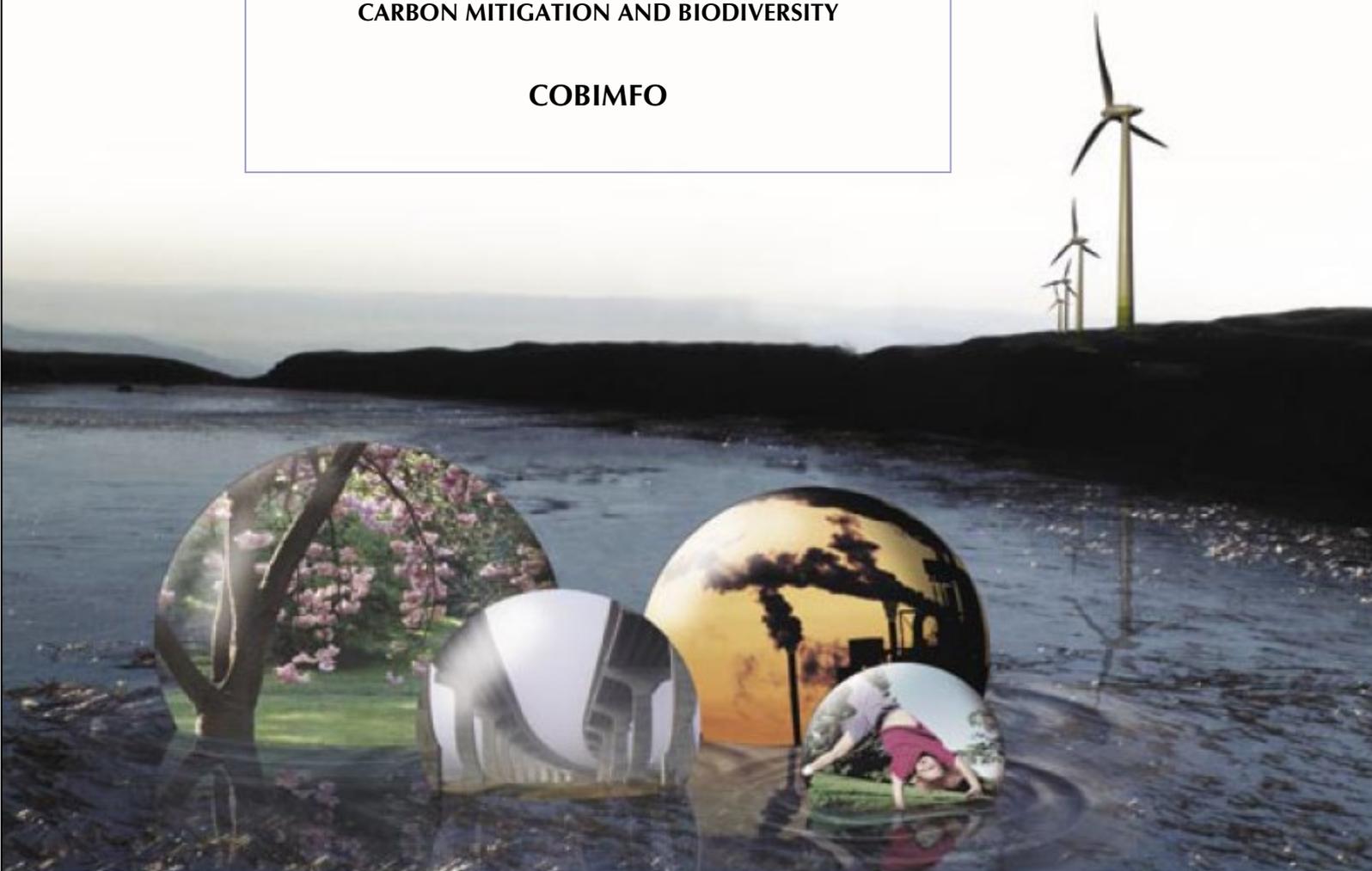
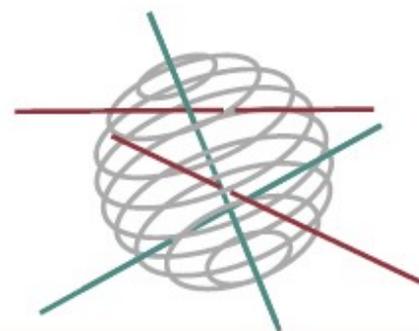


# SSD

SCIENCE FOR A SUSTAINABLE DEVELOPMENT

CONGO BASIN INTEGRATED MONITORING FOR FOREST  
CARBON MITIGATION AND BIODIVERSITY

COBIMFO



BIODIVERSITY

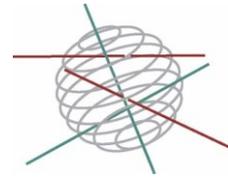


ATMOSPHERE AND TERRESTRIAL AND MARINE ECOSYSTEMS





SCIENCE FOR A SUSTAINABLE DEVELOPMENT  
(SSD)



*Atmosphere and terrestrial and marine ecosystems - Biodiversity*

FINAL REPORT

CONGO BASIN INTEGRATED MONITORING FOR FOREST CARBON  
MITIGATION AND BIODIVERSITY

COBIMFO

SD/AR/01A

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## ACRONYMS, ABBREVIATIONS AND UNITS

A: photosynthetic assimilation rates  
AGB: Aboveground biomass  
APM: Agentschap Plantentuin Meise  
BGB: Belowground biomass  
DBH: diameter at breast height  
DNA: Deoxyribonucleic acid  
FAO: Food and Agriculture Organization  
Gs: stomatal conductance  
PG-CB: Productivity gradient, carbon biodiversity  
PSP: permanent sampling plot  
RBINS: Royal Belgian Institute of Natural Sciences  
REDD: Reducing emissions from deforestation and forest degradation  
SD: standard deviation  
UNEP: United Nations Environment Programme  
UNIKIS: l'Université de Kisangani  
WP: Working package  
WSG: wood specific gravity  
WUE: water use efficiency  
Y-MaB: Yangambi Man and Biosphere reserve

## 1. EXECUTIVE SUMMARY

The overall aim of the COBIMFO project is to increase our knowledge and understanding of the linkage between biodiversity, landscape composition and configuration and above and below ground biomass (AGB and BGB, respectively) in pristine and intervened dense tropical forest of the Congo Basin; which as of yet remains poorly understood. To investigate carbon sequestration and biodiversity and their relation along a forest productivity gradient in one specific biome of the Congo Basin forest, this project (1) measures aboveground and belowground soil carbon stocks and biodiversity indices along a forest productivity gradient in the Yangambi Man and Biosphere reserve (Y-MaB), (2) investigates direct effect relationships between of forest carbon stocks and biodiversity along this productivity gradient, and (3) uses measurements of proxies such as bio-indicators or remote sensing to act as rapid assessment tools or help in the scaling of carbon stock and biodiversity data. As such, the different partners (see contact information section) explore biodiversity and the link with AGB and BGB and this on various ecosystem levels.

Within this context 21 field sites in contrasting forest types along a productivity gradient were selected through careful analysis of high resolution remote sensing data to assess AGB, BGB and their link to lichen, floral and faunal biodiversity as measured within and around these plots (methodology and results see below). The measured data gathered during the pilot study past spring included plant functional traits such as diameter at breast height (DBH), leaf area index but also derived parameters such as specific leaf area and biochemical parameters such as leaf nitrogen content (P 1 – 4, WP2 baseline C inventory). Additionally, research is focussed on the possible presence of an edge effect on wood density in Yangambi reserve.

Biodiversity of vascular plants, small mammals and insects were gathered for DNA barcoding. Specifically, in collaboration with the Royal Belgian Institute of Natural Sciences (RBINS, P7, WP3 biodiversity monitoring) and the Université de Kisangani (UNIKIS), large reference collections of small mammals have been established. These reference collections provide a basis for the unique DNA barcode archive organised by RBINS. Currently, the collections describes the small mammal biodiversity of the Kisangani region in detail, including some species new to science. Continued field sampling as executed within this last and future field campaigns together with DNA barcoding of higher vascular plants would provide us with a detailed account of genetic diversity within different forest types (P6).

The above measurements quantify the structural and species diversity in a direct way. However, indirect ways to assess biodiversity, ecosystem services and other parameters are also actively being explored. For example, in the tropics a special group of lichens lives exclusively on leaves, namely foliicolous lichens. These lichens have an accelerated life cycle and respond rapidly to changes in environmental conditions. Foliicolous lichens are highly susceptible towards micro-climate. Furthermore, they have a two-dimensional growth, well-known taxonomy, are easy to collect and show a high diversity in tropical lowland rainforests. Therefore, they have a great potential to be used as bio-indicators of climate change and other disturbances. Also ants and termites show high potential for biodiversity assessment. Ants and termites constitute up to 1/3 of the animal biomass in tropical rainforests. Termites are major decomposers, acting significantly in the C cycle. Ants have various ecological roles interacting

with plants (mutualism, seed dispersion, pollination) and other arthropods (mutualism, predation).

## 2. INTRODUCTION

### 2.1 Context

The aim of this project is to get baseline reference data on the carbon balance and biodiversity in pristine and intervened dense tropical forests of the Congo Basin and to increase our understanding in the relationship between both variables as a function of forest management. The strategic choice of the tropical forests of D.R. Congo as a study area is inspired by five main reasons: (1) REDD+ projects are active and also REDD+ on a national level has been initiated as D.R. Congo is one of first nine pilot UN-REDD+ countries, UN-REDD+ being the UN program and partnership between FAO, UNEP and UNDP, dealing with support to countries to make part of REDD+; (2) there are large uncertainties associated to impact of forest degradation on the global C budget as a result of the lack of information on current and future C stocks and fluxes in forests of D.R. Congo; (3) Central African tropical dense rainforests are considered an unexplored and endangered biodiversity hotspot; (4) enhanced forest degradation of non-protected areas in D.R. Congo will almost certainly take place in the future at high rates; and (5) the support of the local stakeholders for future REDD+ initiatives in Central African forests will ultimately depend on its associated impacts on biodiversity and associated ecosystem functions. In order to achieve our objectives, we build a scientific consortium that is composed of 8 partners having complementary research expertise (remote sensing, biogeochemistry, biodiversity biologists, landscape ecology, forestry, etc.) and a common interest in African tropical forest ecology and nature conservation. All partners have established scientific contacts and ongoing collaborations in D.R. Congo.

We will measure aboveground and belowground soil carbon stocks and biodiversity indices along a forest productivity gradient (21 sites) in the Yangambi Man and Biosphere reserve (Y-MaB) and investigate direct effect relationships between forest carbon stocks and biodiversity along this productivity gradient (PG-CB). The different sites located along a forest productivity gradient were selected using remote sensing techniques and validated on the ground. Carbon stocks will be investigated in the forest core and edges zones (P 1 – 5, see above). Furthermore, rapid development of slash and burn activities in tropical forested areas has an important impact on carbon stocks and landscape configuration. Indeed, clear cutting tend to fragment forest patches, and expose forested core areas to non-forested ecosystems. These exposed core areas then undergo new constraints (temperature, light, exposure to wind and pests...) that can lead to a shift in their ecological traits, called the edge effect. This edge effect could affect many different ecological traits: floristic composition of the stand, growth, wood microscopic features, wood density... We investigate the possible presence of an edge effect on wood density in Yangambi reserve. Wood density (along with diameter and height) is a key feature for biomass estimations in tropical forests. Thus, fluctuations of wood density in forest edges could lead to fluctuation in estimations of carbon stocks.

To improve the understanding of the dynamics of African tropical forests, the relationship between biodiversity and carbon stock (included here as a function of forest dynamics) is investigated. In a first phase of the project, carbon stocks are calculated for different forest plots forming a production gradient and covering the different types of young regrowth and old growth forests found in the Yangambi area. For these same plots, scientists of the National Botanic Garden of Belgium estimate the botanical diversity using the following groups: higher vascular plants, selected groups of fungi,

lichens and myxomycetes (P 6). Furthermore, we will bring forward a set of biodiversity indices related to termites, spiders, flies, bees, arthropods and rodents (P 7 – 8).

## **2.2 Objectives**

### **2.2.1 WP1 Site selection**

The main objective of the project is to get baseline reference data on the C stocks and biodiversity in pristine and intervened dense tropical forests of the Congo Basin and to increase the understanding in the relationship between both variables. This project has five specific objectives each associated to a Work Package, UCL-Geomatics was responsible for the work package 1, which was finalized during the first year of the project.

#### *Deliverables:*

A series of permanent carbon and biodiversity monitoring plots along a productivity gradient in the tropical forest in Yangambi. These plots will be used for long term monitoring of biomass and biodiversity.

### **2.2.2 WP2 Baseline C inventory**

The objectives of WP2 are aimed at composing a detailed database of above and below ground carbon stocks for the selected PSP (WP1) with deliverable as described below.

#### *Deliverables:*

- Quantify the carbon stock in the region of Yangambi, and predicting future changes through the installation and monitoring of 1 ha PSP on multiple sites in the region, to obtain a representative sampling of the different types of forest in the reserves;
- Characterize tree biodiversity throughout the reserve (see WP3);
- Characterize plant functional diversity and traits, linking this diversity to the carbon stocks;
- Characterize relationships between landscape structure, biodiversity (loss) and carbon stocks;
- Characterize and scale the above findings to the Congo basin using remote sensing data;
- Characterize wood density in function of the distance along a forest edge or disturbances;
- Characterize Wood Specific Gravity (WSG) variability in Yangambi Reserve, and its link with tree DBH, forest typology, age and edge effect.
- Characterize the 'edge effect' over a larger area using remote sensing techniques;
- Quantify the carbon cost of the edge effect and antropogenic disturbances;
- Quantify long term changes in carbon and water relations using (stable isotope) tree ring analysis.
- Contributing to pan-tropical and global studies.

### **2.2.3 WP3 Biodiversity monitoring**

The overall goal of WP3 is the production of multiple baseline biodiversity indices along a forest productivity gradient representative for lowland dense tropical rainforest biome. Besides making species inventories, the biological diversity will be translated into diversity indices that will attempt to account problems with issuing values to diversity. Depending on necessity (life cycle (e.g. flowering) or fluctuations in population densities), the selected animals, plants, fungi, lichens will be studied once during the dry season, or during both rainy and dry season. For further details on temporal intensity of the individual organism that will be monitored, we also refer to the Timetable (Form 14 in the original proposal).

*Deliverables:*

Production of multiple baseline biodiversity indices along a forest productivity gradient representative for lowland dense tropical rainforest biome.

*Fungi and myxomycetes:*

- make an inventory of fungi, myxomycetes, protostelids and dictyostelids in a number of research plots covering the production gradient and including the major forest types;
- describe, characterize and compare the plots using available data and species composition (indicators), biomass production and prevalence of ecological groups of fungi;
- determine the varying levels of human interference and how they relate to the production of useful fungi under natural conditions;
- quantify the actual annual biomass production per plot and per forest type. Assign a monetary value from the fungal perspective;
- identify any current local conservation practise geared towards mushroom production;
- propose methods and recommendations to improve conservation, management and sustainable use of edible and useful fungi;
- record ethnomycological knowledge, compare and synthesize with the existing knowledge on African edible species;
- produce a book, i.e. a tool for identification and study of edible and useful fungi in the area.

*Lichens:*

- to characterize the diversity of epiphytic lichens and their lichenicolous fungi in ecologically diverse forests of the Democratic Republic of the Congo;
- to investigate the factors influencing the richness and composition of the epiphytic lichen communities in those forests;
- to establish a baseline of the lichen vegetation for a long-term monitoring survey in the forests of the bio spherical reserve of Yangambi.

*Higher vascular plants:*

- provide confident determinations for all tree species with a DBH above 10 cm encountered within the selected plots;
- build a DNA barcode reference library for the tree species of the Central African basin;
- complete the checklist of higher vascular plants of the Tshopo area;
- compare tree species diversity patterns with other biodiversity patterns and carbon production.

*Small mammals:*

- Build a DNA barcode reference library for mammal species of the Central African basin;
- Characterize the diversity of rodents and shrews in different forest types of the Yangambi Biosphere Reserve.
- Assess whether the survey on rodent and shrew fauna conducted in Y-MaB are representative of the Congo basin in terms of species richness and abundance.

#### *Insects (ants, flies ...)*

- Compare the community structure (diversity, density) of dominant arboreal ants and in early vs. late stages of the succession gradient of mixed forests corresponding to low and high carbon stocks, respectively;
- Assess whether the ant community structure is affected by tree monodominance (of either *Gilbertiodendron* or *Brachystegia*) occurring due to particular local environmental conditions.
- Study the spatial distribution of arboreal ants: is there an exclusion of dominant species?

### **2.2.4 WP4 Integration of carbon and biodiversity data**

#### *Deliverables:*

- Select a set of diversity parameters that can be calculated for each taxon, and that can be normalised so as to be comparable between taxa. We will assess biotic parameters that describe compositional and functional components of the sampled communities.
- Calculate the chosen measures for alpha diversity for each taxon and sample site.
- Make a statistical model for each biodiversity parameter that models biodiversity as a function of carbon, taking into account the correlation structure of repeated measurements on the clustered data of the same sampling plot (nested within habitat type).
- Generate area-wide predictions of biodiversity based on the biodiversity data obtained from the COBIMFO study plots, using Ecological Niche Modelling techniques and MacroEcological Modelling

## **2.3 Expected outcomes**

### **2.3.1 WP1 Site selection**

The expected outcome of WP1 in the project proposal was to select candidate sites based on the attribute estimation (forest productivity and forest structure) from satellite images. By selecting different sites based on forest and soil type it was assumed that we are covering simultaneously several other gradients: a gradient in productivity, carbon stock, stand age and biodiversity. These possible locations have been updated during the actual fieldwork. This WP is therefore finalized.

### **2.3.2 WP2 Baseline C inventory**

The proposed research will provide us with a baseline inventory and C-stock (both above and belowground) of the Yangambi reserve and by proxy the larger Congo Basin. Furthermore, a link with plant functional traits will be explored as to constrain the controlling factors on differences between the PSP. In addition, we quantify the tree biodiversity in the same areas (coordinating with WP3 partners).

We provide a detailed study of the edge effect on mixed primary forest carbon stock in Yangambi. This will be inferred by the analysis of the data obtained in the heart and edge PSP installed. Rapid development of slash and burn activities in tropical forested areas has an important impact on carbon stocks and landscape configuration. Indeed, clear cutting tend to fragment forest patches, and expose forested core areas to non-forested ecosystems. These exposed core areas then undergo new constraints (temperature, light, exposure to wind and pests...) that can lead to a shift in their ecological traits, called the edge effect. This edge effect could affect many different ecological traits:

population specific ratio, growth, wood microscopic features, wood density, etc. Here we focus on the investigation of the possible presence of an edge effect on wood density in Yangambi reserve.

### **2.3.3 WP3 Biodiversity monitoring**

Within the biodiversity working package the expected outcomes can be summarized as such: a list of foliicolous lichen species suitable as bio-indicators for local and regional environmental changes within the Congo Basin will be identified and a reference list of lichens compiled and published as a baseline for further research. In addition, an updated checklist of the plant diversity of the Tshopo area and a DNA barcode library for plants of the Yangambi area.

DNA barcoding and reference species collection will also be established for small mammals and selected insects, mapping diversity and identifying new species. For all subjects within all WP high impact publications are foreseen or currently outlined.

*In detail we expect:*

- A species-plot list (ATBI all taxa biodiversity inventory) including all the major edible and useful mushrooms of the studied area; the occurrence is given per studied plot (vegetation type), including biomass produced per ha; each plot is characterised and all data treated in a multivariate analysis; bio-indicators are listed and described;
- An understanding of the factors affecting fungal composition and natural biomass production;
- The monetary value of the plots from the mushroom perspectives;
- A package of recommendations for sustainable management of the plots (forest types) for increased production of useful species;
- A list of local names and their significance for edible and useful fungi, as well as a full account on local ethnomycological knowledge;
- A scientific account on the edible mushrooms of the area;
- A species-plot list of myxomycetes, protostelids and dictyostelids of the studied area; the occurrence is given per studied plot (vegetation type);
- A list of the total diversity of myxomycetes, protostelids and dictyostelids of the tropical forests in the Yangambi area;
- A list of the total diversity of corticolous and foliicolous lichens and of lichenicolous fungi of the tropical forests in the Yangambi area;
- An understanding of the factors affecting diversity and composition of lichens in the forest for foliicolous and corticolous lichens;
- A package of recommendations for sustainable management of the plots (forest types) based on the lichens;
- A species-plot list including all the higher vascular plants of the studied area. The occurrence is given per studied plot (vegetation type); each plot is characterised and all data treated in a multivariate analysis; bio-indicators are listed and described;
- An updated checklist of the plant diversity of the Tshopo area and a DNA barcode library for plants of the Yangambi area;
- An understanding of the factors affecting diversity and composition of higher vascular plants in the forest;
- A package of recommendations for sustainable management of the plots (forest types) based on the analysis of the vegetation;

- A herbarium with a fully documented reference collection at the herbarium of Yangambi, the University of Kisangani, the herbarium of Epulu and at the National Botanic Garden of Belgium;
- A cytb DNA barcode database for African murids for fast and reliably identification of 27 murid species for the region of Kisangani, 8 of which are new to science;
- A 16SrRNA DNA barcode database for 23 shrew species;
- A COI DNA barcode database for insect target groups (a complete inventory will be difficult to a certain due to the number of insect species);
- Species richness statistics based upon the identified mammals and insects, and this for all PSP;
- Characterization of population dynamics of selected species;
- Characterization of the genetic variation across PSPs.
- Detailed capture data of rodents and shrews from six PSPs, as well as DNA sequences of all specimens
- Complete dataset of the rodent and shrew captures in the region, surveyed by researchers affiliated with the UA or the RBINS

#### **2.3.4 WP4 Integration of carbon and biodiversity data**

- An established framework of diversity parameters that cover multiple aspects of biodiversity and that are applicable for all sampled species groups
- Spatial extrapolations of the different aspects of diversity for the Y-MaB
- A statistical model linking biodiversity and carbon storage

## 3. SCIENTIFIC METHODOLOGY

### 3.1 WP1 Site selection

#### Site selection Yangambi

This task was finalized during the first year of the project by the UCL-Geomatics team. A preliminary classification of the study area was made using SPOT-4 HRVIR, Landsat and geo-eye satellite images using an object based classification approach. Plot locations were assigned within each classification type before fieldwork. The forest type was validated in the field and permanent inventory plots of 1 ha have been installed. Details can be found in the annual report of 2012 and 2013.

#### *Large scale forest inventory*

To capture the population structure of important tree species we started in 2014 a large scale forest inventory of specific species. This inventory does not overlap with the permanent sampling plots in which the detailed carbon and biodiversity data is collected.

#### *Edge sampling in Yangambi*

Results from the first carbon inventory in Yangambi Reserve indicated an important site and tree species dependence on height-diameter-Wood Specific Gravity relationships in edges plots, blurring the impact of edge effects on these traits. In order to randomize these dependences, a new sampling setup was installed along the edges of Yangambi reserve forests, and into the forests core. For this setup, edge environment was defined as the area located less than 30 m into the forest, measured from the closest tree forming the limit between forest and non-forest environment. Core environment was defined as the area located more than 3 km away from any forest edge. To randomize any site effect on the data, each individual were selected randomly while traveling through forest edges, and forest core. This new setup is expected to describe more closely the edge effect on height-diameter-wood density relationships.

#### *Arboretum*

The arboretum in Yangambi was selected as a new study location for a 77-year-old tree diversity experiment. The arboretum was established in 1938 by the colonial Belgians, which held a large tropical agriculture and forest research center at this site. Information on the setup and the initial follow-up of the experiment could be tracked in the Belgian State Archive, until the decolonization in 1960. Since then, the experimental sites have been under the protection of the INERA (Institut National pour l'Etude et la Recherche Agronomique), the Congolese national institute for agricultural research.

#### Site expansion Yoko

A second site was selected in Yoko, Biaro reserve, south of Kisangani (N00°17'; E25°18'), to address questions related to spatial variability in forest structure and carbon storage. Data acquired at this site is only used for WP2. Details of data acquisition can be found in the annual report of 2014.

#### Site expansion Djolu

A final extension site in Djolu (Equateur) was selected to continue the work on the carbon stocks-functional diversity links. In this site 15 hectare plots were selected and delineated on a forest

succession gradient. This site extension adds to the COBIMFO project because it makes use of the skills and training of the local people, which were generated through COBIMFO.

### **3.2 WP2 Baseline C inventory**

Details on plot inventory in Yangambi and Yoko can be found in the annual report of 2012, 2013 and 2014.

#### Aboveground and belowground carbon storage in Yoko and Yangambi

##### *Tree height and aboveground biomass estimation*

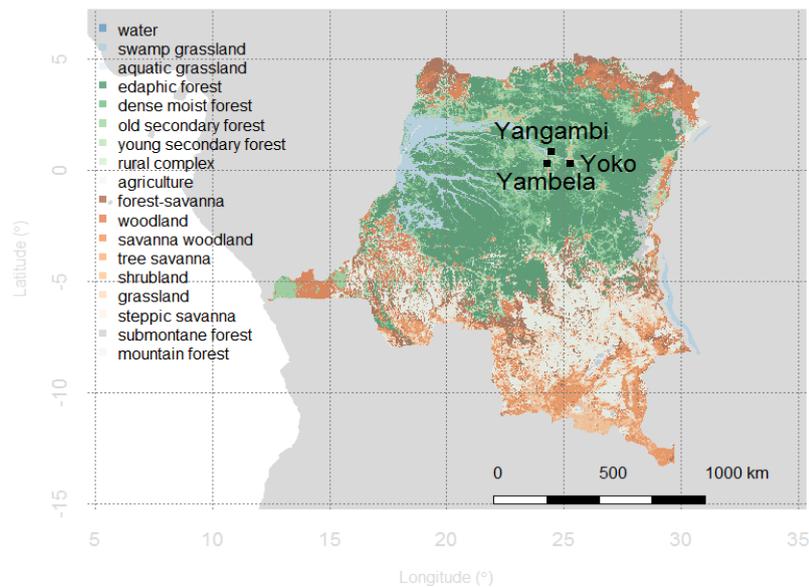
Site-specific height-diameter regression models were developed for each forest type. All trees known to be broken, damaged or leaning more than 10% were excluded from the analysis. Site-specific height-diameter models were set up, for which the three-parameter exponential height-diameter model was selected as optimal model at both sites independently. These models were further used to determine tree heights for aboveground carbon (AGC) stock estimation. Despite the differences in plot size between YGB and YOKO, roughly the same number of trees are height measured with a similar distribution over the different diameter sizes. The pantropical relation of Chave et al. (2014) for moist tropical forest including height and wood density was selected for AGC stock estimation, with biomass assumed to be 50% carbon. Site-specific wood density measurements were used for YGB (Kearsley et al. 2013), and completed with genus level averages if species level data was not available. For species not determined in YGB, values from the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009) were used.

##### *Soil and litter sampling and analysis*

On two plots per study site, ten soil cores have been taken and composed to three depth increments (0–30, 30–60, 60–90) and oven-dried (50°C). At each of the two study plots where soil samples were taken, forest floor litter was sampled in May 2014 from a randomly distributed 0.5 x 0.5m square in triplicate to capture the variability in plant growth/litterfall in the area. The forest in Yoko and Yangambi shows a seasonal pattern in litter production for fine litter (4.57 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) and foliar litter (2.85 Mg C ha<sup>-1</sup> yr<sup>-1</sup>), with the highest rates of litterfall occurring January-March and September-October. This litterfall dynamic is mainly driven by the region's climatic seasonality. After sampling, litter has been dried at 40°C and the dry weight has been taken. For both soil and litter the following parameters have been measured: bulk density (soil only), soil texture, pH (soil only), potential cation exchange capacity, base saturation, bioavailable P, NO<sub>3</sub> and NH<sub>4</sub>, C stock and soil organic carbon (SOC) fractions.

##### Assessment of regional variability in tree allometry

In a previous study (Kearsley et al. 2013; see annual report 2013), we identified significant differences in height-diameter relationships with lower asymptotic tree heights found in the central region of the Congo Basin compared to the outer regions of the Congo Basin (Banin et al. 2012; Feldpausch et al. 2011). Here we enlarge the spatial scale of this study by investigating height-diameter relationships at three old-growth forest sites: Yangambi, Yoko and Yambela (Figure 1). The data for the Yambela site is provided by collaborator Pieter Moonen (KULeuven).



**Figure 1:** Location of the three study sites Yangambi, Yoko and Yambela on a land cover map of DRC (Verhegghen et al. 2012).

The statistical analysis consisted of three main stages. First a selection is made of the best model function for this region, referred to as the local model. Secondly, the selected model is compared to regional models for Central Africa, namely Feldpausch et al. (2012) and Banin et al. (2012), and the pan-tropical model presented by Chave et al. (2014). Finally, site-level variability is assessed by introducing site as random effect in a nonlinear mixed effects (NLME) version of the local model.

#### Recensus at the Yangambi site

All the 21 PSP in Yangambi reserve were reinventoried using the RAINFOR protocol (the same protocol used during the first sampling campaign), 2 years after the first sampling campaign. In addition, for maintenance purposes, PSP labeled using paint in 2012 were relabeled using plastic labels.

#### Sampling in the edge setup

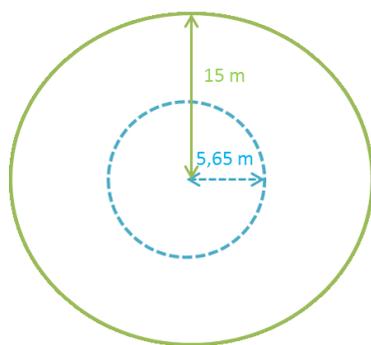
In the edge setup, 5 target species, which total basal area represented, in 2012 PSP, over 40% of the total basal area of mixed forest PSP (that is to say, the MIX and EDG plots), were selected. These species are: *Scorodophloeus zenkeri* (FABACEAE), *Panda oleosa* (Pandaceae) *Petersianthus macrocarpus* (LECYTHIDACEAE) *Strombosiopsis tetrandra* (OLACACEAE) and *Tridestemon claussensii* (SAPOTACEAE). 4 Diameter classes were selected: 10 to 20 cm, 20 to 30 cm, 30 to 50 cm, and more than 50 cm. For both environments (edge and core) and for each species, 5 individuals were sampled in each diameter class. Sampling protocol included: DBH, height, distance to edge (if applicable), and 2 cylindrical wood samples. These samples were 2.5 cm in diameter and 3 to 5 cm in depth under the bark. In edge environment, samples were taken perpendicular to the orientation of the edge: on sample on the side of the trunk facing the interior of the forest, the other on the side facing the non-forest environment. In the core environment, samples were taken on the east and west sides of the trunk. In total, 200 individuals were sampled. Fresh and oven dry wood samples were measured and weighted, and Wood Specific Gravity was calculated.

Inventory of the understory

The understory, here defined as  $DBH < 10$  cm, has been inventoried to investigate its species composition and to assess the biomass it holds. The understory namely has some important aspects of forest dynamics:

- Critical stage for certain species (heliophilous, etc.)
- A fase all individuals most go through,
- Some species never reach the other strata,
- Structural role, specific habitats, etc.

Two plots were inventoried, namely one in undisturbed forest (MIX5) and a forest that has undergone management. Small plots have been installed outside the permanent plots to not disturb them, while remaining in the same environment. These plots consist of two concentric circles, the first having a radius of 5.65 m and the second of 15 m (Figure 2).



**Figure 2:** Plot design for understory inventory.

In the first circle ( $r = 5.65$  m), all individuals with  $DBH < 10$  cm were cut and their woody biomass and leaf biomass was estimated by weighing. The collected data are:

- Scientific name
- Position (polar coordinates)
- Diameter at base
- The diameter at breast height (DBH)
- Total height
- Height stem
- Herbarium
- Sample timber
- DNA Sample
- Fresh weight

In the second circle ( $r = 15$ m), all individuals with  $DBH > 10$  cm were recorded and the following data were collected:

- Scientific name
- Position (polar coordinates)
- DBH

Wood traits and wood specific gravity

In 2012, wood samples were collected from 1102 individuals, among 110 taxa (see previous reports). Wood Specific Gravity, water contents and shrinking ratios were measured. Using

InsideWood database (<http://insidewood.lib.ncsu.edu/>) average fiber thickness and average vessel diameters of each taxa were obtained. A correlation study was then performed.

Additional wood sampling was performed in 2014. The main objective was to establish a monitoring protocol for tree growth (cambial marking) and to collect wood samples (cores) to investigate functional traits of the wood. This analysis focusses on 18 species (Table 1) which are abundant in the mixed forest in Yangambi. All these measures will complement the wood trait dataset which will improve our estimates of carbon stocks in the core of the forest and in the edge zones.

**Table 1:** Selected species for additional wood sampling. Family name given between brackets.

Species present in forest canopy	Species present in understory
<i>Blighia welwitschii</i> (Sapindaceae)	<i>Carapa procera</i> (Meliaceae)
<i>Celtis mildbraedii</i> (Ulmaceae)	<i>Cola griseiflora</i> (Malvaceae)
<i>Chrysophyllum africanum</i> (Sapotaceae)	<i>Garcinia punctata</i> (Clusiaceae)
<i>Erythrophleum suaveolens</i> (Leguminosae)	<i>Polyalthia suaveolens</i> (Annonaceae)
<i>Guarea thompsonii</i> (Meliaceae)	<i>Trichilia gilgiana</i> (Meliaceae)
<i>Pentaclethra macrophylla</i> (Mimosaceae)	<i>Trichilia prieurieana</i> (Meliaceae)
<i>Petersianthus macrocarpus</i> (Lecythidaceae)	
<i>Prioria oxyphylla</i> (Leguminosae)	
<i>Pycnanthus angolensis</i> (Myristicaceae)	
<i>Staudtia kamerunensis</i> (Myristicaceae)	
<i>Strombosiopsis tetrandra</i> (Olacaceae)	
<i>Trilepisium madagascariense</i> (Moraceae)	

#### Collected material

- Tree cores: 2 or 3 tree cores from an individual tree were taken with at least three trees per species. This sample was taken on the 18 species selected within 5 different plots: MIX5, MIX6, BRA1, EDG2, EDG5 depending on the location of the species.
- Bark: bark of 2 individuals per species was collected and placed directly in alcohol. We chose each time two individuals with a thin and thick bark.
- Wood sample: a wood sample was collected on all trees of plot MIX2. The sample was taken at the location where a nail was inserted in 2012 (to attach the tree number). This will allow us to know the growth of all species in the plot in 2 years.
- Leaf and wood samples: Samples are collected to verify different species identification protocols: field identification, herbaria identification, wood anatomical identification and DNA sequencing.

#### Cambial marking

For all 18 species, at least three trees per diameter class (A:10-20 cm, B: 20-30 cm, C: 30-50 cm, D > 50cm) were labeled using a syringe. This will reveal the annual growth of these 18 species according to their diameter.

#### Wood traits measured

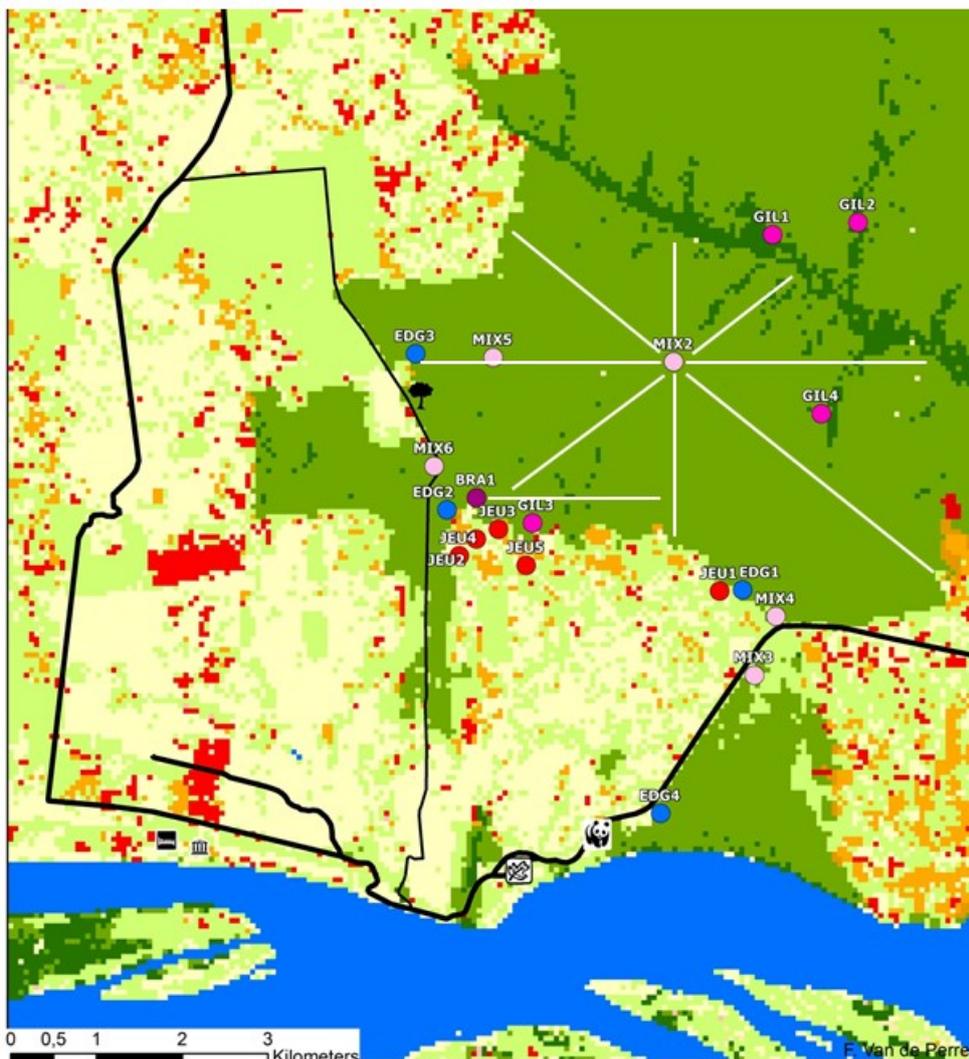
- wood Density
- density of the vessels
- vessel diameter
- heartwood / sapwood ratio

Large scale forest inventory

A species-specific large scale forest inventory (Table 2, Figure 3) is performed focussing on *Pericopsis elata* and *Entandrophragma* spp., which are both valuable timber species. Although this inventory fits and contributed to the COBIMFO project, the implementation and scientific monitoring of the inventory has been made with the financial support of the project Xyladate with MRAC as the prime contractor (financing DGD).

**Table 2:** Characteristics of the inventory system of rods *P. elata* and *Entandrophragma* spp. in the reserve Yangambi.

<b>Inventory threshold</b>	dbh ≥ 5.0 cm ( <i>Entandrophragma</i> spp.)
	dbh ≥ 10.0 cm ( <i>P. elata</i> )
<b>Inventory plots</b>	5.0 – 19.9 cm dbh, 50 m x 15 m on either side of the central transect
	≥ 20,0 cm de dbh, 50 m x 50 m on either side of the central transect
<b>Total length of the transect</b>	25 km
<b>Total area inventory</b>	250 ha



**Figure 3:** Schematic representation of the location of inventory transects in the reserve Yangambi (white lines). The specific plots Cobimfo project are represented indication.

#### *Pericopsis elata* (Harms) Meeuwen (Fabaceae)

*P. elata* is a large tree of the African semi-evergreen forest. Of great commercial value, this species is exploited for its wood throughout its natural range. As is the case for most of the large trees exploited in the Congo Basin, *Pericopsis* is characterized by a more or less extensive regeneration deficiency. This species is known for its gregarious nature and light-demanding characteristics and can form real pockets in forest stands characterized by a high density of adult stems. Forest disturbance is often hypothesized to be crucial for the formation of homogenous groups of *P. elata*.

#### *Entandrophragma* spp. C. DC. (Meliaceae)

The most represented taxon of *Entandrophragma* spp. for commercial use are *E. angolense* (Welw.) C. DC., *E. candollei* Harms, *E. cylindricum* (Sprague) Sprague et *E. utile* (Dawe & Sprague) Sprague, which are sought for varying degrees within the quality of their wood. Like the hypotheses developed for *P. elata*, establishment of this species is light dependent and may be favored following disturbance. Understanding the ecology of these species should allow to understand their possible evolution within the changing climate and environment.

#### Pan-tropical research

Multiple collaborations have been set-up with research groups working on pan-tropical questions. Inventory data from Yangambi represent an important contribution due to the unique location of the site.

### **3.2 WP3 Biodiversity monitoring**

#### Trees species identification

In 2012, all trees with a DBH  $\geq 10$  cm were identified to species level with the help of local botanist. The identification of species has been double checked by a team of botanist of the Botanic Garden Meise (Belgium), and botanical specimens were collected for all individuals for which uncertainty remained. Final identification was then based on a comparison with herbarium material and DNA sequencing when necessary.

#### Plant functional traits and functional diversity of trees

Functional diversity is defined as the value, range, distribution and relative abundance of functional traits of the organisms that make up an ecosystem (Díaz *et al.* 2007). Plant functional traits are characteristics of an individual organism (Garnier & Navas 2012), usually measured at the tissue-level like at the leaves, that bear some relationship to plant functioning (Lavorel *et al.* 2007). More precisely, functional traits are physiological, structural, behavioral, or phenological characteristics associated to the response of organisms to the environment and their effects on the functioning of the ecosystems in which they live (Díaz *et al.* 2007).

#### *Trait selection and analysis*

Within this study, the following traits have been measured on 998 individual trees, covering tree 123 species (Table 3). From each individual tree, 10 leaves were sampled at various tree heights, which were fully expanded and no signs of pathogens or herbivory.

**Table 3:** List of all plant functional traits including the used abbreviations and units. General strategy correlations are provided. (Adapted from Baraloto et al. 2010; Fortunel et al. 2014).

Trait	Abbreviation	Unit	Strategy correlations
Specific leaf area	SLA	m <sup>2</sup> kg <sup>-1</sup>	Resource capture and defense
Leaf dry matter content	LDMC	g g <sup>-1</sup>	Resource capture and defense
Foliar carbon content	LCC	mg g <sup>-1</sup>	Resource capture and defense
Foliar nitrogen content	LNC	mg g <sup>-1</sup>	Resource capture
Foliar phosphorus content	LPC	mg g <sup>-1</sup>	Resource capture
Foliar C:N ratio	C:N	g g <sup>-1</sup>	Resource capture and defense
Foliar N:P ratio	N:P	g g <sup>-1</sup>	Resource capture
Foliar <sup>13</sup> C composition	δ <sup>13</sup> C	‰	Resource capture
Foliar <sup>15</sup> N composition	δ <sup>15</sup> N	‰	Resource capture
Foliar <sup>18</sup> O composition	δ <sup>18</sup> O	‰	Resource capture
Wood density	WD	g cm <sup>-3</sup>	Transport, structure and defense
Vessel density	VD	μm <sup>-2</sup>	Transport, structure and defense
Vessel diameter	VDm	μm	Transport, structure and defense
Minimum ray width	RWMin	cells	Transport, structure and defense?
Maximum ray width	RWMax	cells	Transport, structure and defense?

#### *Functional diversity indices*

Multivariate statistical analysis is performed since the ecology of species inherently relates to a combination of traits. Multivariate functional diversity indices are calculated for each plot. Functional diversity consists of different dimensions, and according to Mason *et al.* (2005) and Villéger *et al.* (2008), at least three different indices are needed to capture these different dimensions, namely functional richness, functional evenness and functional divergence. Functional richness is defined as the amount of niche space filled by species in the community, thus describing trait dissimilarity. Functional richness is measured for each plot as the convex hull volume encompassing all traits. Functional evenness is the evenness of abundance distribution in filled niche space. Functional divergence is the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community. Since a monodominant tree community could have a large influence on the distribution of trait values, we include another measure of divergence, namely functional dispersion (Laliberté & Legendre 2010). Functional dispersion is the mean distance in multidimensional trait space of individual species to the centroid of all species, while functional divergence quantifies how species diverge in their distances from the center of gravity in the functional space (Villéger *et al.* 2008; Laliberté & Legendre 2010). Both functional divergence and functional dispersion are calculated relative to the centroid per plot. All indices are calculated using the R package FD (Laliberté *et al.* 2014).

#### *Monodominant vs mixed forests*

Monodominant forests are frequently found in African tropical rainforests, generally characterized by a low diversity in tree species. However, functional diversity and functional structure of these forests remains poorly understood. We investigated the functional diversity and functional community structure of persistent and non-persistent monodominant forests compared to the adjacent mixed forest, using 15 functional leaf and wood traits covering 95% of the species found over 16 one-hectare plots.

Two main types of monodominant forest are investigated namely non-persistent and persistent dominance (Peh 2009). Non-persistent dominance, by definition, does not have the ability to regenerate under its own canopy, and thus lasts for only one or at most a few generations. This short-term dominance is usually related to secondary forest succession that occurs following anthropogenic clearance or large-scale natural disturbance such as windstorms. In this study, successional forests dominated by the monodominant species *Musanga cecropioides* are investigated. Among the persistent monodominant old-growth forests, multiple types of monodominance and their drivers can be found, including water-logged forest such as mangroves and swamp forests, low-nutrient forests such as Amazonian caatinga and heath forests in Southeast Asia. We study the monodominant forest dominated by *Gilbertiodendron dewevrei* from which naturally occurring monodominant patches are commonly found across Central Africa alongside forests with high species.

### Lichens

#### *Sampled plots and estimation of lichen diversity*

Sampling of corticolous lichens was done according to the European Guidelines of mapping lichen diversity (Asta *et al.* 2002) with some adaptations. For 12 PSP trees were selected and sampled: six trees with a circumference of  $\geq 36$  cm were investigated with four frequency grids with the centre of each frequency ladder oriented N, E, S, W, respectively. For the other six trees with a circumference  $< 36$  cm all species present between 100 and 150 cm above ground were sampled. Tree data collected included species or genus (where possible), girth at breast height and some characteristics of the bark (smooth, peeling, rough,...). All the corticolous lichen species samples that were large enough to allow identification were collected for microscopic and chemical investigation (by spot tests and TLC). All samples collected were labelled with plot and tree number to facilitate data entry, placing each in a separate bag. The trunk was searched for additional species giving total diversity for each tree. Additional species found in the plot were included in plot diversity. This included material from other trees. Within plots species were collected erratically, depending on time available. Lichens were dried in the sun and/or with a drying kiln. To quantify the foliicolous lichens at the 12 collecting sites 10-20 leaves were collected from different ferns and plants in the shrub layer within a radius of five meter around the investigated tree. In every plot at least six of them belonged to *Scaphopetalum thonneri* and six to *Marantaceae* sp. Concerning the leaves of other species of plants it was not possible to collect the same amount of leaves in every plot. So six leaves from different plants were selected at random. In general, only leaves with visible presence of foliicolous lichens were selected. Leaves were pressed between newspapers and dried in a modest way (sunlight and/or a drying kiln). To compare diversity data from the 16 studied plots a similar sample size was chosen. An ellipsoid grid of 16 cm length and 6.4 cm width, covering an area of ca. 100.5 cm<sup>2</sup>, was placed on the leaf in such a manner as to cover the leaf asymmetrically, with one edge of the grid touching the left margin of the leaf. Leaves with a smaller surface were also collected but not investigated. The leaves were studied by means of a binocular. All the species on the up- and underside were noted. Lichen richness of the corticolous lichens corresponded to the total number of corticolous lichen species per plot. Cover data of the corticolous lichens were used to calculate the LDV (Lichen Diversity Values) according to Asta *et al.* (2002). The Shannon-Wiener diversity index was calculated for the foliicolous lichens with the program EstimateS 9 for Windows (Colwell 2013).

*Environmental variables characterising the plots*

Ancillary variables were used to characterize the plots: the mean DBH of all the trees in the plot with a DBH  $\geq 10$  cm (ATD), the mean circumference of the investigated trees (ATCI), the distance of the plot to the main road (DIS) and the number of trees in the plot with a DHD  $\geq 10$  cm (NT) (Table 4).

**Table 4:** Environmental variables characterising the plots. ATD = the mean DBH in cm of all the trees in the plot with a DBH  $\geq 10$  cm, ATCI = the mean circumference in cm of the investigated trees, DIS = the distance of the plot to the main road in m, NTS = the number of trees in the plot with a DBH  $\geq 10$  cm.

Plots	ATD (cm)	ATCI (cm)	DIS (m)	NTS
BRA 1	81,74	87,37	3600	378
GIL 1	80,98	32,46	6600	347
GIL 2	78,95	50,21	7500	436
GIL 3	81,05	50,18	3000	376
GIL 4	77,96	80,79	2500	374
GIL 5	97,90	38,63	890	231
JEU 1	90,94	79,92	680	322
JEU 2	74,11	47,29	3200	448
JEU 3	41,04	42,00	3300	350
JEU 4	72,52	60,86	2900	237
JEU 5	42,00	32,41	2800	132
MIX 2	74,24	46,53	3300	563
MIX 3	87,19	98,70	170	403
MIX 4	84,10	55,38	140	367
MIX 5	82,01	53,23	4200	432
MIX 6	83,23	59,40	3600	328

*Data analyses*

Pearson's correlation analyses were carried out to detect which variables were highly correlated and thus colinear. To avoid unreliable analysis results related to high intercorrelation among independent variables (Sokal & Rohlf 2000), the threshold value for deciding on colinearity was set to a correlation coefficient ( $r$ ) of 0.74 (Variance Inflation Factor  $\gg 1$ ). No environmental variable exceeded  $r = 0.74$  with other environmental variables (Table 5). The total number of foliicolous lichen species per plot was highly positively correlated to SHA ( $r = 0.96$ ,  $p < 0.05$ ) so SHA was not used in the further analyses.

**Table 5:** Pearson's correlation coefficients  $r$  between environmental variables. DIS = the distance of the plot to the main road in m, NT = the number of trees in the plot with a DHD  $\geq 10$  cm, ATD = the mean DBH of all the trees in the plot in cm with a DBH  $\geq 10$  cm, ATCI = the mean circumference of the investigated trees in cm. (Marked correlations are significant at  $p < .05000$ ;  $N = 16$ ).

	NT	ATD	ATCI
DIST	0.237 ( $p=0.4$ )	-0.205 ( $p=0.5$ )	-0.413 ( $p=0.1$ )
NTS		0.253 ( $p=0.3$ )	0.197 ( $p=0.5$ )
ATD			0.403 ( $p=0.1$ )

Since no correlations were significant further analysis were performed with all the four variables.

#### Small mammals

We conducted fieldwork in 2013 and 2014 and supervised the fieldwork of master students of the university of Antwerp in the Y-MaB in 2015 and 2016. The fieldwork was organised in collaboration with the CSB at UNIKIS. During each trapping campaign we sampled three PSP and applied the same protocol. In short, rodents and shrews were collected using the Paceline Method which consists of placing traps at regular intervals on transects. On each trapping station, three types of traps were combined: Sherman LFA traps, Victor snap traps and Pitfall traps (connected with drift fences). Traps were left into place for 21 days and checked daily at dawn. For all collected specimens the weight, length and reproductive status were recorded. Specimens were identified up till the genus level in the field. Animals were dissected after which samples were taken of liver, kidney, spleen, endo- and ectoparasites and blood. Additionally, we collected invertebrates caught in pitfall traps for *Laboulbeniales* research at the Botanic Garden Meise.

Genetic analyses needed to confirm the species identification were carried out at the RBINS. For rodents the cytochrome b, for shrews the 16S rRNA was sequenced. DNA sequences were blasted against a representative database which we compiled using DNA sequences generated during previous research at the UA and RBINS. Collected specimens were also screened for zoonotic diseases such as monkeypox and *Bartonella*.

#### Myxomycetes and protosteloid amoebae

Between 26th October and 19th November 2013 fieldwork was performed in Yangambi Man and Biosphere Reserve. A total of 286 specimens were collected and 15 photographic records of myxomycetes were made in the 11 COBIMFO plots that were visited during this field campaign. In addition 63 samples were collected from three substrate types, AL (33), ground litter (GL, 12) and bark from living trees or aerial bark (AB, 18). These substrates are intended for agar and moist chamber cultures of protosteloid amoebae and additional records of myxomycetes.

Protosteloid amoebae and myxomycetes are two groups of plasmodial slime molds which are bacterivorous, amoeboflagellate protists (Amoebozoa). They represent an important portion of the soil protozoa and play a significant role in unlocking nutrients held by bacteria and, thus assist in soil fertilization. In the context of COBIMFO this group represents a part of the CO<sub>2</sub> unlocking organisms.

The results of this survey in the Yangambi will be combined with the species lists of the Congo 2010 expedition and records from herbaria (APM and GENT) for a paper treating the myxomycetes of D.R. Congo to be submitted by the end of 2015. All new records will be added to the update of the checklist of Africa (Ndiritu et al, 2009B) this publication will be prepared in 2016. Images from typical specimens will be used in the issue treating myxomycetes and protosteloid amoebae of the series Fungus Flora of Tropical Africa published by the Botanic Garden, Meise.

#### *Field collections*

The total sampling time per plot was 6 hours. In some cases, for example due to frequent heavy rainfall sampling was interrupted, and was continued during a second and even third day to obtain the total of 6 hours of sampling. The plot GIL 5 was visited only once for 4 hours, it was advised against returning there by local people because of problems with the inhabitants near that plot. The plot BRA 1 was also visited once for 4 hours, because it was too disturbed by people walking through it. Table 1 shows the visited plots and respective sampling dates. Sampling was done by

walking through the plot and investigating potential substrates. Voucher samples were collected and in some cases, when macroscopic identification was possible and certain, photographic records were taken of common species. Substrates were collected to put into cultures for protosteloid amoebae and additional myxomycetes.

### *Cultures*

The protocol for moist chamber cultures can be found the web site of the Department of Biological Sciences of the University of Arkansas (<http://slimemold.uark.edu/>) or in Stephenson and Stempen (1994).

A total of 63 samples were collected representing three substrate types, aerial litter (AL, 33), ground litter (GL, 12) and bark from living trees = aerial bark (AB, 18). Aerial litter was taken from 4 plant species, *Anonidium mannii* (9), cf. *Microsorium punctatum* (6), *Musa* sp. (8) and *Palisota* sp. (10). The substrates from *Musa* sp. were all taken outside, but some were in the close vicinity of the plots. There are two types of AB samples. The first type, ABT (11), represents samples taken from the trunk of a selection of living trees in the central area of the plot between 1.5 m and 2 m from the ground level. The second sample type ABB (7) was taken from a branch that was cut from a living tree for sampling lichens. The GL samples are a mix of plant litter collected in the central area of the plots. All of the collected material was air-dried on site in separate paper bags.

### *Primary isolation plates of aerial litter samples*

A representative portion of each substrate sample was cut into strips of about 0.5 cm wide and 4 cm long and soaked in sterile water for 30 min in an empty, sterile Petri dish. About six strips of one substrate sample were distributed evenly on a 9.4 cm x 16 mm Petri dish containing a weak malt yeast nutrient agar medium (1 liter of wMY medium: 0.002 g malt extract, 0.002 g yeast extract, 0.75 g K<sub>2</sub>HPO<sub>4</sub> and 15 g agar in distilled water) representing one primary isolation plate (PIP).

After an incubation-period of three days at room temperature the PIPs were examined under a compound microscope (System Biological Microscope BK 5000 Series) at x200 and x400 magnification every three days during the first three weeks, once a week for the next 8 weeks and from then on once a month. Usually after one month no more new records of protosteloid amoebae are to be expected, but myxomycetes can still develop in these cultures and therefore the plates were kept for two months extra, sometimes up to 5 months. Positive observations of the taxa were counted per strip in each plate. Species abundances were determined and divided in four classes according to Ndiritu et al. (2009A). A record of a taxon on one strip corresponds with a positive observation made in one field of view at x200 magnification. The relative abundance is the percentage of the number of records made on all strips and is divided by total number of strips made on the PIPs from all the samples. Abundance Categories are: > 10% of samples = abundant (A); 5–10% = common (C); 1–5% = occasional (O); < 1% = rare (R).

### *Moist chamber cultures of aerial litter and ground litter*

The remaining portion of the substrate AL samples which was not used for the PIPs was soaked for an additional 30 min. After this period the excess water was poured off and pH was measured with indicator strips (pH-Fix, Carl Roth). The plate was kept at room temperature for a minimum of 3 months. Sterile water was added regularly to prevent the plate from drying out. The plates were observed in the first 4 weeks 2 to 3 times per week with a stereomicroscope (Olympus SZX 10) with zoom magnification of max x126. Positive results, meaning the appearance of plasmodia and

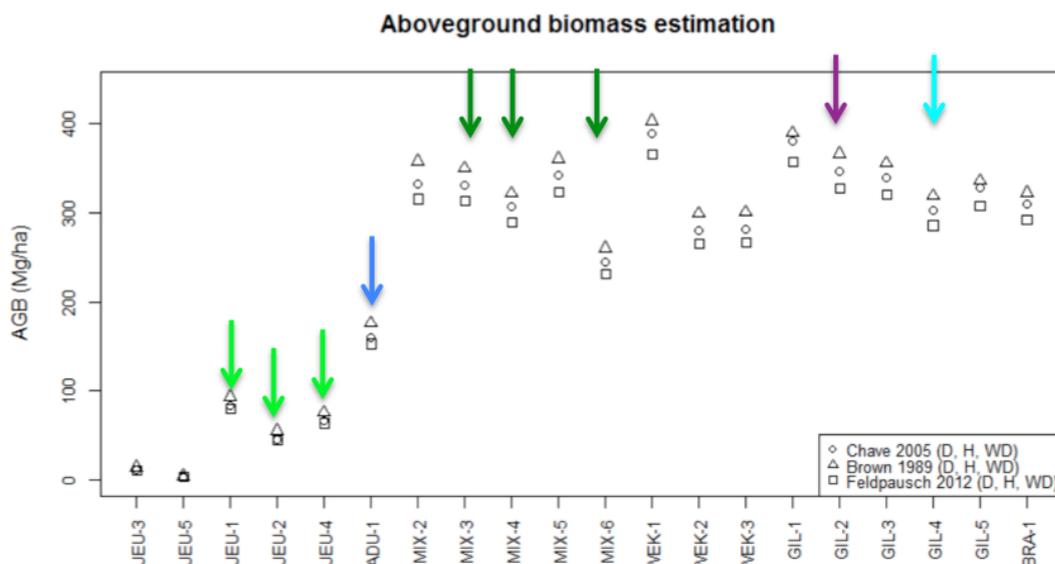
the development of fruiting bodies, were noted. In most cases voucher samples were taken from the fruiting bodies, in the case of assured visual identification photographic records were made. The same method was used for the GL samples, only larger 15 cm x 25 mm Petri dishes were used because of the larger dimensions of the substrate pieces like twigs and nuts.

### Ant monitoring

#### Study sites

According to the study of Kearsley et al. (Fig. 4) there are no significant differences in aboveground carbon stocks between forest types in old growth forest types, namely the mixed forests (with *Scorodophloeus zenkeri* as major -but not dominant- species, MIX), the *Gilbertiodendron dewevri* forests (GIL) and the *Brachystegia laurentii* forests (BRA). The young regrowth forest (JEU) has a lower stock and the old regrowth forest (ADU) an intermediate one.

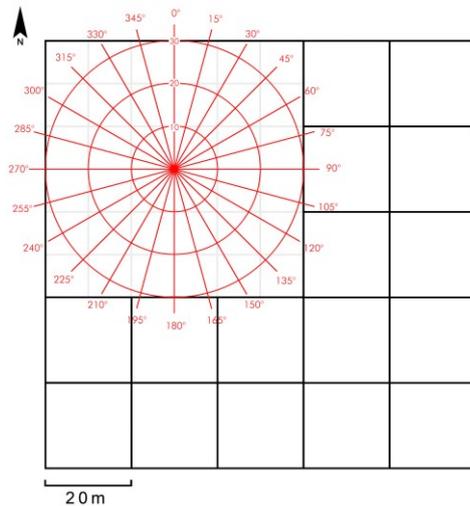
An inventory of all 21 COBIMFO plots was not possible due to time limitations. To address objective #1, we focussed on the major forest type (MIX) and compared 3 plots (JEU 1,2,4) with low carbon stock vs. 3 plots (MIX 3,4,6) with high carbon stock. In addition to address objective #2 we compared these mixed forests with 2 monodominant ones (GIL4, BRA1). Sampling of an intermediate carbon-stock plot (ADU) was started but finally aborted due to problems with land-owners.



**Figure 4:** Above ground carbon stock in the 21 COBIMFO plots calculated on the basis of the 3 allometric equations. The nine representative plot sampled for ants are indicated by arrows.

#### Arboreal ant sampling – mapping of colony spatial extension

The protocol, developed by Maurice Leponce and Alain Dejean, is based on baits spread every 5m along a rope. One end of the rope is tied around the trunk and, with the help of a sling-shot, the other is slung over a branch in the canopy, forming a loop that enables the baits to be easily brought back down for inspection (Fig. 6). Baits are composed of a mixture of proteins and carbohydrates, and are left for maximum 24 hours before being collected. The protocol allows the presence of dominant arboreal-nesting ants to be easily detected. A stratified ant distribution at the baits can be detected on tall trees. To address objective #3, on-site confrontations between dominant ants colonizing baits were performed to allow identifying colony spatial distribution among neighbour trees.



**Figure 5:** circular ant sampling area (in red, radius = 30m) located inside a 1ha botanical plot.



**Figure 6:** A sling shot (yellow pole) is used to install a rope at the top of tree. A bait is placed every 5 meters along the tree trunk and attracts arboreal ants.

## Diptera

### *Taxonomic impediment*

All species have been identified by now, resulting in 127 hybotid species with 120 species being new for science.

At the moment we paid special attention to the genus *Elaphropeza*, which are small hybotid flies that use leaves as their hunting substrate. All species have been described and keyed and their genitalia illustrated in order to produce a monograph for the Hybotid species of the Congo Basin. Most species have been barcoded using the COI gene, but more specimens should be sequenced during the next months in order to do an analysis of the phylogenetic diversity. Such an analysis will provide further insights in the evolution of the diversity of these flies in these rather young forests.

### 3.4 WP4 Integration of carbon and biodiversity data

#### Diversity analysis for all taxa

##### *Diversity measures*

A literature study is conducted on the current advances in the field of diversity measuring, focussing on community diversity measures. We characterized the taxonomic dimension of biodiversity using metrics of alpha and beta diversity. In this study we define alpha diversity as local measurements of diversity including species richness, Shannon entropy (Shannon & Weaver, 1949) and the Gini-Simpson's index (Simpson, 1949). Each metric was transformed into effective number of species (or Hill number) to represent "true" biodiversity (Jost, 2006), which is the effective number of equally abundant species that would be needed to produce the same value as that of an empirical metric (Chao et al., 2014). Species richness is a count of the number of species, and already expressed as a Hill number. In contrast, metrics weighed by species abundances are entropies and consequently require transformation. We therefore used the exponential of Shannon entropy (hereafter Shannon diversity), and the inverse Simpson concentration (hereafter Simpson diversity). Because empirical species diversity, regardless of metric, is a function of the number of sampled individuals, regardless of plot size, estimates were standardized for completeness. Sample completeness is the proportion of the total number of individuals in an assemblage that belong to the species represented in the sample, and can be estimated based on sampling curves; as recommended, extrapolation for each metric at each site was executed to twice the empirical sample size before standardization (Chao & Jost, 2012).

Beta diversity was expressed as pairwise dissimilarities in species composition between plots and were quantified by Sørensen (Sørensen, 1948) and Morisita-Horn (Morisita, 1959) indices. The Sørensen index quantifies similarity based on the ratio of the number of shared species ( $S_{12}$ ) in two plots (1 and 2) to the mean number of species in those same plots ( $(S_1 + S_2)/2$ ). Because the Morisita-Horn index is based on the squared differences of the relative abundances of species, its magnitude is dominated by the most abundant species, with rare species contributing relatively little (Jost, Chao, & Chazdon, 2011). When two assemblages are equally diverse and consist entirely of equally abundant species, the Morisita-Horn index is equal to the Sørensen index. Based on additive inverse relationships, we transformed each similarity measure to its corresponding dissimilarity measure (beta diversity).

To identify species of local or regional conservation concern, we assessed the occurrence of species in low carbon forests (LCF) and high carbon forests (HCF), represented by regrowth and old growth forests, respectively. We used two different methods: one based on species presences and one based on the abundance distribution of species. Firstly, we counted the number of species that were observed only in LCF or only in HCF versus the species that occurred in both habitats. Secondly, we used a statistical classification approach (Chazdon et al., 2011) to identify habitat specialists versus generalists. Using a multinomial model based on relative abundances of species in each of two habitats, the method minimizes bias due to differences in sampling intensities between two habitat types as well as bias due to insufficient sampling within each habitat. The method permits a robust statistical classification of habitat generalists and specialists without excluding rare species a priori. We used a threshold of 0.67, to classify species into one of four groups: (1) generalist; (2) low carbon habitat specialist; (3) high carbon habitat specialist; and (4) too rare to classify with confidence.

Because we wished to use the most robust estimates, plots with an extrapolated coverage lower than 0.85 were omitted from consideration in all analyses (except for the identification of specialist species). When abundances were unavailable, as in the case of slime molds and fungi, only species richness, Sørensen index and specialist species based on occurrences were determined. All calculations were performed in R 3.1 (R Core Team, 2014) using the packages iNEXT (sample completeness; Hsieh, Ma, & Chao, 2016) and SpadeR (similarity indices; Chao, Ma, & Hsieh, 2015).

We will also use the framework of Hill numbers to estimate phylogenetic and distance-based functional diversity, in order to achieve our main goal: using a wide range of parameters to measure biodiversity.

### *Statistical analyses*

To quantify relationships between aspects of taxonomic alpha diversity and carbon storage (i.e., random, linear, and non-linear relationships), we employed orthogonal polynomial regression analyses (Dutka & Ewens, 1971). Because we have no a priori empirical evidence or theoretical argument on which to base the exploration of higher-order polynomials, we considered second-order polynomials to capture linear and nonlinear relationships. Orthogonal polynomial regression decomposes the general relationship from ordinary polynomial regression into a suite of additive independent polynomials (e.g. zero-, first- and second-order relationships), whose coefficients ( $b^*0$ ,  $b^*1$  and  $b^*2$ ) represent their independent contributions, and whose statistical significance can then be evaluated in an unbiased fashion. Metrics of biodiversity were weighted by inverses of their standard deviation, thereby giving a higher weight to values with a higher certainty. We considered relationships to be significant if both the model and the linear or non-linear components were significant at an  $\alpha$ -level of 0.05. Relationships with significant quadratic terms were subsequently subjected to the Mitchell-Olds and Shaw test (MOS; Mitchell-Olds & Shaw 1987) to distinguish monotonic relationships from those with peaks or troughs. The MOS test is based on a determination of whether the predicted maximum or minimum of a quadratic relationship occurred within the bounds of the empirical data and we executed in R using *vegan*.

We used Mantel tests (Mantel, 1967) to quantify associations between differences in species composition (beta diversity) and differences in carbon storage among all possible pairs of plots. The Mantel test is a preferable alternative to simple Pearson correlation analysis because the former circumvents the problem of pseudoreplication by addressing partial dependence between the cells of matrices (Legendre & Legendre, 1998). We hypothesized that dissimilarity in species composition would increase with an increasing difference in carbon stock (i.e. a one-sided test). A Pearson correlation coefficient was used to determine the direction of association in cases for which the Mantel test was significant. To assess pseudoreplication, we used a Mantel test to evaluate the extent to which differences in species composition are related to differences in geographic distance between pairs of plots; we did so for each forest type separately and for the entire data set (Edwards et al., 2014). Mantel tests were performed with the R-package *ecodist* (Goslee & Urban, 2007) and significance was assessed with a Monte-Carlo procedure with 10000 permutations.

### Functional diversity indices and rarity of trees

The rarity or commonness of a species can reflect how much this species contributes to the total amount of carbon in the forest stand. In this study, the relationship between species rarity and its contribution to the functional diversity of the community is investigated.

Two aspects of rarity are investigated, namely an abundance-based rarity and a carbon-based rarity. The abundance-based rarity is expressed as the relative number of stems of each species

to the species with the highest number of stems, and represents rare species based on low number of occurrence. The carbon-based rarity is quantified using the species-specific AGC storage, with species-specific carbon as a percentage of the total AGC stock. The relationship between the abundance-based and carbon-based rarity is assessed to identify importance of occupancy and size within our definition of rare species. Additionally, a combined rarity rank with both relative abundance and AGC stock is addressed to quantify the functional contribution of species with both low presence and low AGC storage. This combined rarity rank is a normalized index calculated by multiplying log-transformed relative abundance and AGC stock.

Functional diversity indices are assessed for the aggregate of all plots within each forest type, thus for the combined 5 hectares within mixed and monodominant forest. To determine the contribution of each species to functional diversity we calculated the community convex hull volume which quantifies the volume inside the minimum convex hull containing all the species belonging to the community (Cornwell *et al.* 2006). This volume can be interpreted as a four dimensional structure containing all four selected traits for each species represented in the community and corresponds to a multivariate functional range, namely the functional trait space (FTS). The relative contribution of each species to the community divergence was quantified by separately removing each species and calculating the subsequent change in total FTS from the whole community.

However, relative changes in FTS do not quantify how different a species is from the other species in the community in terms of their functional traits. Therefore a distance-based functional diversity measure is calculated to address the functional distinctiveness (FD) of each species. Following Mouillot *et al.* (2013), the functional traits are used to estimate a Euclidian distance matrix between all species pairs and the most reliable functional dendrogram is used to link all species in functional space. Subsequently, the FD of each species is estimated using an equal-split approach of the dendrogram which reflects how functionally isolated a species is and therefore approximates how functionally distinct it is from other species (Redding & Mooers 2006). The equal-split of the dendrogram was performed using the R package 'ade4' and the function 'originality' (Dray & Dufour 2007). The association between the FTS contribution and FD for all species is tested by Spearman correlation.

The relationship between rarity ranking of species and FTS contribution and FD is assessed through linear and quantile regression. The linear relationship indicates trends of the means of the response variables, while quantile regressions (5<sup>th</sup> and 95<sup>th</sup> quantiles) quantify a linear relationship along upper and lower quantiles of the response variable (FTS or FD). The combination of both 5<sup>th</sup> and 95<sup>th</sup> quantile regressions will improve our understanding of the ranges of the two functional diversity indices along the rarity ranking.

### 77-year-old tree diversity experiment

#### *The role of species identity and diversity on carbon accrual*

This study was performed in a 77-year-old tree diversity experiment, in the surrounding of the Yangambi Man and Biosphere Reserve (N00°47'; E24°30'), in the DRC. The experiment was established in 1938 by the colonial Belgians, which held a large tropical agriculture and forest research center at this site. Information on the setup and the initial follow-up of the experiment could be tracked in the Belgian State Archive, until the decolonization in 1960. Since then, the experimental sites have been under the protection of the INERA (Institut National pour l'Etude et la Recherche Agronomique), the Congolese national institute for agricultural research, which means that there have been no logging activities until today. The total experimental plantation holds more than 50 ha of experimental plots. These were planted with a wide variety of tree

species in different tree species diversity levels (ranging from monospecific plots up to mixtures of six species). The total planted species pool consisted of 23 tree species, listed in Table 1. However, the majority of the plots contained only one or two planted tree species. Almost no repetitions of the different configurations were planted. The experiment contains plots of both 60 by 60 m (0.36 ha) and 40 by 40 m (0.16 ha). All plots were nursed and kept clear of spontaneous ingrowth, for ten years after planting, except those where *Pericopsis elata* [(Harms) Meeuwen] was planted, which were nursed for 20 years. After that, the plots were deliberately left unmanaged, so spontaneously in-growing species now accompany the planted species, augmenting the total realized species pool to 143 tree species in all plots.

For this study, we wanted to assess both the tree species identity and admixture effects, i.e. the effect of adding one other species in the monoculture, on the long-term carbon sequestration. We therefore selected 13 target tree species, i.e. the species which were planted in at least one monospecific and one two-species mixture, as shown in Table 1. We grouped the plots in 13 groups, each time consisting of the monoculture(s) and admixture(s) of the target species with the admixed species. Remark that in some cases, the admixed species is also a target tree species, and thus also found as a monoculture in the plantation. We inventoried a total of 29 plots, consisting of 14 monocultures and 15 two-species mixtures. Each plot was subdivided in either 4 (for the 0.16 ha plots) or 9 subplots of 20 by 20 m (for the 0.36 ha plots), resulting in a total dataset of 201 subplots.

An international standardized protocol for tropical forest inventories (RAINFOR, Malhi et al. 2002) was used. We considered both the planted tree species (one or two) and the species that spontaneously established in the subplots. In each subplot, the diameter of all live stems with a diameter larger than 10 cm was measured at 1.3 m height and the trees were identified to species level. Tree height was measured on 20% of all individuals in each plot, selected across all the diameter classes, using a hypsometer (Vertex III, Haglöf, Sweden). We use abbreviations of the planted species, of which the full scientific name can be found in Table A1. Extra parameters were assigned to each plot to indicate the nursing treatment (group of *P.elata* was kept clear of spontaneous ingrowth for a longer time) and the inclusion of nitrogen fixing tree species in the plantation scheme. We treated all *Fabaceae* members as potential nitrogen fixers (see Table A1).

At five different places within every plot, soil samples were taken at five depth increments (0-10, 10-20, 20-30, 30-50 and 50-100 cm) and these samples were pooled per depth increment. All samples were dried for 48 hours at 60°C. Carbon and nitrogen content were analyzed using an elemental analyzer (Automated Nitrogen Carbon Analyser, interfaced with a Sercon 20-20 IRMS; SerCon, Cheshire, UK). In addition, spread over the whole study area, seven soil pits to 1 m depth were dug, and bulk density was measured in the wall of these pits at different depths (20, 40 and 80 cm) using container rings of known volume (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). We determined the bulk density for the upper soil layer (0 -10 cm) at three locations within each plot using container rings.

For the calculation of the aboveground carbon stock (AGC) in the trees, we used the formula of Chave et al. (2005), including wood density and tree height. First, we fitted different diameter-height relationships from literature (see Table A2 in Supporting Information) by non-linear least-squares estimations for every plot, using the actual tree height measurements from the field. The best fit for every plot was selected based on the Akaike Information Criterion (AIC) and the

residual variation. Broken and strongly leaning trees were measured separately and were not included in the fitting process. The best fit was then used to estimate the unknown tree heights. We used wood density data that were collected in the surrounding natural forest by taking 5 x 5 x 5cm<sup>3</sup> wood samples from under the bark (Kearsley et al., 2013). If no species data was available from this dataset, we used species averages from the DRYAD global wood density database (Jerome Chave et al., 2009; Zanne et al., 2009) or genus averages from both databases to assign wood densities to the individual trees. We assumed a carbon content of 50% in the woody biomass for the final carbon stock calculations.

For the soil organic carbon stock (SOC) down to one meter depth, the averages of the bulk density measurements from the soil pits were used in combination with the specific carbon content from the plot-level composite samples for the bottom four increment layers. Because of the higher variation of the bulk density of the topsoil and the high contribution of this soil layer to the total SOC stock to 1 m depth, we used the plot-specific bulk density and C measurements for the topsoil.

Based on the results of the inventory, we derived subplot-level planted tree species richness (monospecific or two species mixture), effective tree species richness (planted tree species as well as spontaneous ingrowth), effective Simpson diversity, and the proportion of planted species in the stand basal area ( $BA_{pl}$ ). In a second stage, we replaced the taxonomic target species group as a fixed effect with functional types that summarized the functional role of the planted species (*functional type*). For that purpose, we compiled a simple trait matrix with information on wood density and shade tolerance of all the planted tree species. Wood density is an important trait, strongly linked to the functional ecology of tree species (e.g. Chave et al. 2009), while shade tolerance is a crucial life-history trait, associated with a wide range of physical and chemical plant traits (Valladares & Niinemets 2008). Information on shade tolerance was derived from literature (Lebrun & Gilbert 1954; Hawthorne 1995; Hubau et al. 2012), giving priority to the publication of Lebrun & Gilbert (1954), who based their classification on field observations of seedlings in natural forest in Yangambi. They used three classes – light-demanding, shade-tolerant and shade species - with increasing tolerance to shade. Based on this trait matrix, we performed a hierarchical clustering on the different tree species, and divided them in functional types. We choose four functional types, since there were two distinct groups of light-demanding species with differing wood density properties (Table 2). We tested the differences in wood densities between the types using a non-parametric Kruskal-Wallis test, and the significant association of the shade tolerance with the types using a non-parametric chi-square test.

To analyze the influence of tree species diversity and composition on subplot-level AGC (n=201), we applied linear mixed effects models. Plot was set as random intercept and AGC was log-transformed. We started off with a model containing all calculated compositional parameters for the subplots as fixed effects (i.e. the target species group, planted tree species richness, effective species richness, effective Simpson diversity, the  $BA_{pl}$ , the presence/absence of nitrogen fixers among the planted species and the nursing treatment). The non-categorical variables were standardized to make the parameter estimates of the fixed effects comparable. First, we tested the random structure, keeping the fixed effects structure constant (with parameter estimation via restricted maximum likelihood). Once the optimal random structure was found, the fixed effects were backwards selected, based on the AIC and likelihood ratio tests using maximum likelihood estimations. Finally, the marginal and conditional  $R^2$  were calculated for the final model, which indicate the proportion of the variance that is explained by the fixed

structure, respectively the fixed and random structures together (Nakagawa & Schielzeth 2013). We additionally checked Spearman correlations in the pooled dataset ( $n=201$ ) between  $BA_{pl}$ , effective species richness and AGC, to increase the interpretability of the mixed effects model results.

Subsequently, we used the functional types to replace the taxonomic target species groups as a fixed effect in the model. Both final models were compared using likelihood ratio tests and AIC. To gain insight in how  $BA_{pl}$ , as an important fixed effect, was linked to the functional identity of the planted species, ANOVA was additionally done, with  $BA_{pl}$  as dependent variable and the functional types as independent variable on the plot level ( $n=29$ ).

Finally, we checked whether the SOC stock (to 1 m depth) was correlated to AGC on the plot level, by calculating Spearman correlation coefficients. Subsequently, we repeated the modelling steps on the plot-level for the SOC with all the compositional parameters in the first model as fixed effects. All statistical analyses were conducted with R version 3.1.1 (R Development Core Team, 2015). We used the 'nmle' package for the mixed effects modeling (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2013).

#### *Tree species effects*

We characterized the nutrient concentration of the topsoil, litter layer and tree canopy in three randomly chosen subplots per plot (87 subplots in total; 3 replications per plot). In each subplot, we took a composite sample of the top 0-5 cm and 5-10 cm layer of mineral soil at 5 random locations (4 or 9 replications per plot). Additionally, we collected plot-level composite samples of deeper soil layers from five different places within every plot (10-20, 20-30, 30-50 and 50-100 cm; no replications). The litter layer was collected from one randomly located 0.25 m by 0.25 m square per subplot (4 or 9 replications per plot). The canopy of every subplot was characterised by selecting the most abundant tree species, constituting 95% of the basal area of the selected subplots, and by sampling mature leaves of a minimum of two individuals per species using tree climbers. This sampling was carried out at the level of the total experiment. Species occurring in multiple subplots were not sampled in every subplot, resulting in a total of 65 tree species and 354 individuals sampled.

Topsoil (0 - 5 cm), litter and leaf samples were dried for 48 hours at 60°C. Roots were picked out of the soil samples before grinding and subsequently C and nitrogen (N) concentration of tree and soil samples were analysed using an elemental analyser (Automated Nitrogen Carbon Analyser), interfaced with an Isotope Ratios Mass Spectrometer (IRMS; 20-20, SerCon, UK). The soil pH ( $pH_{KCl}$ ) of each sample was analysed using a glass electrode (Model 920A, Orion, England) after suspension of 14 ml soil in a 70 mL KCl (1 M) solution (ISO10390). Exchangeable Ca, Mg and K were quantified by saturating cation exchange sites with ammonium acetate buffered at pH 7.0 and by subsequently measuring the cation concentrations in the filtrated extracts with Atomic Absorption Spectroscopy (AAS) (AA240FS, Agilent Technologies, US). Exchangeable Al was extracted by 1 M KCl solution and determined by inductively coupled plasma (ICP; Iris intrepid II XSP, Thermo Scientific, US) and optical emission spectrometry. Additionally, we titrated this extract with sodium hydroxide to determine the exchangeable acidity ( $H^+$  and  $Al^{3+}$ ) (Van Ranst, Verloo, Demeyer, & Pauwels, 1999). For total P, soil samples were treated with  $HClO_4$ ,  $HNO_3$  and  $H_2SO_4$  for 4 hours at 150°C, after which phosphate concentrations were measured colorimetrically with malachite green (Varian Cary50, Agilent Technologies, US; Lajtha *et al.* 1999). Resin P was analysed as a proxy for plant-available P (A. H. Johnson, Frizano, & Vann, 2003; Saggar, Hedley, & White, 1990). This was done by shaking

1 g of soil for 16 hours with distilled water and activated resin membranes, and subsequently shaking the membranes for 16 hours in a 0.5 M HCl solution. P analysis of the extracts was done using standard colorimetry kits. Fresh leaf and litter samples were dry-ashed at 550°C for 5.5 hours; the ash was dissolved in 2M HCl solution and subsequently filtered through a P-free filter. The aliquots were then analysed for total P by colorimetry and for calcium (Ca), magnesium (Mg) and potassium (K) by AAS (Ryan, Estefan, & Rashid, 2001). Additionally, to have a general idea of the topsoil texture, sand vs silt and clay concentration of 11 randomly selected, pre-treated (organics destroyed with 20% H<sub>2</sub>O<sub>2</sub>; aggregates disaggregated with 0.1M Na<sub>4</sub>P<sub>2</sub>O<sub>7</sub>) soil samples of the 0 - 5 cm layer was determined. The procedure for C and pH was repeated for the soil samples of the deeper soil layers.

Average leaf chemical trait values (C, N, P, C:N, N:P, Ca, Mg, K) were calculated for every selected species. Subsequently, we assigned a basal area weighted-average canopy value to every subplot using the subplot's species composition, to calculate an average nutrient concentration for the canopy of every selected subplot (n=87). For litter and soil, we had one (composite) sample per subplot. We then averaged all subplot values for canopy, litter and soil variables to plot-level variables (n=29), and further used these plot-level variables in the statistical analyses. Principal component analyses (PCA's) were done on the standardized variables for every compartment (soil, litter, and canopy) separately to check variability and correlations within each of these compartments. For interpretability we rotated the first two principal components of the soil, litter and canopy compartment, using a Varimax rotation. For the links between canopy, litter and topsoil, we calculated bivariate Pearson correlations between all the variables and subsequently used multiple linear regression to link canopy and litter characteristics to multiple key topsoil variables: C concentration, N concentration, available P, C:N ratio, N:P ratio (with available P), pH and exchangeable acidity (H<sup>+</sup> and Al<sup>3+</sup>).

We considered both canopy and litter chemical variables as plant-related traits to relate the biotic aboveground part to the topsoil for two reasons: (1) each species has specific nutrient resorption strategies, meaning that the canopy nutrient values and ratios can deviate from the actual litterfall input, and (2) each species and individual has a different leaf productivity, which is not accounted for in our basal-area weighted mean. As such, litter layer sampling includes freshly fallen leaves as well as partly decomposed leaves. To avoid problems with collinearity, because of the strong correlations of some of our predictor variables, we (1) first did preliminary stepwise multiple regression with the canopy and litter variables separately (using a starting set of 8 variables for both compartments, as shown in SI 2) for the different response variables, and (2) used only the retained variables from this first step for a stepwise regression including both canopy and litter variables. In stepwise multiple regressions, Akaike's information criterion (AIC) was used as stopping criterion, which penalizes for the number of predictor variables that are retained in the model. After every parameter selection step, the variance inflation factors (VIF) were calculated to verify if the retained variables did not cause multicollinearity problems. If the VIF of two or more variables was greater than 3, we retained the single variable with the strongest Pearson correlation with the response variable (Zuur, Ieno, & Elphick, 2010).

Finally, we estimated the extent of the tree-community effects on soil carbon and soil pH. For this, canopy and litter layer characteristics of the different plots were related to the pH and the carbon concentrations of the different soil layers, using the same multiple linear regression model. All statistical analyses were conducted with R version 3.2.3 (R Development Core Team, 2015).



## 4. INTERMEDIARY RESULTS

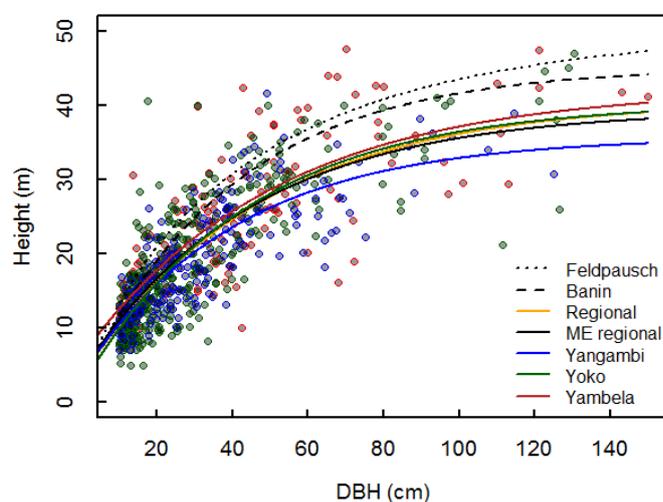
### 4.1 WP2 Baseline C inventory

#### Tree allometry and carbon stocks

In the previous annual report, it is shown that a lower aboveground carbon storage is found in Yangambi related to a lower tree stature at this site. We can now show the generality of these results for 2 other sites in this region, namely Yoko and Yambela.

#### *Lower tree height generally found in this region*

We present a general height-diameter relationship for this region in the central Congo Basin based on measurements in three old-growth forest sites (Yangambi, Yoko and Yambela; Figure 7). A lower asymptotic tree height is found compared to the current general relationships by Feldpausch *et al.* (2012) and Banin *et al.* (2012). These generalized models for Central Africa systematically overestimate tree height in this region. Additionally, all site-specific random deviations from the mixed effects height-diameter model show a lower height-diameter relationship compared to the general Central African relationships, emphasizing the generality of the results. This confirms that the lower tree heights found earlier locally in Yangambi (*Chapter 3*) is probably applicable for a larger area in the central Congo Basin. The central Congo Basin region as defined by Feldpausch *et al.* (2012) is possibly too large for a uniform height-diameter relationship, bringing forward the need for better demarcation of regions with similar forest structure in tropical Africa. Banin *et al.* (2012) showed that tree allometry is altered by environmental conditions, forest structure and wood density. However, the mean environmental and forest structure variables of our study region do not differ from those in the central African region as indicated by Feldpausch *et al.* (2011), with similar mean annual precipitation, temperature and dry season length. Therefore, other factors driving this differentiation may be related to soil properties, the local available species pool or past natural and anthropogenic disturbances (Clark & Clark 2000; Malhi *et al.* 2006). Within this study, we are not able to identify the importance of each of the different drivers. Yet, this result emphasizes the poor knowledge on spatial distributions of forest structure in tropical Africa (Saatchi *et al.* 2011; Batjes 2008), resulting in large uncertainties for carbon storage.



**Figure 7:** Height-diameter models for the studied region, namely the regional model (orange), the mixed effects regional model (full black line) with site-specific deviations for Yangambi (blue), Yoko (green) and Yambela (red). The generalized models for Central Africa by Feldpausch *et al.* (2012) (black dotted line) and Banin *et al.* (2012) (black dashed line) are indicated.

Soil organic carbon storage

While the focus of estimating carbon stocks traditionally lies on the living aboveground biomass, belowground soil organic carbon (SOC) stocks have received little attention. We now investigate SOC stocks in Yangambi and Yoko sites. We show that despite similar vegetation, soil and climatic conditions, SOC stocks in an area with greater tree height/aboveground biomass (Yoko) were only half compared to an area with lower tree height/aboveground biomass (Table 7). This suggests a substantial variability in the root:shoot carbon allocation strategy of two similar tropical tree communities for nutrient mining, especially potassium, and is reflected in changes of the SOC mass stored in fractions with differing functional interpretation. We argue that adaptation of tree communities to nutrient limitation as well as nutrient limitation as a constraint on microbial activity offers some explanation, specifically potassium. Our study highlights that a large and unaccounted variability in SOC stocks is to be expected in African tropical rainforests, introducing additional uncertainty in the response of tropical forest systems to climate change and its contribution to the current terrestrial carbon budget.

**Table 7:** Summary on average carbon stocks at both sites in different pools, and the combination of the measured pools (Total C), including standard deviations.

	C mass Mg ha <sup>-1</sup>			
	Litter	SOC	AGC	Total C
Yoko	1.8 ± 0.4	44.2 ± 4.0	189 ± 28	<b>234.8 ± 32.4</b>
Yangambi	2.0 ± 0.7	109.5 ± 21.4	157 ± 21	<b>268.5 ± 43.1</b>

Recensus

Data from the reinventory of the 21 PSP is currently being encoded.

Sampling in the edge setup

While analyses are still underway, preliminary result suggested a trade-off between wood density and height for trees located in core and edges forests.

Understory

The amount of wood mass and leaf mass of all individuals in the undisturbed and managed forest, within the small circle of the plot ( $r = 5.65$  m) is summarized in Table 8.

**Table 8:** wood mass and leaf mass of all individuals in the undisturbed and managed forest

plot	Plot radius (m)	Latitude	Longitude	catégorie de l'individu	Woody mass (kg)	Leaf mass (kg)
MIX5	5.65	0.81494° N	24.49374° E	Diameter at base < 1cm	4.56	2.15
				Diameter at base > = 1cm	208.97	23.41
managed	5.65	0.80137° N	24.47622 E	Diameter at base < 1cm	1.42	0.59
				Diameter at base > = 1cm	141.01	10.68

Table 8 highlights the existence of a historical impact of forestry on the biomass present in the understory. Indeed, in the plot of mixed forest which corresponds to a less disturbed forest (MIX5), as well as woody mass of leaves is higher than that measured in the plot of managed forest. The biomass in the plot PMIX5 is about twice higher than in the managed plot.

The number of individuals per family found in each plot is presented in table 9. The three families with the highest number of individuals in the plots are Fabaceae, Malvaceae and the Meliciaceae. The number of individuals of the most abundant family is always higher in the mixed plot.

**Table 9.** Number of individuals per family in both plots.

<b>Family</b>	<b>Mangaged</b>	<b>MIX5</b>	<b>Total</b>
Fabaceae	61	99	160
Malvaceae	34	105	139
Meliaceae	37	70	107
Annonaceae	14	82	96
Myristicaceae	4	64	68
Euphorbiaceae	17	37	54
Huaceae	26	19	45
Apocynaceae	4	32	36
Clusiaceae	12	21	33
Rubiaceae	4	22	26
Sapotaceae	12	11	23
Inconnue	6	15	21
Lecythidaceae	8	10	18
Ebenaceae	4	8	12
Olacaceae	7	4	11
Moraceae	3	7	10
Thomandersiaceae	1	9	10
Ochnaceae	0	8	8
Sapindaceae	3	4	7
Menispermaceae	1	5	6
Flacourtiaceae	0	4	4
Cannabaceae	3	0	3
Chrysobalanaceae	3	0	3
Pandaceae	0	3	3
Melastomataceae	0	2	2
Connaraceae	0	1	1
Icacinaceae	0	1	1
Urticaceae	1	0	1

#### Wood traits and wood specific gravity

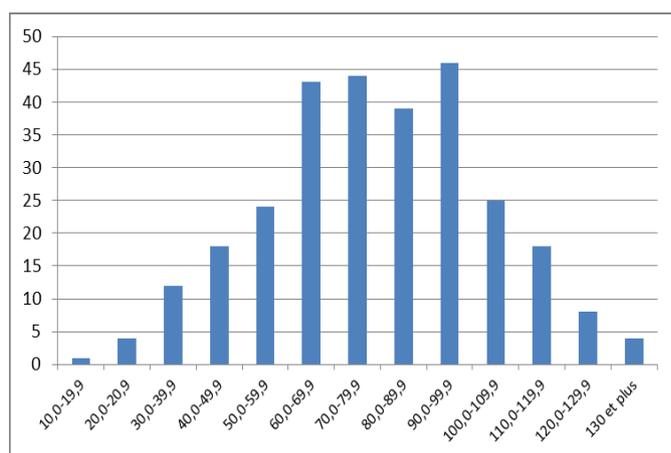
Preliminary results suggest a direct correlation between Wood Specific Gravity and fiber thickness, while a weak inverse correlation between Wood Specific Gravity and vessel diameter was observed. Furthermore, we showed that the Wood Specific Gravity is inversely correlated with water content, while the shrinkage ratio does not seem to be correlated to Wood Specific Gravity nor to the water content.

#### Large scale forest inventory

At this point only preliminary results are available, as presented in Table 10, 11 and Figures 8, 9, 10.

*Pericopsis elata***Table 10:** Estimated stem density per hectare (SD) by diameter class for *Pericopsis elata* after inventory in the reserve Yangambi.

Diameter class	Number of stems inventoried	SD /ha
10,0-19,9	1	0,008
20,0-20,9	4	0,016
30,0-39,9	12	0,048
40,0-49,9	18	0,072
50,0-59,9	24	0,096
60,0-69,9	43	0,172
70,0-79,9	44	0,176
80,0-89,9	39	0,156
90,0-99,9	46	0,184
100,0-109,9	25	0,1
110,0-119,9	18	0,072
120,0-129,9	8	0,032
> 130	4	0,016

**Figure 8:** Diameter distribution of all individuals of *Pericopsis elata* in the large scale forest inventory.

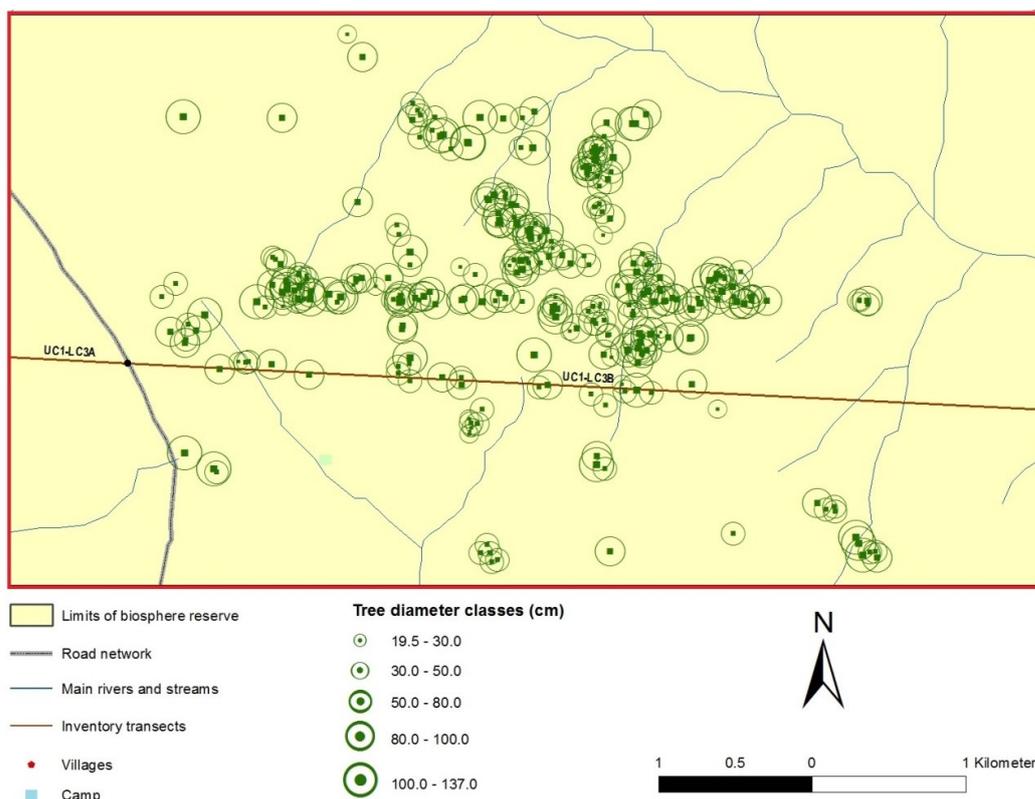


Figure 9: Geographical location of all individuals of *Pericopsis elata* inventoried in the reserve.

*Entandrophragma* spp.

Table 11: Number of inventoried stems by diameter class for the four species of *Entandrophragma* spp. encountered in the reserve Yangambi.

Species	Diameter classes										Total	
	0	1	2	3	4	5	6	7	8	9		10
<i>Entandrophragma angolense</i>	3	13	3	6		1	2	1	1	1	5	36
<i>Entandrophragma candollei</i>		11	1				2	1		3	20	38
<i>Entandrophragma cylindricum</i>	2	13	6	4		2	1	1		3	15	47
<i>Entandrophragma utile</i>	3	12	3	1	1	1	2	1				24
<b>Total</b>	<b>8</b>	<b>49</b>	<b>13</b>	<b>11</b>	<b>1</b>	<b>4</b>	<b>7</b>	<b>4</b>	<b>1</b>	<b>7</b>	<b>40</b>	<b>145</b>

Diameter classes 0: 5,0-9,9 cm ; 1: 10,0-19,9 cm ; 2: 20,0-29,9 cm ; ... ; 10: > 100,0 cm.

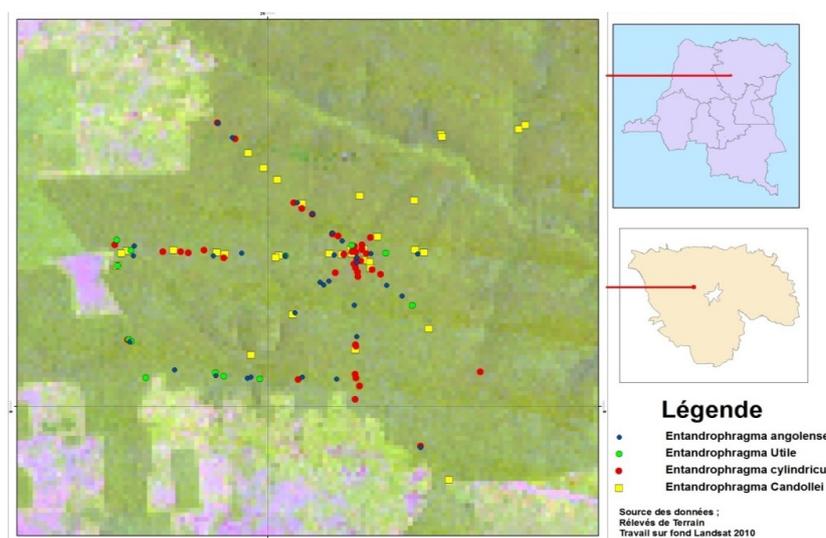


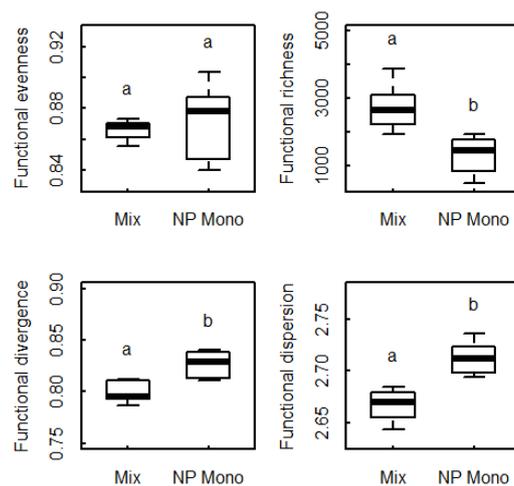
Figure 10: Geographical location of all individuals of *Entandrophragma* spp. inventoried in the reserve Yangambi.

## 4.2 WP3 Biodiversity monitoring

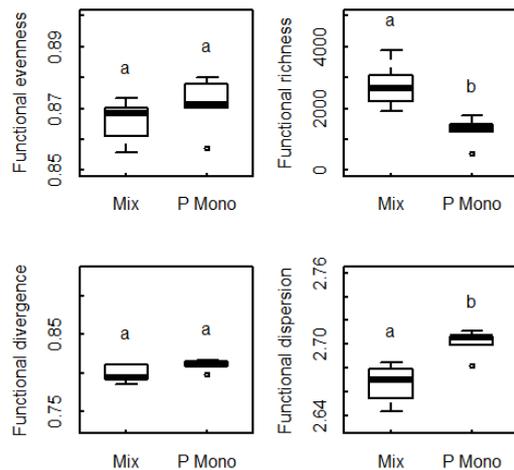
### Functional diversity of the tree community

#### *Monodominant vs mixed forests*

Species and trait diversity of persistent and non-persistent monodominant forest has been compared with an adjacent mixed forest. Lower species diversity is found both in the persistent and non-persistent monodominant forest compared to the mixed forest, with a lower overall species richness, species evenness index and Simpson's index. Both types of monodominant forest have a significantly lower functional richness compared to the mixed forest (Non-persistent monodominance  $p < 0.01$ , Figure 10; Persistent monodominance  $p < 0.01$ , Figure 11). Additionally, functional divergence and dispersion indicate a similar relationship for both monodominant forest types with the mixed forest (Figure 10 & 11). In the non-persistent monodominant forest, both functional divergence and dispersion show significantly higher values compared to the mixed forest ( $p < 0.01$ ; Figure 10). In the persistent monodominant forest, functional dispersion is also significantly higher, although the difference is not significant for functional divergence (Figure 11). Functional evenness is similar for both types of monodominant forest and the mixed forest.



**Figure 10:** Comparison of functional diversity measures of the non-persistent monodominant forest (NP Mono) and the adjacent mixed forest (Mix). Young and old Musanga regrowth forest make up the non-persistent monodominant forest. Functional diversity measures are calculated on a plot level and represented per forest type. Letters indicate if there is a significant difference ( $p < 0.01$ ) between the forest types.



**Figure 11:** Comparison of functional diversity measures of the persistent monodominant forest (P Mono) and the adjacent mixed forest (Mix). Functional diversity measures are calculated on a plot level and represented per forest type. Letters indicate if there is a significant difference ( $p < 0.01$ ) between the forest types.

We thus identified similar differences in functional diversity in both monodominant forest types compared to the adjacent mixed forest, with lower functional richness and higher functional divergence in the monodominant forests. In the persistent monodominant forest, shifts in community-level means are identified for nutrient contents, water use efficiency traits and specific leaf area. These shifts are driven by environmental filtering, possibly enforced by presence of the monodominant species by altering probabilities of traits suitable for this environment. In the non-persistent monodominant forest, differences in community-level means have also been identified, with its successional stage after deforestation the main driver of this difference. Shifts in N-P limitation have been identified for this young monodominant regrowth forest, in combination with shifts in resource acquisition and stress tolerance strategies. The non-persistent monodominant species itself does not show signs of influence on other species in this community.

## Lichens

### *Corticolous lichens*

In the 16 forest plots 3536 corticolous lichens specimens were observed and 721 samples collected. All species are crustaceous. Fruticose and foliose lichens are seldom encountered on canopy branches fallen on the ground. Forty-nine tree species could be identified up to species level, 11 to genus level and 15 could not be identified at all. The most investigated tree species was *Musanga cecropioides* with 16 specimens, followed by *Scorodophloeus zenkeri* with 13 specimens. Of the tree species identified up to species level 20 species (40%) were only once investigated. Ninety-nine corticolous lichen species were encountered. On tree stems with a circumference at BH of  $< 36$  cm ca. 61 species have been discovered, on tree stems with a circumference at BH of  $\geq 36$  cm ca. 90 species have been noted.

The most common species is *Porina* sp. followed by *Herpothallon* sp. and *Bacidia* sp. Most of the corticolous species are not yet identified to species level. Some of the species of the families of *Arthoniaceae* and *Graphidaceae* have been studied morphologically and chemically. The

study of *Graphidaceae* resulted in the discovery of a new species, described meanwhile as *Redingeria desseiniiana* (Van den Broeck et al. 2014) and in new records for DRC of some other species. The species of the family *Arthoniaceae* are current under study in the framework of a PhD concerning a revision of the genera *Arthonia* and *Arthothelium* in tropical Africa.

Fourteen species were only encountered in old grown forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii*. Twenty-one were only found in regrowth forests and eight in forests dominated by *Scorodophloeus zenkeri*. In total ca. 43% of the species was encountered only in one of the three forest types.

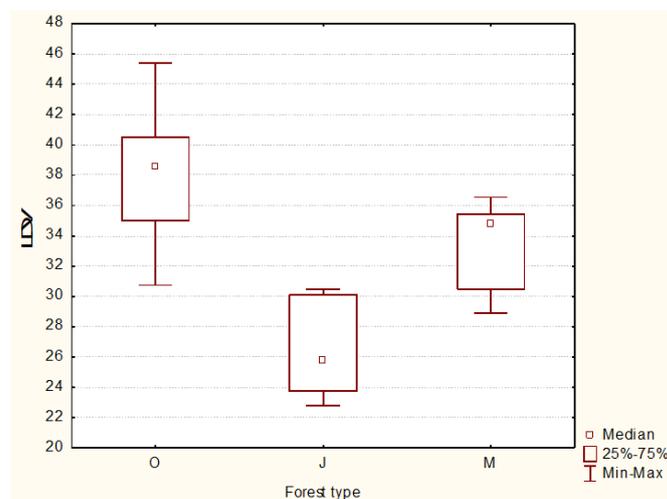
#### Relation between the forest type and the corticolous lichen diversity

The highest number (32) of corticolous species have been found in two forests: JEU 1 and GIL 2, the lowest (19) in MIX 3 (Table 12). The forest with the highest Lichen Diversity value is the forest dominated by *Brachystegia laurentii* (BRA 1), the forest with the lowest Lichen Diversity Value is JEU 2.

**Table 12:** Number of corticolous species (NC) per forest plot and Lichen Diversity Values (LDV).

	BRA1	GIL1	GIL2	GIL3	GIL4	GIL5	JEU1	JEU2	JEU3	JEU4	JEU5	MIX2	MIX3	MIX4	MIX5	MIX6
NC	30	25	32	27	23	23	32	24	22	28	22	28	19	24	20	23
LDV	25,7	22,8	21,3	22,9	13,6	21,2	15,3	14,2	17,0	18,4	15,0	20,5	15,3	20,2	20,3	16,9

To investigate if the corticolous lichen diversity differs between the tree forest types a non-parametric Kruskal-Wallis test was performed.



**Figure 12:** Differences in the diversity of corticolous lichen communities. O = old growth forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii*, J = regrowth forests, M = old growth mixed forests, LDV = Lichen Diversity Values.

The differences in Lichen Diversity Values between the tree forest types are only significant for the difference between the old growth forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii* and the young regrowth forest types (test Kruskal-Wallis  $H_{(2, 16)} = 1,13$ ;  $p < 0.05$ ). Old growth forests are characterized by a higher occurrence of lichen species in comparison with regrowth forests. The number of corticolous species (NC) do not significantly

differ between the tree forest types (results not shown). Lichen Diversity Values seems to allow a better differentiating.

#### *Effect of environmental variables on lichen diversity*

The relationships between Lichen Diversity Values (LDV), the number of corticolous lichens (NC) and the environmental variables (ATD, ATCI, DIST and NTS) were investigated using multiple linear regression with a forward stepwise selection procedure. The analyses were performed using STATISTICA.

**Table 13:** Result of multiple regressions (forward selection) between LDV as dependent variable and the environmental variables: the mean diameter of all the trees in the plot (ATD), the mean circumference of the investigated trees (ATCI), the distance of the plot to the main road (DIS) and the number of trees in the plot (NTS) as independent variables. Only the significant results are shown.

	Beta	Std.Err. of Beta	B	Std.Err. of B	t(13)	p-level
<b>Intercept</b>			12.681	7.382	1.718	0.110
<b>DIST</b>	0.593	0.209	0.002	0.0006	2.839	0.014
<b>ATD</b>	0.467	0.209	0.192	0.086	2.234	0.044

Regression Summary for Dependent Variable: LDV (Corticolous lichens): R= 0.675, R<sup>2</sup>= 0.456, Adjusted R<sup>2</sup>= 0.373; F(2,13)=5.454, p<0.01906, Std.Error of estimate: 4.962

The distance to the main road and the average DBH of the trees with a DHB  $\geq$  10 cm present in the plot are positively correlated with the LDV. Following the same procedure but with NC as dependent variable yielded no significant results. Forests further away from the main road have not less corticolous species but the species have a higher frequency of occurrence indicating that the ecological conditions for those species are better.

#### *The composition of the corticolous lichen communities*

To identify the corticolous species typical for the different forest types an indicator species analysis was performed. Only one species, *Agonimia papilata*, occurs significantly more in old growth mixed forests. Species occurring more in old growth forests are members of *Graphidaceae* (*Diorygma antillarum*, *Ocellularia* sp., *Stegobolus actinotus*, *Wirthiotrema santesonii*), *Ramalinaceae* (*Bacidia* sp.) or unidentified crusts. Species of *Herpothallon*, *Malcolmiella* and one species of *Graphidaceae* are more typical for young regrowth forests (Table 14)

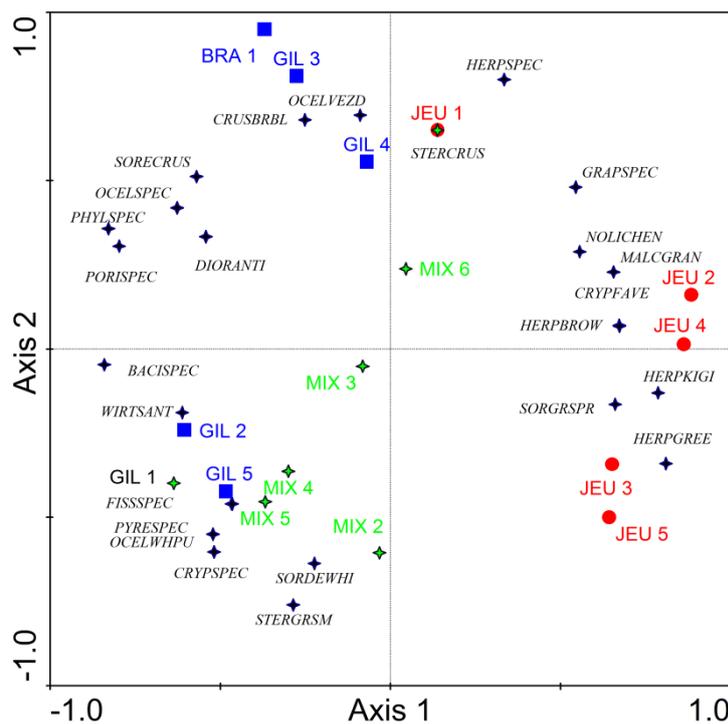
**Table 14:** Result of an indicator species analysis of corticolous species calculated with method of Dufrêne & Legendre (1997) with respect to the forest type. Only those species (with indication of the strength of the significance) are listed that were significantly ( $p \leq 0.05$ ) for a forest type after Monte Carlo test of significance of observed maximum indicator value for species (4999 permutations).

	old growth forests	old growth mixed forests	young regrowth forests
<i>Agonimia papilata</i>		$\leq 0.05$	
<i>Bacidia</i> sp.	<0.05		
<i>Diorygma antillarum</i>	$\leq 0.05$		
<i>Graphis</i> sp.			<0.05
<i>Herpothallon kigienze</i>			<0.01

<i>Herpothallon sp.</i>	< 0.05
<i>Malcolmiella granifera</i>	< 0.05
<i>Malcolmiella sp.</i>	< 0.01
<i>Ocellularia sp.</i>	< 0.01
<i>Sorediate crust</i>	< 0.01
<i>Sorediate crust with green spreading soralia</i>	< 0.01
<i>Stegobolus actinotus</i>	< 0.05
<i>Wirthiotrema santesonii</i>	< 0.05

*The composition of the foliicolous lichen communities*

To investigate the patterns of variation in lichen community composition and to identify the main factors shaping the composition of the lichen communities a Principal Component Analysis (PCA) was performed using the lichen composition of 16 forest plots using the computer package Canoco 4.5 (ter Braak & Šmilauer 2002). We used a linear ordination method because the largest length of gradient in a DCA was shorter than 3.0 suggesting that most of the corticolous species have a linear response to the environmental gradients (Lepš & Šmilauer 2000). Since all data were collected in a comparable forest habitat (rain forest) it can be expected that the gradients of the environmental variables are rather small.



**Figure 13:** PCA-ordination diagram (axes 1 and 2) of forest plots and corticolous lichen species (fit range > 39%). BRA = old growth forests dominated by *Brachystegia laurentii* (blue), Gil = old growth forests dominated by *Gilbertiodendron dewevrei* (blue), JEU = young regrowth forests (red), MIX = mixed old growth forests (green).

The corticolous lichen communities differ clearly between the forest types. Most young regrowth forests are characterized by the presence of hydrophobic cryptothecioid *Arthoniaceae* together with *Malcolmiella granifera* and an unidentified sorediate crust with green spreading soralia.

Trees devoid of lichens are also more occurring in young forests. Most of the forests dominated by *Scorodophloeus zenkeri* (mixed forests) are also characterized by sterile crusts together with another member of the hydrophobic cryptothecioid *Arthoniaceae*. But also some genera of the family of the *Graphidaceae* (*Ocellularia*, *Fissurina*, *Wirthiotrema*) and the genus *Pyrenulla* are more frequent in most of those forests. Forests dominated by *Gilbertiodendron dewevrei* are clearly split up in two groups. The forest dominated by *Brachystegia laurentii* is a member of the first group characterized by *Ocellularia vezdana* and a brown-black sterile crust. The other group shares more or less the same lichen communities as most of the mixed forests.

#### *Foliicolous lichens*

On 288 leaves a total of 154 taxa (139 foliicolous lichens and 15 lichenicolous fungi) from 41 genera and 21 families were recorded (App. 1, table 4). Not all species could be identified to species level. So new taxa are to be expected. Three of them have already been described as new to science and were published together with other new foliicolous species found during the expeditions in 2009 and 2010 (Van den Broeck *et al.* 2014). The most common species, occurring on 46% of the leaves, is *Mazosia phyllosema*. As is usual in biotic community data sets, most species are rare. Thirty-three species occurred only on one of the 288 leaves whereas 69% of the taxa occurred on less than 5% of the leaves.

On 96 leaves of *Scaphopetalum thonneri* 108 foliicolous lichens and 11 lichenicolous fungi were identified. Out of these, 93 were identified to a species level, 24 were identified to a genus level and two species could not be assigned to any particular species or genus. On 96 leaves of *Marantaceae* sp. 89 foliicolous lichens and five lichenicolous fungi were identified. Out of these 24 were identified to a genus level and two could not be assigned to any particular species or genus. On 96 leaves of other unidentified plants and shrubs 101 foliicolous lichens and five lichenicolous fungi were noted. Out of these 82 were identified to a species level, 16 were identified to a genus level and tree species could not be assigned to any particular species or genus.

Fourteen species were only encountered in old grown forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii*. Thirteen were only found in regrowth forests and eight in forests dominated by *Scorodophloeus zenkeri*, most of them only one or two times indicating that it are generally rare species. In total ca. 23% of the species was encountered only in one of the three forest types.

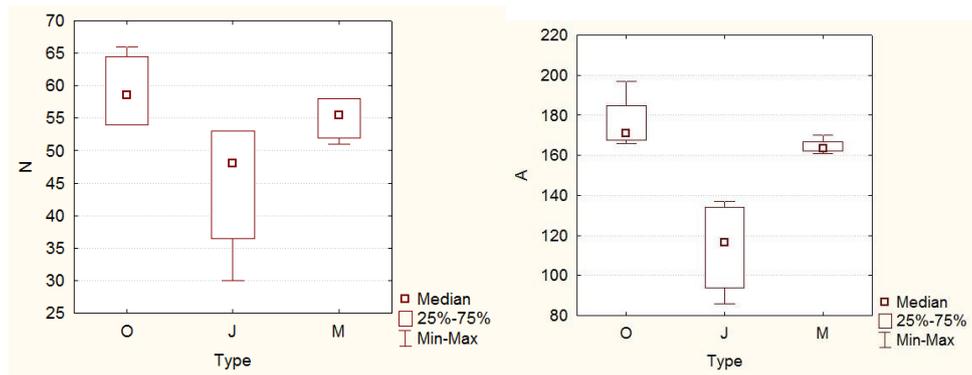
#### *Relation between the forest type and the foliicolous lichen diversity*

The highest number (65) of foliicolous species has been found in GIL 2, the lowest (29) in JEU 5 (Table 15). The forest with the highest Shannon-Wiener Diversity Index (3,9) is GIL 4, the forest with the lowest Shannon-Wiener Diversity Index (3,1) is JEU 5.

**Table 15:** Number of foliicolous species (NF) per forest plot and the Shannon-Wiener Diversity Index (ShF).

	BRA1	GIL1	GIL2	GIL3	GIL4	GIL5	JEU1	JEU2	JEU3	JEU4	JEU 5	MIX2	MIX3	MIX4	MIX5	MIX6
<b>NF</b>	53	57	59	62	65	53	43	53	37	53	29	56	60	62	53	51
<b>ShF</b>	3,7	3,7	3,8	3,7	3,9	3,6	3,5	3,6	3,4	3,6	3,1	3,7	3,8	3,8	3,6	3,5

To investigate if the foliicolous lichen diversity differs between the tree forest types a non-parametric Kruskal-Wallis test was performed.



**Figure 14:** Differences in the diversity of foliicolous lichen communities. O = old growth forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii*, J = regrowth forests, M = old growth mixed forests, N = number of species on leaves in a plot, A = the number of occurrences of the species on the 18 investigated leaves in a plot (max = 18).

Old growth forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii* show a higher diversity than regrowth forests ( $p < 0.05$ ) (Figure 1). Mixed forests are most similar in lichen diversity while young forests are the less similar. The number of species on leaves in a plot (N) is strongly correlated with the abundance of species on leaves in that plot (A) ( $r = 0.92$ ).

To identify the foliicolous species typical for the different forest types an indicator species analysis was performed. Significant indicator values with respect to the forest type were recorded for 12 species (Table 15).

**Table 15:** Result of an indicator species analysis calculated with method of Dufrêne & Legendre (1997) with respect to the forest type. Only those species (with indication of the strength of the significance) are listed that were significantly ( $p \leq 0.05$ ) for a particular forest type after Monte Carlo test of significance of observed maximum indicator value for species (4999 permutations). Only those species are listed which have been identified to species level.

	old growth forests	old growth mixed forests	young regrowth forests
<i>Arthonia accolens</i>	< 0.01		
<i>Arthonia intermedia</i>	< 0.001		
<i>Byssoloma leucoblepharum</i>			< 0.01
<i>Coenogonium hypophyllum</i>	< 0.01		
<i>Coenogonium pocsii</i>		< 0.05	
<i>Echinoplaca leucotrichoides</i>			< 0.05
<i>Fellhanera lambinonii</i>			< 0.05
<i>Fellhanera rubida</i>			< 0.01
<i>Mazosia melanophthalma</i>	< 0.01		
<i>Porina follmanniana</i>	< 0.05		
<i>Porina rubentior</i>	< 0.01		
<i>Trichothelium porinoides</i>			< 0.001

Six species occur significantly ( $P \leq 0.05$ ) more in old growth forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii*. One species is typical for old growth mixed forest. Five species are more present in young regrowth forests. Young regrowth and old growth forests have clearly more unique species than old growth mixed forests.

#### *Effect of environmental variables on foliicolous lichen diversity*

The relationships between the number of foliicolous lichens (NF) and the environmental variables (ATD, ATCI, DIST and NTS) were investigated using multiple linear regression with a forward stepwise selection procedure. The analyses were performed using STATISTICA.

**Table 16:** Result of multiple regressions (forward selection) between NF as dependent variable and the environmental variables: the mean diameter of all the trees in the plot (ATD), the mean circumference of the investigated trees (ATCI), the distance of the plot to the main road (DIS) and the number of trees in the plot (NTS) as independent variables. Only the significant results are shown.

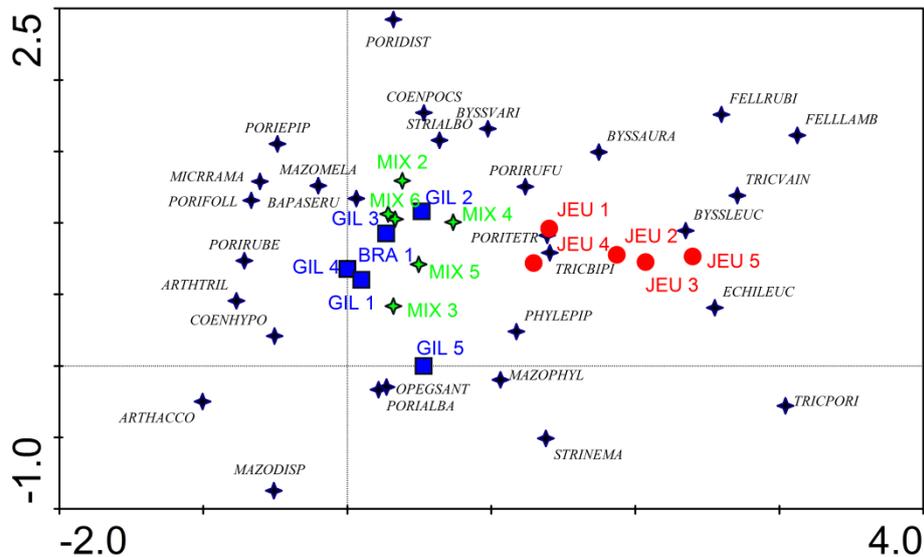
	Beta	Std.Err. of Beta	B	Std.Err. of B	t(13)	p-level
<b>Intercept</b>			11.551	9.341	1.237	0.238
<b>ATD</b>	0.576	0.179	0.360	0.112	3.214	0.007
<b>NTS</b>	0.401	0.179	0.038	0.017	2.238	0.043

Regression Summary for Dependent Variable: NF (Foliicolous lichens):  $R = 0.781$ ;  $R^2 = 0.609$ ; Adjusted  $R^2 = 0.549$ ;  $F(2,13) = 10.143$   $p < .00222$  Std.Error of estimate: 6.3727

The number of trees present in the plot and the average DBH of the trees with a DHB  $\geq 10$  cm present in the plot are positively correlated with the foliicolous species richness. More species prefer dense forests with ecological conditions created by the presence of more and larger trees.

#### *Differences in the composition of the foliicolous lichen communities*

To investigate the patterns of variation in lichen community composition and to identify the main factors shaping the composition of the lichen communities a Principal Component Analysis (PCA) was performed using the lichen composition of 16 forest plots using the computer package Canoco 4.5 (ter Braak & Šmilauer 2002). We used a linear ordination method because the largest length of gradient in a DCA was shorter than 3.0 suggesting that most of the corticolous species have a linear response to the environmental gradients (Lepš & Šmilauer 2000).

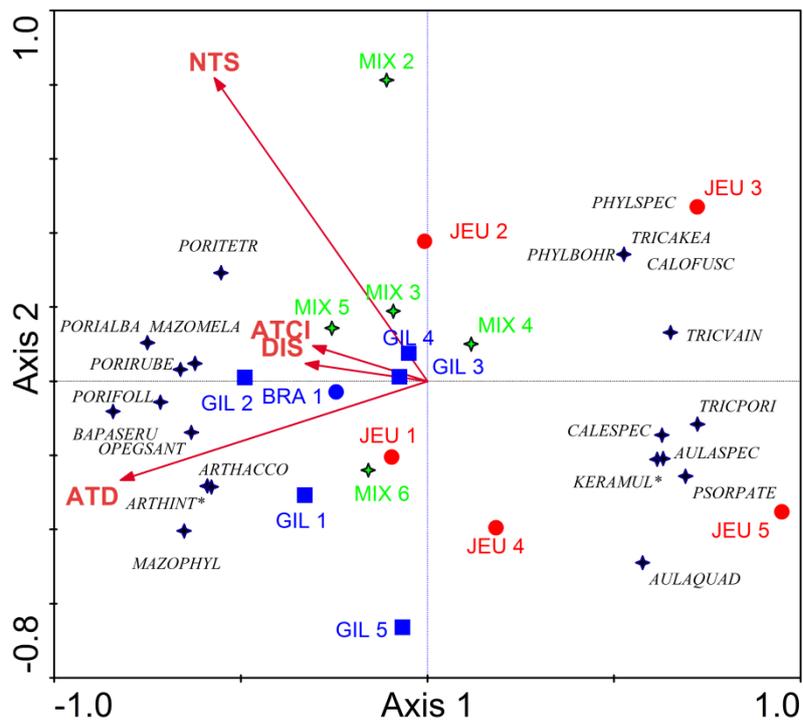


**Figure 15:** PCA-ordination diagram (axes 1 and 2) of forest plots and foliicolous lichen species (fit range > 39%). BRA = old growth forests dominated by *Brachystegia laurentii* (blue), Gil = old growth forests dominated by *Gilbertiodendron dewevrei* (blue), JEU = young regrowth forests (red), MIX = mixed old growth forests (green).

The ecological conditions for foliicolous lichens differs clearly between young regrowth forests (JEU) and old growth forests (Figure 15). *Arthoniaceae*, *Porinaceae* and *Roccellaceae*, species typical for the shady understory, including most hypophyllous taxa (lichens growing partly or completely on the underside of the leaves) and most of the rare and lichenicolous species are more present in old growth forest with the highest diversity. *Gomphilaceae* and *Pilocarpaceae*, representatives of light gaps and canopies in lowland rain forests, are more found in regrowth forests showing a lower diversity (Figure 15).

#### *Factors influencing the composition of the foliicolous lichen communities*

To relate the patterns of variation in foliicolous lichen community composition to the environmental variables, a redundancy analysis (RDA) was performed using the lichen composition of 16 forest plots and the environmental variables (ACD, ACTI, DIST, NTS) using the computer package Canoco 4.5 (ter Braak & Šmilauer 2002). We used a linear ordination method because the largest length of gradient in a DCA was shorter than 3.0 suggesting that most of the foliicolous species have a linear response to the environmental gradients (Lepš & Šmilauer 2000).



**Figure 16:** RDA-ordination diagram (axes 1 and 2) of forest plots and foliicolous lichen species (fit range > 39%). BRA = old growth forests dominated by *Brachystegia laurentii* (blue), Gil = old growth forests dominated by *Gilbertiodendron dewevrei* (blue), JEU = young regrowth forests (red), MIX = mixed old growth forests (green), ATD = the mean diameter of all the trees in the plot, ATCI = the mean circumference of the investigated trees, DIS = the distance of the plot to the main road, NTS = the number of investigated trees.

The average tree diameter is significant ( $p < 0.01$ ) higher in old regrowth forests than in young regrowth forests and explains 15% of the variance. The tree other variables explain another 20 of the variance but are not significant. Most of the young forests are characterized by a different foliicolous lichen vegetation than those of forests dominated by *Gilbertiodendron dewevrei*. Mixed forests seem to have also a mixed foliicolous lichen composition with species characteristic for young and old growth forests. Species of the genera *Arthonia*, *Mazosia* and *Porina* have a preference for old growth forests in contrast to species of the genera *Aulaxina*, *Phyloblastia* and *Trichothelium* who have a preference for young forests. Young forests are in general characterized by less tree species and a shorter distance to the road.

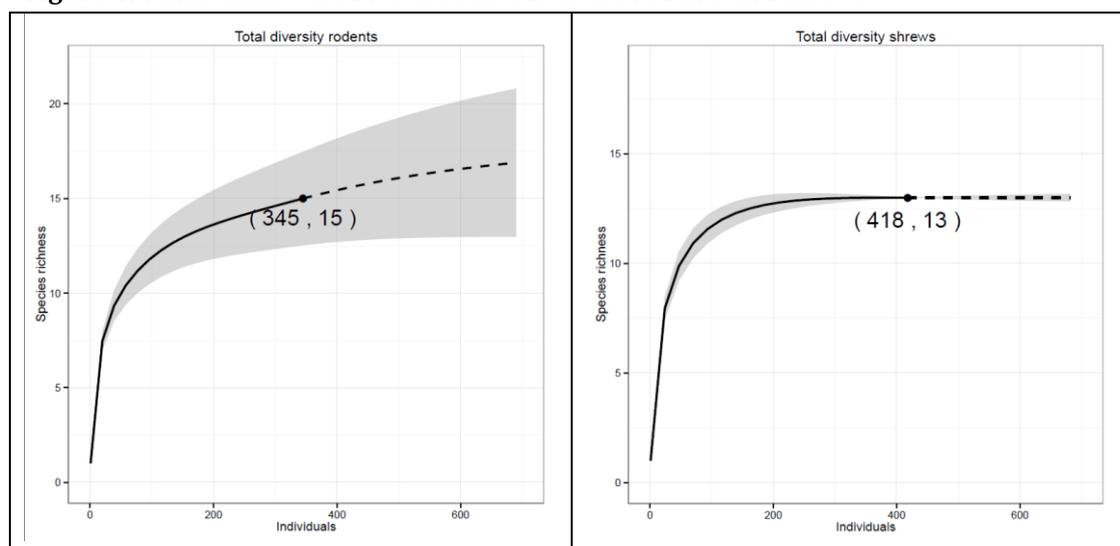
**Table 17:** Follicolous families present in the 16 forest plots. Dominant families in bold.

Family	BRA1	GIL1	GIL2	GIL3	GIL4	GIL5	JEU1	JEU2	JEU3	JEU4	JEU5	MIX2	MIX3	MIX4	MIX5	MIX6	Sum
Arthoniaceae	10	26	9	16	18	5	0	2	0	0	0	7	11	3	5	5	117
Asterothyriaceae	4	5	0	2	2	3	3	3	2	2	1	2	1	3	2	4	39
Coenogoniaceae	14	13	12	24	10	4	5	2	7	4	0	10	15	12	14	24	170
Gomphillaceae	3	2	16	4	2	6	1	8	11	3	11	3	3	15	7	4	99
Graphidaceae	1	3	0	4	4	4	2	0	1	2	0	1	0	2	1	1	26
Lyrommaceae	2	4	0	1	2	3	0	0	0	2	0	0	4	2	4	3	27
Microtheliopsidaceae	2	10	4	4	5	0	0	0	1	3	0	4	4	4	1	2	44
Monoblastiaceae	0	1	2	0	4	1	0	0	0	0	0	3	0	1	2	0	14
<b>Pilocarpaceae</b>	17	45	32	25	25	16	21	38	21	29	21	25	15	28	19	14	<b>391</b>
<b>Porinaceae</b>	45	73	45	44	55	31	19	14	31	15	8	52	33	31	43	39	<b>578</b>
Pseudoperisporiaceae	0	0	0	0	0	2	0	0	2	0	1	3	0	0	0	1	9
Ramalinaceae	7	3	3	2	3	0	1	1	0	2	0	1	2	3	3	0	31
<b>Roccelaceae</b>	28	36	29	30	29	33	7	7	4	14	6	19	31	26	28	24	<b>351</b>
Strigulaceae	7	6	7	6	12	8	4	7	0	6	0	9	4	6	4	9	95
Thelenellaceae	0	0	0	0	0	3	0	0	1	0	0	0	0	0	1	0	5
Verrucariaceae	1	0	2	1	0	0	3	0	1	2	0	0	0	1	0	0	11
Veizdaeaceae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2

The family of *Porinaceae* is best represented, followed by *Pilocarpaceae* and *Roccelaceae* (in bold in the table). Those families seem to have adapted themselves to very different ecological conditions (Table 17).

### Small mammals

We have so far sampled 12 plots. For the PSP sampled in 2016 the identification of specimens is still ongoing. In the remaining 9 plots we found in total 15 rodent ( $n=345$ ) and 13 shrew ( $n=418$ ) species. Rarefaction indicates that one or two more rodent species can be expected (Fig. 17). We recently compiled the capture data for different sites up to 250km distant from Y-MaB.

**Figure 17:** Individual-based rarefaction curves for rodents and shrews.

### Protosteloid amoebae

The jackknife estimator ( $S_j2$ ) (Burnham & Overton 1979) and Chao estimator ( $Sc2$ ) (Chao 1984) both predict that 24 species are expected to be present in the studied area, the survey at Yangambi recovered 23 species. This is a normal number for this type of survey. Two species are new for D.R. Congo.

Myxomycetes

The number of species collected is currently at 99, this number is expected to increase with 5-10% after all the results from the substrate cultures are known. Twenty-seven species are new records for D.R. Congo.

The jackknife estimator (Sj2) and Chao estimator (Sc2) predict calculate that 162 or 173 species are predicted to be present in the studied area. This field campaign recovered around 60% of this estimated number, which is high considering the survey was limited to one campaign and also because essential problems arise when conducting surveys of myxomycetes. First of all the production of ripe fruiting bodies, which are used for the identification, is cryptic and erratic, morphological characters exhibit wide-ranging phenotypic plasticity, populations contain apomictic strains, defining an individual is difficult and, for the moment, it is impossible to obtain data on the distribution and abundance of the two trophic stages.

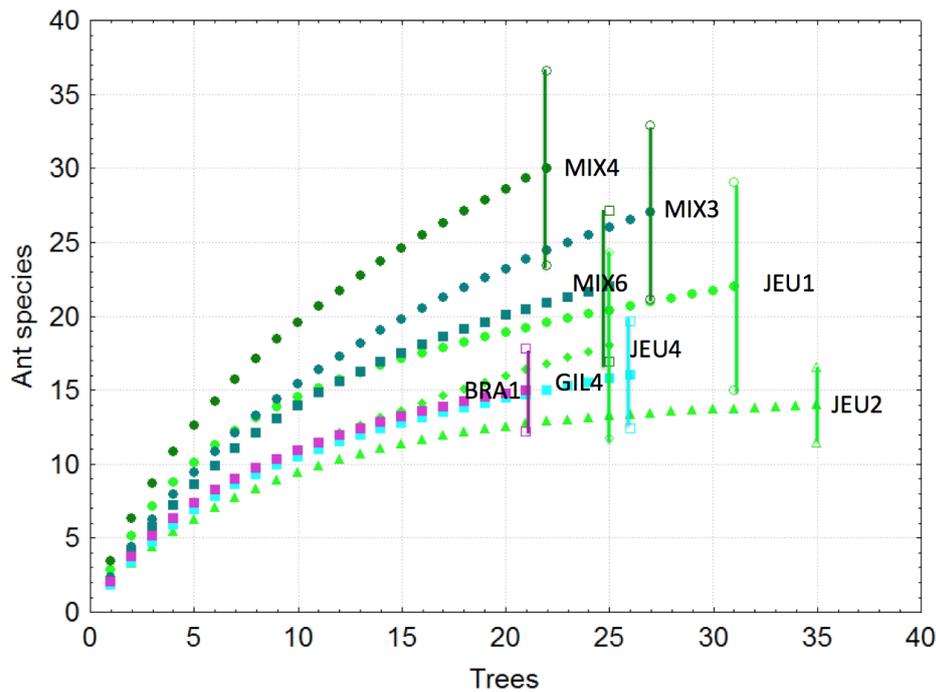
Ants*Ant community structure in early vs. late stages of the succession gradient*

A total of 65 ant species (4651 specimens, 483 occurrences) were collected. Local sampling completeness varied between 62 and 90% (Table 18).

There was a general trend for lower diversity in early (JEU) vs later stages (MIX) of the succession gradient.

**Table 18:** Diversity statistics for each plot. Sest: expected number of species in pooled samples, given the reference sample, and its 95% unconditional confidence interval; Occ. = occurrences; Chao2: Chao2 estimator mean and 95% confidence interval; Completeness, calculated as the ratio of observed against total species richness; q indicate the Hill number.

Plot	Sest	Trees observed	Ant Occ.	Chao 2	Completeness	Shannon Exponential Mean (q = 1)	Simpson Inv Mean (q = 2)
JEU1	<b>22 ± 3.59</b>	31	88	35.55 ± 12.84	90%	16.5	14.1
JEU2	<b>14 ± 1.31</b>	35	65	14.49 ± 1.27	85%	10.1	7.3
JEU4	<b>18 ± 3.21</b>	25	48	32.4 ± 12.37	62%	12.6	9.6
MIX3	<b>27 ± 3</b>	27	63	37.73 ± 7.95	97%	20.6	16.1
MIX4	<b>30 ± 3.35</b>	22	76	44.32 ± 9.9	56%	21.6	16.4
MIX6	<b>22 ± 2.6</b>	25	53	28.91 ± 6.21	72%	17.9	14.9
GIL4	<b>16 ± 1.85</b>	26	47	18.88 ± 3.31	68%	12.5	10.7
BRA1	<b>15 ± 1.43</b>	21	43	16.59 ± 2.12	76%	11.6	9.5
All plots	<b>65 spp.</b>	<b>212</b>	<b>483 occ. 4651 specimens</b>				



**Figure 17:** Sample-based interpolation (rarefaction) of ant species richness with 95% unconditional confidence intervals.

*Effect of tree monodominance (of either Gilbertiodendron or Brachystegia) on ant community structure*

Monodominant mature plots (GIL4 & BRA1) tend to be less diverse than mature mixed plots, showing a diversity comparable to young mixed plots (table 18, fig. 17).

*Spatial distribution of arboreal ants*

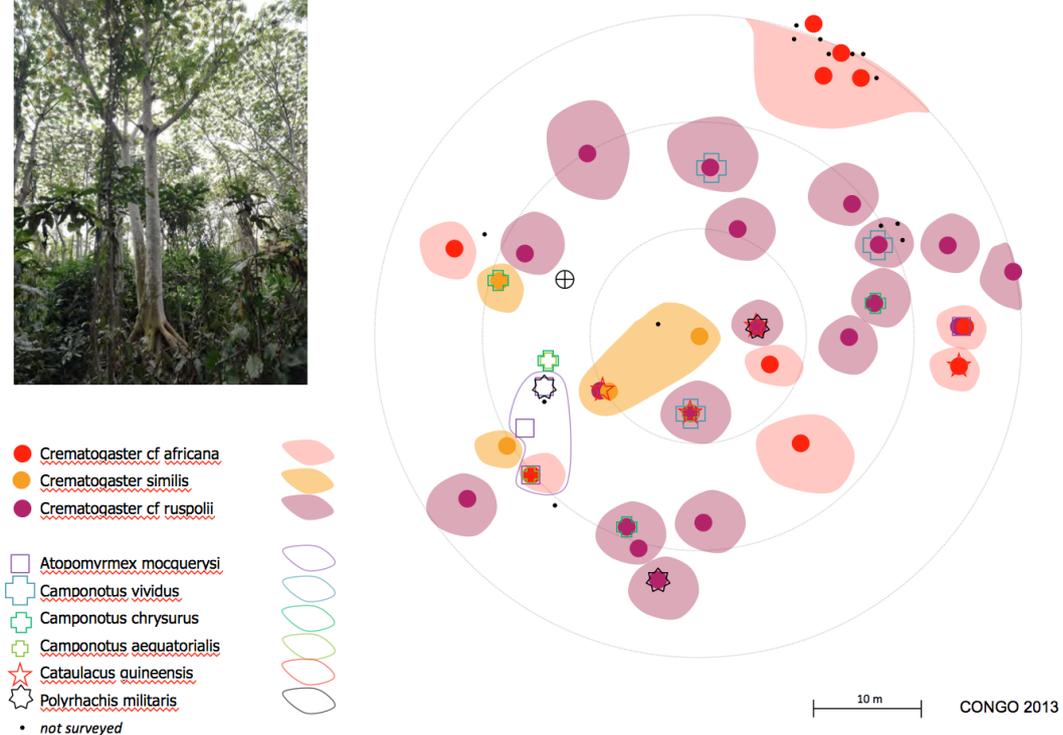
Positive and negative associations were observed between ant species (table 19). Competitive exclusion from tree crowns was obvious in both early and late succession stages of the forest (figs 17 & 18). Early stages were dominated by *Crematogaster* cf. *ruspolii* colonies which colonized single trees (fig. 17). This species is apparently a pioneer species since it is much less present in mature forests where species such as *Crematogaster* cf. *africana* become more present with large colonies extending on several trees (fig. 18).

**Table 19:** Positive (green) and negative (red) associations observed between ant species. Result of paired Chi-square tests with Yates correction.

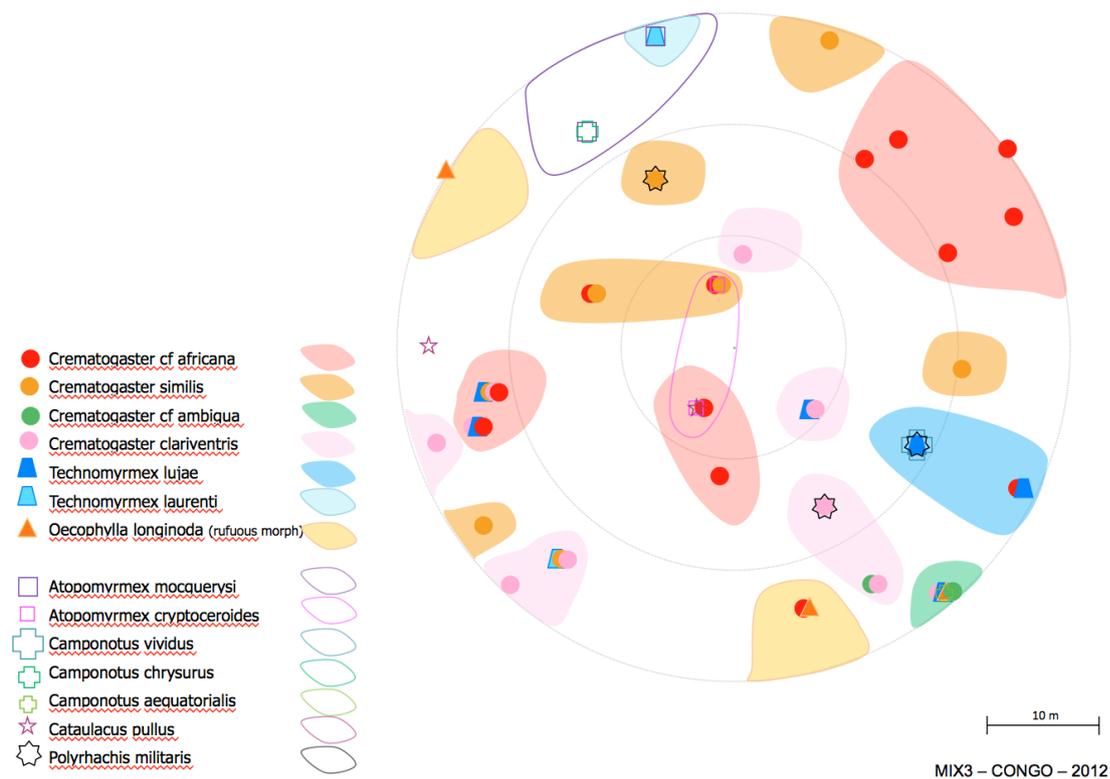
Frequency		<i>Crematogaster cf ruspolii</i>	<i>Crematogaster similis</i>	<i>Oecophylla longinoda</i>	<i>Atopomyrmex mocquersyi</i>	<i>Crematogaster cf africana</i>	<i>Pheidole sp.02RDC</i>	<i>Camponotus vividus</i>	<i>Polyrhachis militaris</i>	<i>Crematogaster transiens</i>
30%	<i>Crematogaster cf ruspolii</i>									
20%	<i>Crematogaster similis</i>									
15%	<i>Oecophylla longinoda</i>	0	0							
14%	<i>Atopomyrmex mocquersyi</i>		0	0						
14%	<i>Crematogaster cf africana</i>				0					
13%	<i>Pheidole sp.02RDC</i>		0	0	0	0				
11%	<i>Camponotus vividus</i>	0	0		0	0	0			
11%	<i>Polyrhachis militaris</i>	0	0	0	0	0	0	0		
10%	<i>Crematogaster transiens</i>		0	0	0	0	0	0	0	
9%	<i>Crematogaster muralti</i>	0	0	0		0		0	0	0



Young trees (height: 10m)



**Figure 17:** Schematic distribution of dominant ant colonies on trees in a young mixed forest. Symbols represent the ant identity on each tree while lines indicate the colony extension.



**Figure 18:** Schematic distribution of dominant ant colonies on trees in a mature mixed forest. Symbols represent the ant identity on each tree while lines indicate the colony extension.

## Diptera

### *Taxonomic impediment*

All species have been identified by now, resulting in 127 hybotid species with 120 species being new for science. The species accumulation curve does not reach the asymptote at all, showing that many species are still to be discovered in these forests around Yangambi. We definitely challenge Ashley Kirk-Spriggs's (2009) statement: rich savannahs, poor forests (chapter In: Diptera Diversity: status, challenges and tools, 2009), we state that forests along the Congo river contain a very high diversity that is likely to be richer than the savannahs.

### *Ecology*

The number of specimens collected per time unit is much lower in primary forest than in young forest. This is probably due to the more diverse architecture density of the vegetation in young forest, especially the understory and the variety of light intensity that reaches the understory thus creating much more microhabitats and niches for the insect species. Primary forest lacks a dense understory which is used by predators as hunting ground and food source for herbivores. Only 18 species of the 127 are represented by more than 20 individuals and as such available for a statistical ecological analysis. With a Detrended Canonical Analysis (DCA) we can see clearly a relation between species and their presence in respectively primary, secondary and young forest. A number of indicator species could be detected.

### 4.3 WP4 Integration of carbon and biodiversity data

We used three different groups of taxonomic diversity metrics in our analyses: alpha diversity (species richness, Shannon and Simpson diversity), beta diversity (community dissimilarity; Sørensen and Morisita-Horn index), and species of conservation concern. Each of the three groups contained metrics that are only based on presence data and metrics that take into account abundances. For appropriate combinations of plot and taxon, the metrics for taxonomic diversity evinced the same functional form with respect to carbon storage and therefore only differed in levels of significance (Table 20). The effect size and shape of the associations between alpha diversity (standardized for sample completeness) and carbon differed considerably among taxa. The diversity of fungi, bark lichens, flies, ants, rodents, and shrews was not related to above-ground carbon. The diversity of trees and leaf-inhabiting lichens increased with above-ground carbon, but did so in a saturating fashion for the latter group. Diversity of slime molds decreased with increasing carbon stock. For birds Shannon diversity decreasing nonlinearly, while species richness and Simpson diversity showed no significant correlation.

**Table 20:** Parameter estimates for orthogonal polynomial regression between each of three measures of taxonomic biodiversity and carbon storage, separately for each of the taxa. Significance ( $\alpha = 0.05$ ) of regression coefficients ( $b_1^*$  and  $b_2^*$ ) is indicated by asterisk.

	Species richness			Shannon diversity			Simpson diversity		
	$b_1^*$	$b_2^*$	$R^2$	$b_1^*$	$b_2^*$	$R^2$	$b_1^*$	$b_2^*$	$R^2$
Trees	<b>68.168*</b>	-13.535	0.780	<b>28.439*</b>	-2.940	0.540	<b>13.881*</b>	-0.344	0.407
Slime molds	<b>-26.981*</b>	-5.48	0.839	-	-	-	-	-	-
Fungi	44.776	6.306	0.127	-	-	-	-	-	-
Lichens - leaf	<b>20.618*</b>	<b>-17.616*</b>	0.686	<b>16.231*</b>	<b>-10.968*</b>	0.632	<b>14.654*</b>	-5.282	0.556
Lichens - bark	1.412	-1.847	-0.225	-2.140	-1.909	-0.210	-3.173	3.580	-0.091
Flies	-20.249	19.082	0.519	-5.488	9.370	0.576	-1.687	6.274	0.393
Ants	6.924	-1.619	-0.184	4.503	-3.062	-0.028	3.097	-3.954	0.176
Birds	-3.367	2.913	-0.145	<b>-2.942*</b>	<b>2.802*</b>	0.623	-1.036	2.122	0.278
Rodents	-3.460	-3.612	0.416	-2.943	-2.022	0.443	-2.413	-1.302	0.386
Shrews	-2.355	-2.155	-0.021	-1.794	-0.161	-0.142	-1.368	0.635	-0.161

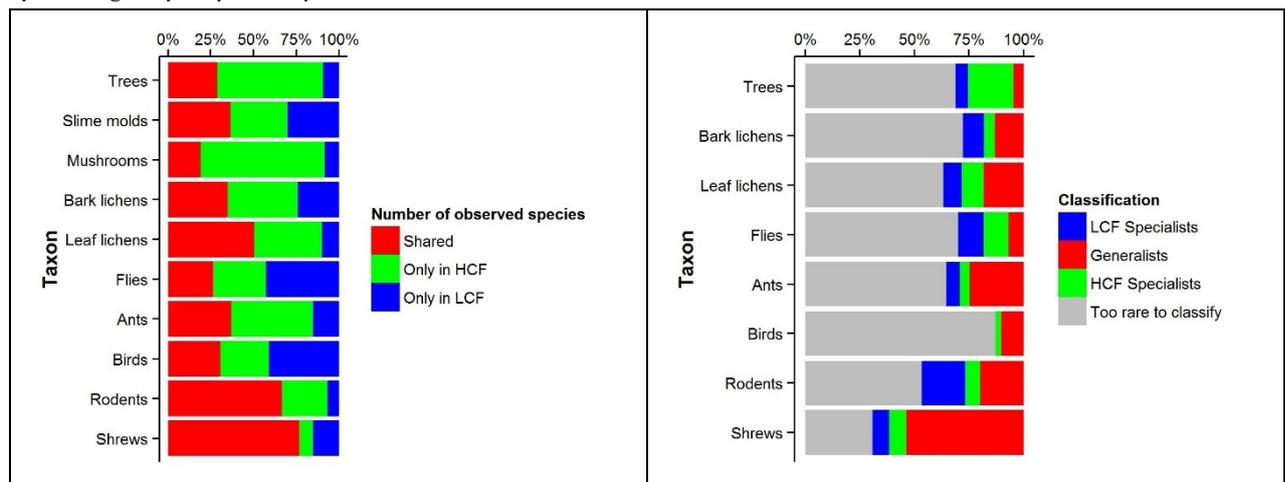
Differences in species composition increased with differences in carbon storage between sites for all taxa, except slime molds, rodents and shrews (Table 21). The largest differences in carbon stock occur between regrowth and old-growth forest plots, thus a positive correlation implies that plots within the same forest type are compositionally more similar to each other than are plots from different forest types. Generally, taxa comprising many ( $> 20$ ) generalist species show no relationship between dissimilarity and difference in carbon storage. Compositional dissimilarity (Sørensen and Morisita-Horn) was unrelated to geographic distance between pairs of plots (each of 18 Mantel tests,  $p \geq 0.15$ ; each of 36 tests between forest types,  $p \geq 0.25$ ) except for Sørensen dissimilarity of trees in HCF ( $p = 0.005$ ).

**Table 21:** Estimated parameters of mantel correlations (Mean and S.D.) between species dissimilarity and difference in carbon stock for a variety of taxa. For both Sørensen and Morisita-Horn indices, the Pearson correlation coefficient (R) illustrates the direction of association. Significance ( $\alpha = 0.05$ ) is indicated by an asterisk.

	Sørensen		Morisita-Horn	
	R	Mean and S.D.	R	Mean and S.D.
Trees	<b>0.801*</b>	0.63 ± 0.20	<b>0.601*</b>	0.75 ± 0.32
Slime molds	-0.119	0.64 ± 0.08	-	-
Fungi	<b>0.279*</b>	0.76 ± 0.10	-	-
Leaf lichens	<b>0.774*</b>	0.43 ± 0.14	<b>0.812*</b>	0.25 ± 0.21
Bark lichens	<b>0.588*</b>	0.56 ± 0.14	<b>0.658*</b>	0.42 ± 0.20
Flies	<b>0.620*</b>	0.65 ± 0.12	<b>0.397*</b>	0.56 ± 0.21
Ants	0.271	0.55 ± 0.08	<b>0.412*</b>	0.49 ± 0.16
Birds	<b>0.662*</b>	0.53 ± 0.15	0.155	0.11 ± 0.07
Rodents	0.008	0.44 ± 0.15	0.286	0.46 ± 0.23
Shrews	-0.074	0.29 ± 0.14	-0.133	0.25 ± 0.20

Except for flies, birds and shrews, more species were only found HCF compared to LCF. For rodents and shrews, more than half of all species occurred in both habitats. The classification results corroborate that tropical rainforests are species rich with most species occurring at low abundances. Consequently, many of the species are too rare to be classified (Fig. 19).

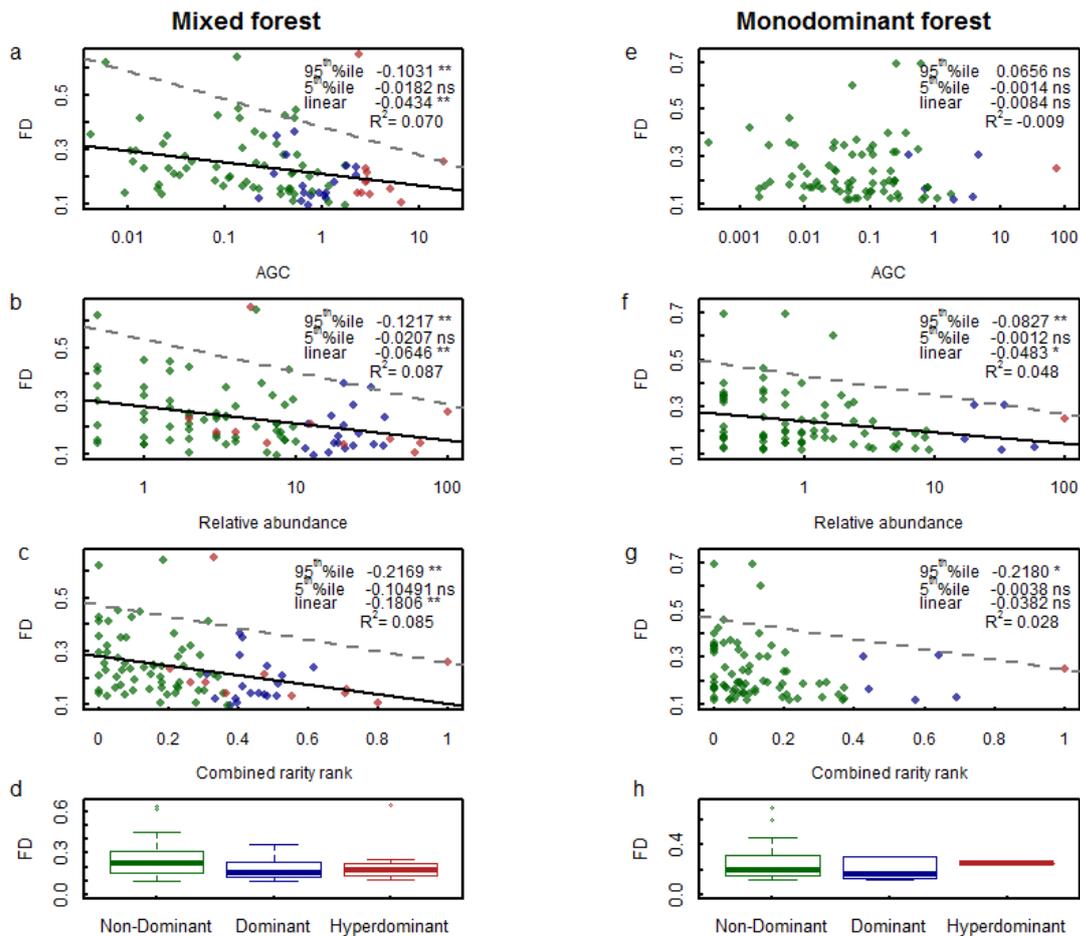
**Figure 19:** a) Percentage of observed species occurring only in high carbon forests (HCF), low carbon forests (LCF), or both. b) Percentage of species classified as HCF specialists, LCF specialists, generalists, or too rare to classify. See text for details; assessments executed for each species group separately.



The described objectives and methodology were translated into an application for a 4-year fellowship at the research foundation Flanders, which was accepted and started October 2015. The results and discussion were translated into a manuscript.

### Functional diversity and species rarity

We examined the relationship between the rarity of tree species and their contribution to functional diversity. Our main finding is that within mixed and monodominant forest ecosystem, rare species support the trait combinations with the highest functional distinctiveness. Rare species however cover the entire range of low and high functional distinctiveness, contributing both unique and redundant functions. Common species only show a low contribution to functional diversity but are crucial for aboveground carbon storage. We argue that within carbon sequestration initiatives, inclusion of both functional diversity and biodiversity conservation is imperative not only for conservation purposes but also to sustain the stability of the ecosystem.



**Figure 20:** Functional distinctiveness (FD) of species within the mixed (a, b and c) and monodominant forest (e, f and g) for all 5 ha plots combined. All dots show the FD of a single species as a function of their aboveground carbon stock (AGC), their relative abundance and the combined rarity rank which incorporates both the species specific carbon stock and their abundance. FD quantifies the uniqueness of species traits compared to the rest of the pool in the ecosystem. The relative abundance is expressed as a percentage of the maximal observed abundance within the community. The AGC stock is expressed as a percentage of the total AGC stock within the community. Significant linear regressions are presented as full black lines. Significant 95<sup>th</sup> quantile regressions are presented as dotted grey lines. ns  $p > 0.05$ , \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . FD of hyperdominant (red), dominant (blue) and non-dominant (green) species is indicated with the mixed (d) and monodominant (h) forest.

From a carbon stock perspective, a low number of highly abundant species and less abundant species with a large size maintain a large amount of the total AGC stock within each forest type. Eleven species in the mixed forest are classified as hyperdominant and contain over half of the AGC. Within the monodominant forest, only *Gilbertiodendron dewevrei* is classified as hyperdominant containing 73% of the total AGC. As these species contain a large fraction of the tropical tree community biomass, both theory (biomass ratio hypothesis) and experimental evidence have shown they highly determine ecosystem properties such as productivity, carbon sequestration, water relations, nutrient cycling etc. The large influence of hyperdominants, and to a lesser extent of dominants, does not exclude non-dominants from involvement in the determination of ecosystem function and sustainability.

Namely from a functional diversity perspective, we found that common species show a high degree of functional similarity and a low degree of functional divergence compared to other species within the community, both in mixed and monodominant forests. The presence of a strong habitat filtering could be the underlying cause of this difference. In particular, the establishment of monodominant forest could have been caused by environmental filters such as soil conditions, microclimate or disturbance, driving habitat filtering. This habitat filtering is subsequently reinforced by the dominance of *Gilbertiodendron dewevrei* which through specific trait combinations alters the environment favoring these traits (Peh *et al.* 2011b; Maire *et al.* 2012). As such, the high functional similarity could be advantageous for dominant species as it increases their importance as a competitor compared to less abundant species. Contrary, rare species benefit more by niche differentiation in order to coexist with competitors within a community which is passively or actively driven by strong habitat filtering (Maire *et al.* 2012). The high contribution to functional divergence of rare species suggests that species with a low occupancy in communities experiencing a strong habitat filtering need to specialize for a specific niche, with trait combinations diverging from the community mean. Consequently, these species are predominantly associated with extreme trait values. For example *Drypetes angustifolia* Pax & K. Hoffm., one of the rarest species in the mixed forest based on both abundance and AGC, shows the lowest SLA combined with lower LNC and  $\delta^{13}\text{C}$  and a long leaf lifespan. Yet, the rare species *Isolona thonneri* (De Wild & Th. Dur.) Engl. & Diels does not show extreme trait values but has distinct trait relations, namely a low SLA combined with an above average LNC, which contrasts with the positive correlation that is generally observed (Wright *et al.* 2004). Furthermore, *I. thonneri* shows a longer leaf lifespan but combined with a higher LNC, potentially enhancing photosynthetic rates (Wright *et al.* 2004). In this study we have, nevertheless, limited understanding of the functional role of traits and trait combinations of particular rare species or their relationships across trophic levels / food webs.

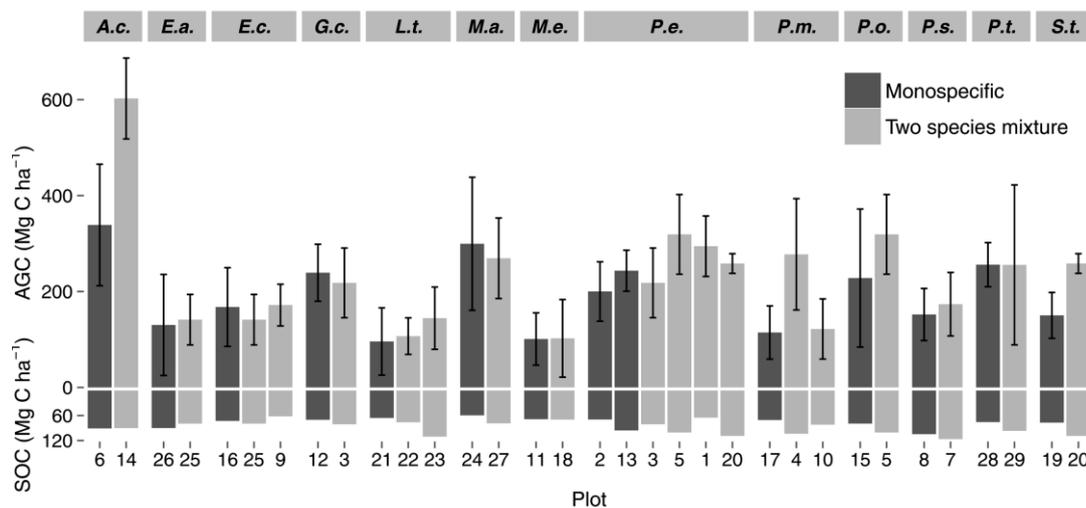
The loss of rare species, supporting important traits, in tropical forests could affect long-term carbon storage by inducing shifts in carbon dynamics (Díaz *et al.* 2009). Consequently, the loss of species with distinct traits, adding to the functional diversity within the community (Cardinale *et al.* 2006), may affect ecosystem functioning more than would be expected as a result of numerical species loss (Mouillot *et al.* 2013). At the same time, rare species are more vulnerable due to their low abundances, restricted geographic distribution, susceptibility to habitat loss, overexploitation, invasion and climate change (Hansen *et al.* 2001; Brooks *et al.* 2002; Thomas *et al.* 2004). Yet, rare species with a high functional similarity with other species are found alongside rare species with distinct traits. This functional similarity suggests trait redundancy which might act as a buffer against species loss (Gaston & Fuller 2008) insuring ecosystem functioning through replacement with more common species following biodiversity erosion (Yachi & Loreau 1999; Fonseca & Ganade 2001).

Conversely, rare species could maintain the stability of ecosystem functioning if they become more abundant (MacDougall *et al.* 2013) when common species go locally extinct due to environmental change (Walker *et al.* 1999; MacDougall *et al.* 2013). In short, functional redundancy in the context of biodiversity loss and environmental change safeguards the ecosystem against the loss of ecosystem functioning following biodiversity erosion, while the unique set of traits of rare species enables optimal ecosystem functioning and efficient use of resources.

### 77-year-old tree diversity experiment

#### *Functional identity and carbon accrual in the experiment*

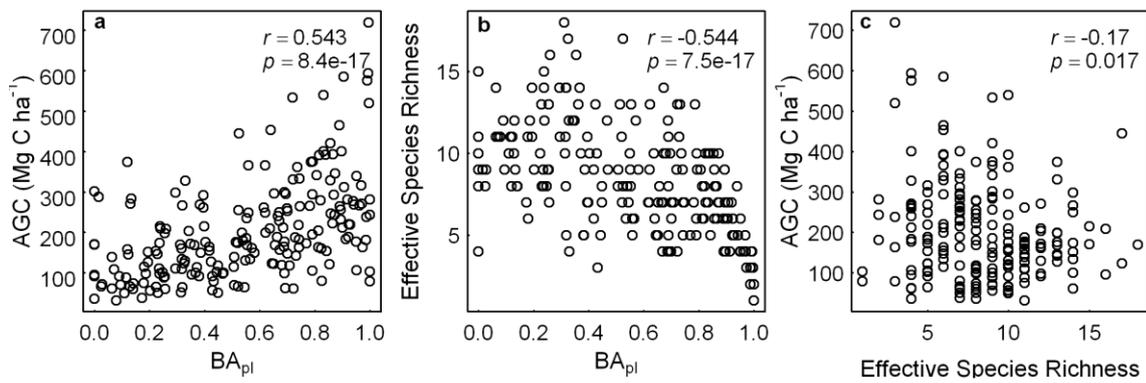
The overall AGC and SOC is  $212 \pm 106 \text{ Mg C ha}^{-1}$ , respectively  $83 \pm 16 \text{ Mg C ha}^{-1}$  (Fig. 21), with the standard deviations calculated on the plot-level averages, resulting in coefficients of variation of 0.50 (AGC) and 0.19 (SOC). The subplot-level AGC stocks in the complete dataset ( $n = 201$ ) range from  $31 \text{ Mg C ha}^{-1}$  to  $731 \text{ Mg C ha}^{-1}$ .



**Figure 21:** Aboveground carbon (AGC) ( $\text{Mg C ha}^{-1}$ ) and Soil organic carbon (SOC) ( $\text{Mg C ha}^{-1}$ ) stocks in the different plots.

The functional clustering resulted in four distinct types: two light demanding types with different wood densities (further called short-lived pioneers (SLP) and long-lived pioneers (LLP)), a class with high wood density and mediate shade tolerance (partial shade-tolerant species (PST)) and a high-wood density class with high shade tolerance (shade-tolerant species (ST)). The wood densities and shade tolerance significantly differed between the types ( $p = 0.003$ , respectively  $p = 0.001$ ).

The optimal model structure for the taxonomical approach contained plot as a random intercept. The backward selection of fixed effects resulted in a model with three significant effects: the  $BA_{pl}$ , the effective species richness and the target species groups (significant,  $p < 0.1$ , for four groups). This resulted in a final model with a marginal and conditional  $R^2$  of respectively 0.51 and 0.55. Simple Spearman-correlations in the dataset ( $n = 201$ ) show a significant positive correlation between  $BA_{pl}$  and AGC, a significant negative correlation between effective species richness and  $BA_{pl}$ , and a weak correlation between effective species richness and AGC (Fig. 22). The parameter estimates of the functional types in the model pointed out that planting species of type PST had a positive effect on AGC, in contrast with LLP, ST and especially SLP.



**Figure 22:** Interrelationships between aboveground carbon (AGC), BA<sub>pl</sub> and effective species richness in the different subplots (n=201). AGC stands for above ground carbon in the woody biomass of the subplots. BA<sub>pl</sub> is the ratio of basal area of the planted species to the total stand basal area in the plot (including spontaneous ingrowth). The effective species richness is the number of tree species with a DBH > 10 cm that were present in the subplot. The r-values are Spearman correlation coefficients, along with their p-value.

Fixed effects selection resulted in the same model as the first model, with functional types replacing the target tree species groups, and the differences in nursing as an additional significant, positive fixed effect. The optimal taxonomical and functional model performed equally well. The ANOVA analysis revealed a significant negative effect of the presence of the SLP class in the plantation scheme on the BA<sub>pl</sub> ( $p = 0.004$ ).

The top soil layer (0-10 cm) held on average 33% of the total SOC stock to 1 m depth. The coefficient of variation of the bulk densities decreased with increasing soil depth; 0.16 (5 cm), 0.15 (20 cm), 0.07 (40 cm) to 0.03 (80 cm). There was no significant correlation between AGC and SOC to 1 m depth on plot-level. Including N-fixers in the plantation scheme was the only significant, positive, effect on SOC stocks ( $r^2 = 0.11$  and  $p = 0.03$ ).

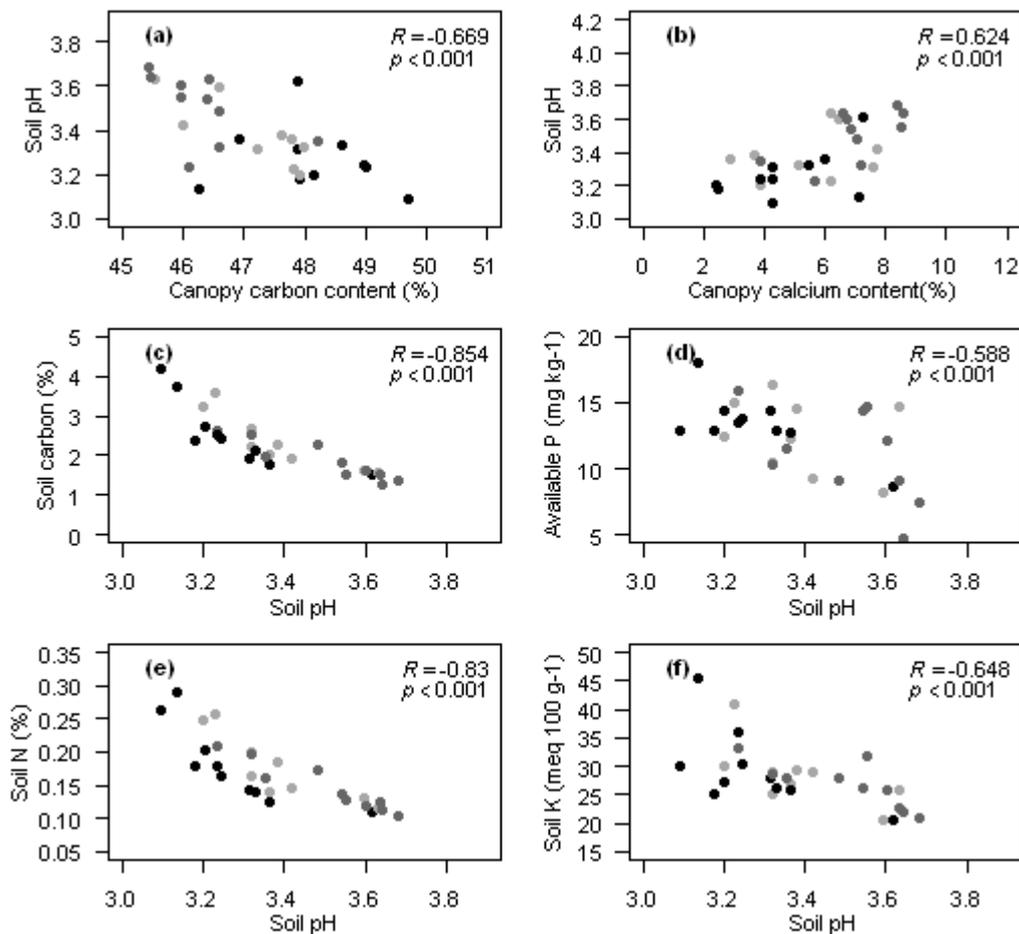
#### *Tree species effects*

Topsoil texture was considered fairly constant on the experimental area with average sand concentration of  $85.3 \pm 2\%$ . Furthermore, the sandy and acidic topsoils were characterized by very low concentrations of exchangeable non-hydrolyzing cations, with pH<sub>KCl</sub> ranging from 3.09 to 3.72. The relative ranges of element concentration in the three compartments were comparable, except for C, C:N and Ca (Table 20). Carbon concentration in the soil, on average  $22.5 \text{ g kg}^{-1}$ , ranged three-fold, while only 10 to 25% in litter and canopy. On the contrary, the C:N ratio and N concentration ranged three-fold in the canopy and two-fold in the litter compartment, while only 20% in the soil, with an average of 13.4. The Ca concentration ranged four- and two-fold in the canopy and litter layer, while ten-fold in the soil compartment. Total soil P ranged two-fold while bio-available P ranged more than five-fold, with averages of respectively  $240 \text{ mg kg}^{-1}$  and  $12 \text{ mg kg}^{-1}$ . On average, the litter N:P concentration was higher than the canopy N:P, while the C:N ratios were similar. Soil exchangeable aluminium and exchangeable acidity ranged two-fold and were two orders of magnitude higher than the non-hydrolyzing cation concentrations.

The rotated PCAs visualize the correlations of the nutrient chemistry within the soil, litter and canopy. Both canopy and litter show a similar structure of variation, with N:P ratio and Ca and Mg concentration along the first axis, and C:N ratio and N concentration along the second axis.

In the canopy compartment, PCA axis 1 and 2 together explained 84% of the variation, while for the litter layer only 65% of the variation was explained by the first two axes. For soil, we included more variables in the analysis and 64% of the variation was explained. A total of 43% of the variation was explained by the first axis, and visualises a clear relation between pH on the one hand and acidity, available P, C, N, K and C:N on the other. The N:P ratio, together with Ca and Mg concentration were strongly correlated with the second axis.

In general, canopy and litter chemical variables were well correlated. The bivariate statistics will not be discussed in full detail here. The link between topsoil and both canopy and litter, is expressed via multivariate regression for topsoil C, N, available P, C:N, pH and acidity (Table 21). This revealed that canopy C concentration explained as much variation in topsoil C concentration as three litter variables; C concentration, C:N ratio and Mg concentration, with the latter having negative predictor coefficients. With canopy and litter both in the model, only canopy C concentration and C:N ratio of the litter were retained, explaining 30% of the variation in topsoil C. For N concentration, the sets of significant predictors were very similar to those for the topsoil C concentration, but K concentration was also retained as significant predictor for litter, which now explained more variation than the canopy. For the canopy variables, again only canopy C concentration was retained as a significant parameter and a selection on the combined predictor sets resulted in a model explaining 44% of the variation in topsoil N concentration. For soil *bio-available P*, Ca concentration was the only significant, and negative, predictor of the canopy, while for litter the P concentration, N:P ratio, K concentration and Ca concentration were retained. Together the N:P ratio of the litter, the litter K concentration and the (negative) Ca concentration significantly explained 48% of the variation of bio-available-P. Overall,  $pH_{KCl}$  and C:N showed the strongest links to the plant-related predictors (respectively 58 and 60% of the variation explained by canopy and litter; Table 21). The stepwise regression parameter selection for the C:N ratio resulted in respectively canopy C concentration and C:N ratio, and litter C:N ratio and Ca concentration to predict the topsoil C:N ratio. By a selection on both retained sets of predictors, only canopy C:N ratio and litter Ca concentration were retained. Similar, bivariate correlations were found between *topsoil pH* and canopy C, P, K, Mg and Ca concentration and N:P ratio. For litter, only Mg and Ca concentration were correlated with topsoil pH. In the regression models, respectively the canopy C and P concentration were retained, with the N:P ratio, while for litter the C concentration and (negative) N concentration were the significant predictors for topsoil  $pH_{KCl}$ . The regression combining the retained predictors of the canopy and litter, canopy C concentration and litter N and Ca concentration explained 60% of the variation. For *acidity*, only the Mg concentration was retained as significant predictor for the canopy, while C and Mg concentration were retained as significant predictors for the litter. The latter were the only significant variables in the regression with both predictor sets, which explained only 24% of the variation.



**Figure 23:** Correlation plots illustrating the links between canopy chemistry and topsoil properties (0-5 cm) in this experiment. Canopy chemistry was correlated with soil pH (shown for canopy carbon (a) and canopy calcium concentration (b)). This range in soil pH was linked to a strong range in soil carbon (c), available phosphorus (d), soil total nitrogen (e) and exchangeable potassium (f) concentration. The points represent the different plots in the setup ( $n=29$ ), plots with high above-ground carbon (AGC) are black, mediocre dark grey and low AGC light grey.

*Mineral soil C concentration in every soil layer* was significantly explained by a variable set of canopy and litter chemical characteristics (Table 22). The  $R^2_{adj}$  of the models combining canopy and litter predictor sets ranged between 0.21 and 0.34 in the soil layers of the upper 30 cm and the lower 50 cm, while for the 30-50 cm layer it was very low and not significant ( $R^2_{adj}=0.08$  and  $p=0.08$ ). For soil pH, canopy and litter traits significantly explained the variation in the soil layers until 30 cm depth (Table 22). In these layers, the multiple regressions in general better explained the pH variation than the C concentration of the corresponding layer, except for the 10-20 cm depth layer.

**Table 20:** Correlation plots illustrating the links between canopy chemistry and topsoil properties (0-5 cm) in this experiment. Canopy chemistry was correlated with soil pH (shown for canopy carbon (a) and canopy calcium concentration (b)). This range in soil pH was linked to a strong range in soil carbon (c), available phosphorus (d), soil total nitrogen (e) and exchangeable potassium (f) concentration. The points represent the different plots in the setup (n=29), plots with high above-ground carbon (AGC) are black, mediocre dark grey and low AGC light grey.

	Canopy	Litter	Soil (0-5 cm)
C (g kg <sup>-1</sup> )	471.7±12.5 (448.0 – 497.0)	426.7±28.3 (359.2 – 475.6)	22.5±7.3 (13.1 – 41.9)
N (g kg <sup>-1</sup> )	32.2±6.7 (17.3 – 41.9)	26.4±3.7 (18.6 – 33.1)	1.7±0.5 (1.1 – 2.9)
C:N	16.27±4.58 (11.6 - 29.51)	16.62±3.00 (12.63 - 25.42)	13.39±0.88 (11.91 - 15.79)
P (g kg <sup>-1</sup> )	1.4±0.3 (0.7 – 2.2)	0.8±0.2 (0.4 – 1.2)	0.24±0.04 (0.16 - 0.30)
N:P	24.19±4.05 (16.95 - 32.88)	32.24±5.01 (24.55 - 46.22)	7.04±2.39 (3.96 - 13.92)
K <sup>†</sup>	10.72±2.94 (5.94 - 18.44)	2.01±0.58 (0.65 - 3.42)	0.07±0.01 (0.05 - 0.11)
Mg <sup>†</sup>	2.57±0.92 (1.03 - 4.42)	2.66±0.82 (0.94 - 5.60)	0.07±0.02 (0.04 - 0.10)
Ca <sup>†</sup>	5.75±1.96 (2.40 - 9.39)	9.30±2.77 (3.54 - 20.15)	0.06±0.04 (0.02 - 0.21)
P available (mg kg <sup>-1</sup> )			12.23±3.69 (4.70 - 26.15)
Al (meq 100 g <sup>-1</sup> )			3.98±0.77 (2.66 - 6.33)
pH (KCl)			3.38±0.18 (3.09 - 3.72)
Acidity (meq 100 g <sup>-1</sup> )			7.06±1.45 (5.01 - 10.67)

**Table 21** Retained significant predictors of multiple regressions on different soil (0-5 cm) response variables. The stepwise regression was done with separate predictor sets for canopy (subscript 'can') and litter (subscript 'lit') first, of which the retained predictor variables were combined in a third multiple regression. Variable abbreviations used: carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), C:N and N:P ratio. Significance levels for the retained predictor variables were  $P > 0.1$  (non-significant; ns);  $P < 0.1$  (\*),  $P < 0.05$  (\*\*) and  $P < 0.001$  (\*\*\*). Negative parameter estimates were indicated with (-).

Soil Response	$R^2_{adj}$	$P$	Explanatory	Significant Predictors
C	0.26	0.003	Canopy	$C_{can}^{**}$
	0.26	0.016	Litter	$C_{lit}^{**}$ , $C:N_{lit}^{**(-)}$ , $Mg_{lit}^{**(-)}$
	0.30	0.007	Canopy + Litter	$C_{can}^{**}$ , $C:N_{lit}^{*(-)}$
N	0.17	0.032	Canopy	$C_{can}^{**}$
	0.29	0.015	Litter	$C_{lit}^{**}$ , $C:N_{lit}^{**(-)}$ , $K_{lit}^*$ , $Mg_{lit}^{**(-)}$
	0.44	<0.001	Canopy + Litter	$C_{can}^{***}$ , $C:N_{lit}^{*(-)}$ , $K_{lit}^{**}$
Available P	0.15	0.021	Canopy	$Ca_{can}^{**(-)}$
	0.37	0.003	Litter	$P_{lit}^*$ , $N:P_{lit}^{**}$ , $K_{lit}^{**}$ , $Ca_{lit}^{**(-)}$
	0.48	<0.001	Canopy + Litter	$Ca_{can}^{***(-)}$ , $N:P_{lit}^{**}$ , $K_{lit}^{***}$
Total P	0.00	>0.1	Canopy	$P_{can}^{ns}$ , $N:P_{can}^{ns}$ , $Ca_{can}^{ns(-)}$
	0.02	>0.1	Litter	$C_{lit}^{ns(-)}$ , $P_{lit}^{ns(-)}$ , $Mg_{lit}^{ns(-)}$
	0.07	>0.1	Canopy + Litter	$Ca_{can}^{ns(-)}$
C:N	0.50	<0.001	Canopy	$C_{can}^{**}$ , $C:N_{can}^{**}$
	0.36	0.001	Litter	$C:N_{lit}^*$ , $Ca_{lit}^{**(-)}$
	0.58	<0.001	Canopy + Litter	$C:N_{can}^{**}$ , $Ca_{lit}^{**(-)}$
pH	0.48	<0.001	Canopy	$C_{can}^{**(-)}$ , $N:P_{can}^{**(-)}$
	0.49	<0.001	Litter	$N_{lit}^{**(-)}$ , $Ca_{lit}^{***}$
	0.60	<0.001	Canopy + Litter	$C_{can}^{**(-)}$ , $N_{lit}^{**(-)}$ , $Ca_{lit}^{**}$
Acidity	0.15	0.050	Canopy	$Mg_{can}^*(-)$
	0.24	0.011	Litter	$C_{lit}^{**}$ , $Mg_{lit}^{**(-)}$
	0.24	0.011	Canopy + Litter	$C_{lit}^{**}$ , $Mg_{lit}^{**(-)}$

**Table 22** Multiple regression for soil C and pH in different soil layers with the plant-related canopy (subscript 'can') and litter (subscript 'lit') chemistry as explanatory variables and the soil organic carbon concentration of the different depth increment layers as response variables. Variable abbreviations used: carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), C:N and N:P ratio. Significance levels for the retained predictor variables were  $P > 0.1$  (non-significant; ns);  $P < 0.1$  (\*),  $P < 0.05$  (\*\*) and  $P < 0.001$  (\*\*\*). Negative parameter estimates were indicated with (-).

Depth (cm)	C concentration				pH			
	$R^2_{adj}$	$P$	Explanatory	Predictors	$R^2_{adj}$	$P$	Explanatory	Predictors
0-5	0.26	0.003	Canopy	$C_{can}^{**}$	0.49	<0.001	Canopy	$C_{can}^{**}(-)$ , $N:P_{can}^{**}(-)$
	0.26	0.01	Litter	$C_{lit}^{**}$ , $C:N_{lit}^{**}(-)$ , $Mg_{lit}^{**}(-)$	0.46	<0.001	Litter	$N_{lit}^{**}(-)$ , $Ca_{lit}^{***}$
	0.26	0.003	Canopy + Litter	$C_{can}^{**}$ , $C:N_{lit}^{**}(-)$	0.6	<0.001	Canopy + Litter	$C_{can}^{**}(-)$ , $N_{lit}^{**}(-)$ , $Ca_{lit}^{**}$
5-10	0.2	0.02	Canopy	$C:N_{can}^{**}(-)$ , $K_{can}^{**}(-)$	0.42	<0.001	Canopy	$Ca_{can}^{***}$
	0.32	0.003	Litter	$N_{lit}^{**}$ , $P_{lit}^{*}(-)$	0.39	<0.001	Litter	$N_{lit}^{***}(-)$ , $Mg_{lit}^{**}$
	0.34	0.002	Canopy + Litter	$K_{can}^{**}(-)$ , $N_{lit}^{***}$	0.42	<0.001	Canopy + Litter	$Ca_{can}^{***}$
10-20	0.17	0.04	Canopy	$C_{can}^{**}$ , $C:N_{can}^{**}(-)$	0.09	0.06	Canopy	$N_{can}^{*}(-)$
	0.21	0.02	Litter	$P_{lit}^{**}$ , $Ca_{lit}^{**}(-)$	0.13	0.06	Litter	$P_{lit}^{**}(-)$ , $Ca_{lit}^{*}$
	0.21	0.02	Canopy + Litter	$P_{lit}^{**}$ , $Ca_{lit}^{**}(-)$	0.13	0.06	Canopy + Litter	$P_{lit}^{**}(-)$ , $Ca_{lit}^{*}$
20-30	0.1	0.05	Canopy	$N_{can}^{*}$	0.5	<0.001	Canopy	$C_{can}^{**}(-)$ , $N_{can}^{***}(-)$ , $K_{can}^{**}$
	0.32	0.005	Litter	$C_{lit}^{**}(-)$ , $P_{lit}^{**}$ , $Ca_{lit}^{**}(-)$	0.43	<0.001	Litter	$C_{lit}^{**}$ , $P_{lit}^{***}(-)$ , $Ca_{lit}^{**}$
	0.32	0.005	Canopy + Litter	$C_{lit}^{**}(-)$ , $P_{lit}^{**}$ , $Ca_{lit}^{**}(-)$	0.5	<0.001	Canopy + Litter	$C_{can}^{**}(-)$ , $N_{can}^{***}(-)$ , $K_{can}^{**}$
30-50	0	ns	Canopy	-	0	Ns	Canopy	-
	0.08	0.07	Litter	$K_{lit}^{*}(-)$	0	Ns	Litter	-
	0.08	0.07	Canopy + Litter	$K_{lit}^{*}(-)$	0	Ns	Canopy + Litter	-
50-100	0	ns	Canopy	-	0	Ns	Canopy	-
	0.23	0.004	Litter	$N:P_{lit}^{**}(-)$	0	Ns	Litter	-
	0.23	0.004	Canopy + Litter	$N:P_{lit}^{**}(-)$	0	Ns	Canopy + Litter	-



## 5. CONCLUSIONS AND RECOMMENDATIONS

### 5.1 WP2 Baseline C inventory

#### Biomass in old-growth forest

Forests cover an area of over 300 million ha (FAO 2011) in the Congo Basin. However, the distribution of forest biomass or carbon storage over these forests is highly uncertain (Saatchi *et al.* 2007 & 2011). These uncertainties propagate and further decrease the reliability of estimates of carbon flux from land-cover and land-use change (Houghton 2005).

Our synthesis of aboveground carbon storage data across old-growth forest of Yangambi contributes to the extensive ground data required to increase this reliability. Here we show consistently lower values compared to the outer regions of the Congo Basin, due to a difference in tree height-diameter allometry. We estimated an average aboveground carbon stock of  $162 \pm 20$  Mg C ha<sup>-1</sup> for old-growth forest in Yangambi, which is significantly lower than stocks recorded in the outer regions of the Congo Basin, respectively 243 Mg C ha<sup>-1</sup> and 259 Mg C ha<sup>-1</sup> for western and eastern Congo Basin sites (Lewis *et al.* 2009). The best available tree height-diameter relationships derived for Central Africa (Feldpausch *et al.* 2012; Banin *et al.* 2012) do not render accurate canopy height estimates for our study area where the forests have a lower stature.

In addition, we explored the regional validity of this trend. Extending our study to new study areas in the region, Yoko and Yambela, confirmed the lower stature throughout the region. Our results hereby represent an important scientific contribution due to the central location of Yangambi, Yoko and Yambela within the Congo Basin. These results confirm earlier results by Saatchi *et al.* (2011), indicating that the Western Congo Basin in Gabon and Southern Cameroon, and Eastern D. R. Congo support higher carbon stocks. However, a high variability in local tree allometry between sites was found and results might not scale properly to the entire central Congo Basin. Increases of the spatial coverage of ground-based inventory plots as well as extensive remote sensing based measurements are therefore necessary to properly account for fine grained spatial variability. Yet, the expansion of a plot inventory network in the central Congo Basin is impeded mostly by logistical complications and poor infrastructure (Verbeeck *et al.* 2011; Malhi 2013).

Exploring the causes of this high local variability in tree allometry, we found differences in forest structure, species composition, soil texture and soil potassium levels as main explanatory variables. Forest structure and soil physical constraints are accepted variables influencing allometry (Poorter *et al.* 2003; Heineman *et al.* 2011). Furthermore, our results suggest that potassium might influence forest structure and above and belowground biomass. More so, a two-fold difference is found in soil organic carbon (SOC) stock between two old-growth tropical forest systems (Yoko:  $44.2 \pm 4.0$  Mg C ha<sup>-1</sup> and Yangambi:  $109.5 \pm 21.4$  Mg C ha<sup>-1</sup> respectively) with opposite asymptotic tree heights and aboveground biomass (Yoko: 42.5 m /  $189 \pm 28$  Mg C ha<sup>-1</sup>; Yangambi: 36.3 m /  $157 \pm 21$  Mg C ha<sup>-1</sup>), but very similar species composition, soil geochemistry and climate.

Our data indicates that small changes in nutrient availability can have large effects on the resulting biomass allocation in tropical lowland rainforest systems. We specifically propose that

the differences in above and belowground carbon stock are a result of substantial variability in the root shoot carbon allocation strategy of two similar tree communities for nutrient mining. We argue that adaptation of tree communities to nutrient limitation offer some explanation, as well as nutrient limitation as a constraint on microbial activity (Wright *et al.* 2011). Tropical forest soils are generally assumed to be phosphorus limited while limitation of potassium is often overlooked (Wright *et al.* 2011). This topic should be further developed by analyzing the relationships between leaf potassium concentrations, available soil potassium content and above and belowground biomass. Furthermore, quantification of root traits could also improve our knowledge on the functional structure of a community as they provide information on anchoring of a plant, water and nutrient absorption, transportation and storage (Jackson *et al.* 2007). However, root traits are not easily measured and a number of challenges still have to be addressed (Lavorel *et al.* 2007). Namely, an evaluation needs to be made of which root traits best represent certain root functions such as nutrient acquisition, anchoring, rhizospheric activity, decomposition rate. Additionally, the identification of relationships between root traits and aboveground traits (i.e. leaf or stem) could allow for the use of these second group of traits as proxies, which are more easily measurable (Lavorel *et al.* 2007).

These findings of highly variable SOC stocks have important consequences for the assessment of total carbon stored in tropical forests leading to different conclusions regarding the carbon storage capacity of the entire system, i.e. above and belowground carbon mass combined. The large and unaccounted variability in SOC stocks introduces additional uncertainty in the response of tropical forest systems to climate change and its contribution to the current terrestrial carbon budget.

## 5.2 WP3 Biodiversity monitoring

### Tree taxonomic and functional diversity

Not all tropical forest types display the known high species diversity as often observed in most tropical forests. For example, the species *Gilbertiodendron dewevrei* dominates riparian forests within the Congo Basin, shaped by environmental filtering. *Gilbertiodendron dewevrei* in particular shows a combination of functional traits highly suitable for gaining dominance over other species, where the remaining species present in this forest show trait combinations that increase their likelihood for competition and survival in this forest type. Our trait-based analysis corroborates mechanisms of monodominance proposed by Peh *et al.* (2011b), and support the mechanism suggesting that the slow leaf decomposition rate of *Gilbertiodendron dewevrei* aids in attaining monodominance. Furthermore, our data also indicates that mechanisms related to xylem and WUE traits could be beneficial in adaptation to the moist soils of riparian forests.

On the other hand, high species diversity in tropical forest is maintained by rare species which rely on niche differentiation. Consequently, these species are predominantly associated with extreme trait values. The high contribution to functional divergence of rare species suggests that species with a low occupancy in communities, even within communities experiencing a strong environmental filtering, need to specialize for a specific niche, with trait combinations diverging from the community mean. As such, rare species benefit from niche differentiation in order to coexist with competitors within a community, which is passively or actively driven by strong environmental filtering (Maire *et al.* 2012).

Although these results are well established in literature (Belyea & Lancaster 1999; Cornwell & Ackerly 2009; Kraft *et al.* 2008; Maire *et al.* 2012), we show that rare species show both unique and redundant functional traits, both of high importance for long-term stability of ecosystem functioning. In contrast more common species mainly support redundant traits. Our study provides accurate descriptions of (rare) species composition and functional community structure related to the local environmental conditions of African tropical forests, which will allow us to better understand current and future species distributions and biodiversity in the African tropical forest.

Although a growing number of studies are investigating the relationship between functional diversity and ecosystem functions (Loreau *et al.* 2001; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Díaz *et al.* 2007), only a limited amount of studies are performed in tropical forests. Most studies are conducted in grassland ecosystem (e.g. Balvanera *et al.* 2006; Clark *et al.* 2012; Maire *et al.* 2012), and the conclusions are not easily transferable to tropical forest systems. It is therefore obvious that additional work on functional diversity in tropical forests is needed, especially within the Congo Basin. We therefore emphasize that protection of rare species, or highly biodiverse areas, is imperative to safeguard the ecosystem against the loss of ecosystem functioning.

#### Lichens

Old growth forests dominated by *Gilbertiodendron dewevrei* or *Brachystegia laurentii* show a significantly higher diversity of corticolous and foliicolous lichens than regrowth forests. More species, even the foliicolous ones, prefer dense forests characterized by the presence of large trees. Nevertheless young forests are characterized by lichen communities with species that are not or only rarely present in old grown forests. Especially ca. 20% of the corticolous species were only found in young forests, sometimes even in great quantities as for instance *Cryptothecia faveomaculata* and *Malcolmiella granifera*. It seems that the ecological conditions of the understorey between the different forest types is more alike than the ecological conditions of the trunks. This can easily be observed in the field where much more trunks in young regrowth forests are well exposed to the sun than in old growth forest types, thus creating an environment more suited for species with a preference for less shady conditions. Trees with a circumference of <36 cm are often more devoid of lichens than trees with a circumference of  $\geq 36$  cm. On 14 of the smaller trees not any lichen on the trunk between 100 and 150 cm above the ground was found. On larger trees only two trees were devoid of lichens.

#### Ants

Arboreal ant species diversity tend to be higher in late succession stages of the forest but this seems to be more linked to tree diversity (generating a variety of food and nesting resources for ants) than to carbon stock since old monodominant forest show ant diversity values comparable to young polydominant forests.

### **5.3 WP4 Integration of carbon and biodiversity data**

#### Biodiversity – carbon storage relationships

Previous studies have been unable to uncover general or pervasive relationships between biodiversity and carbon storage, in part because of the limited spectrum of taxa and diversity metrics used. Our study demonstrates that relationships are complex and taxon-specific, even

when analyses are restricted to a single region (Congo Basin) and based on identical quantitative approaches.

As expected, tree diversity increases linearly with carbon storage. Carbon storage is determined by the volume of the tree as well as its wood density. Although the volume does not change, regrowth forests are dominated by low wood density trees while old-growth forests are dominated by trees with dense wood, therefore containing the highest biomass.

The link between the diversity of trees and the carbon stored in a forest is direct and causal. This is not the case for each of the other studied taxa; they dependent on, or contribute indirectly to the biomass of the forest. Indeed, primary producers as trees show a positive diversity – carbon storage correlation, whereas taxa that can be categorized as consumers within the food web (ants, rodents, shrews) do not have a significant DC relationship. The shape of relationship between the diversity of these taxa and carbon storage can be influenced by a multitude of ecological as well as conceptual factors (Scheiner et al., 2011).

We assume that most differences in the specific diversity – carbon correlations can attributed to the effect of scale. In concordance with other studies on the relationship between carbon and biodiversity, we analyzed this relationship at a resolution relevant for carbon storage (namely 1ha). However, the scale at which biodiversity might correlate with carbon storage is defined by the biology of the focal taxa (Scheiner et al., 2011). For instance, many of the taxa that have random correlation with carbon storage are more mobile organisms (ants, rodents, shrews); their perception of scale therefore differs radically from that of plants and fungi (trees, lichens, fungi). Mittelbach et al. (2001) found that for animals, the odds of finding no significant relationship declined with increasing scale. We covered the whole extent of the forest carbon gradient except for flies and ants. These taxa were not sampled in the plots with the lowest carbon storage. As it is known that ants are sensitive to disturbance (Folgarait, 1998), the inclusion of these youngest regrowth forests might influence the shape of the relationship between alpha diversity and carbon storage.

Secondly, there is the effect of sampling: plots where more individuals were caught can have a higher species richness by chance (Scheiner et al., 2011). In our dataset, this effect is most pronounced for flies where many more individuals were caught in forests with a dense undergrowth, the low carbon forests. Thirdly, although all taxa were sampled within the forest in the 1ha plots, the environmental conditions might not be homogenous. For instance, leaf lichens were collected on leaves found at different heights in the canopy, while bark lichens were sampled at the same height throughout the forest (Table 1). The forest understory is a more stable environment in terms of environmental conditions, while the canopy is subjected to a higher variation in environmental factors. The environmental heterogeneity in the forest canopy can promote species coexistence for leaf lichens.

The anthropogenic changes in our study area influence the observed correlations between carbon and biodiversity in two important ways. First of all, the regrowth forests in our study area occur in a fragmented landscape. We can therefore assume that the biodiversity is influenced more by edge effects in regrowth than in old growth forests (Harris, 1988). Especially for mobile organisms like birds or mammals, faunas of low carbon forests can be found in high carbon forests and vice versa. This spillover of species explains the lack of correlation between alpha diversity and carbon storage, and inflates the number of species classified as generalists. Secondly, although the forests in the Yangambi Biosphere reserve have been protected from logging, the fauna and fungi of the reserve are not protected. Edible fungi are regularly collected and due to bushmeat hunting the forest plots in our study area are largely defaunated. The high

demand for bushmeat driven from the city of Kisangani (van Vliet et al., 2012), made our study area devoid of large-bodied animals (Toirambe, 2010). The removal of apex predators is known to disrupt the trophic web while the loss of frugivorous species influences seed dispersal and forest regeneration. Furthermore, as there is a positive (if weak) correlation between seed size and wood density (Jansen, Muller-Landau, & Wright, 2010), tree species dispersed by large animals, contribute a high proportion of the overall carbon-storage capacity of tropical forests. Carbon storage may therefore decrease over time if tree regeneration is hampered by extinction of large specialized disperser species or increases in seed-predating species enjoying ecological release from their predators (Abernethy, Coad, Taylor, Lee, & Maisels, 2013). Both habitat fragmentation and defaunation can make the relationships we found differ from biodiversity-carbon relationships found under natural conditions. However, the layout of our study area, where regrowth forests occur in a fragmented landscape around old growth forests found near centers of high human population densities is a situation that is found increasingly in the tropics, particularly in Central Africa (Abernethy et al., 2013; de Wasseige et al., 2009). We therefore argue that our observed relationships are relevant for conservation practitioners.

As stated earlier, our study area is dominated by either pristine forest types or recently disturbed, young, regrowth forests. However, old regrowth forests, i.e. forests storing intermediate quantities of carbon, are rare in the area. Older regrowth forests may be preferentially converted to agricultural land because of its sparse undergrowth and dominance of soft wood trees (H. Beeckman, pers. comm.). Consequently, it was not possible to install a series of research plots representing a continuous gradient of carbon storage. In general, old regrowth forests converge with old growth forests both in terms of species richness and species composition of the tree community (Letcher & Chazdon, 2009). Although this gap in our carbon gradient might influence the shape of carbon-diversity relationship, we found no evidence for differing diversity patterns in those forest types

#### Rare tree species

From the study concerning rare species we can conclude that rare species, which contribute little to carbon storage, show both unique and redundant functional traits, both of high importance for long-term stability of ecosystem functioning. Functions supported by rare species are however more vulnerable to extinction due to the low number of species and individuals supporting them. The loss of species with distinctive traits may thus affect ecosystem functioning more than would be expected. Within the context of forest conservation for carbon mitigation initiatives, limitation of biodiversity loss for long-term resilience of ecosystem functioning is crucial, beyond the classic motivations of preserving the diversity of life. Emphasis on common species with distinct functional traits is needed within monodominant forest systems of *Gilbertiodendron dewevrei* to ensure the stability of its ecosystem functioning. Combined efforts of conservation of rare and common species are needed for the success of carbon mitigation. Similar results to our African study in mixed forest are reported within the Neotropical forest (Mouillot et al. 2013) enabling a similar conservation policy, irrespective of the different dynamics in both tropical forests and highlighting the potential co-benefit within carbon mitigation projects (Greve et al. 2013) of safeguarding functional diversity.

#### 77-year-old tree diversity experiment

##### *Functional identity and carbon accrual in the experiment*

Both the average and the coefficient of variation of the AGC stocks were considerably higher than SOC stocks. This shows that the impact of the management choices of tropical plantations have a relatively higher impact on AGC in terms of absolute C sequestration compared to SOC

stocks. Although soils are an important carbon stock globally, we target management guidelines for carbon sequestration in tropical plantations, so devote more attention to AGC (Houghton, 2005). Remark that we did not assess carbon stocks related to the below-ground biomass.

The classification of the functional groups was done using only shade tolerance and wood density, which is consistent with previous work (e.g. Poorter, Bongers & Bongers 2006). We stress that these functional types should also be mainly interpreted in terms of shade tolerance and wood density. Tree species in functional types SLP and LLP have a high light requirement, but differ in their allocation to mechanical stability or growth rate (Selaya & Anten, 2008). PST species can establish in low light conditions but need gaps to grow, while the ST species can grow in the low light conditions (Poorter et al., 2006).

Setting the plot factor as a random intercept allowed us to quantify unwanted local differences in e.g. soil conditions. The effect of the target species groups is an identity effect that is to be expected from this type of experiment, and has been observed in similar contexts (e.g. Balvanera et al. 2006; Redondo-Brenes 2007; Ruiz-Jaen & Potvin 2011). In terms of AGC, two species mixtures did not outperform the monocultures of the target species (Fig. 21). This shows that other processes, such as the species identity effect and spontaneous ingrowth of tree species, were more important in the long-term development of these plantations. In the target species group of *A.congolensis* (A.c. in Fig. 21), the AGC increase in the mixture with *D. likwa* compared to the monoculture is remarkable. However, it is important to be cautious with the interpretation of the results; in case there is no monoculture of the admixed species, a positive or negative mixing effect could be falsely reported using only this dataset (Hulvey et al., 2013).  $BA_{pl}$  and effective species richness both have a significant positive effect on the AGC and SOC of this plantation. In the pooled dataset ( $n = 201$ ), however, these two predictors are negatively correlated to one another and the positive effect of effective species richness is masked (small negative correlation with AGC; Fig. 22). Based on these combined observations, we conclude that  $BA_{pl}$  has a more important effect than species number. We state that, given a high  $BA_{pl}$ , the species that manage to grow into the stand spontaneously are probably using different niches than the planted species. This way, spontaneous ingrowth can enlarge the resource use of the stand (Loreau & Hector, 2001). Considering a low  $BA_{pl}$ , spontaneous ingrowth is of large importance to compensate for the failure of the planted species to establish. In this case, effective species richness reflects the success of spontaneous species to establish, and augment the carbon storage. Hence within each configuration, both parameters show a positive effect on the AGC, although the  $BA_{pl}$  is the dominant driver (Fig. 22), and should thus be priority in tropical plantation design.

The lack of a significant difference in model performance when summarizing the 13 taxonomic groups into 4 functional groups proves that the species identity effect is strongly linked to the functional life-history of species. From the final model results, we conclude that planting with species of class PST, has a bigger carbon storage potential in the long-term, while using SLP is clearly not a good practice. *P. elata* was the only target species which was nursed for ten years longer in all plots (two species mixture and monospecific). This is a light demanding species, belonging to class LLP, and performed in general better than the other, functionally equal species. We cannot safely generalize this observation of a positive effect of extra nursing, since only one functional class and one species had this treatment. In this case, however, keeping the plantation free of spontaneous ingrowth for a longer time, did not only affect the  $BA_{pl}$ , but also the AGC in the plantations with light-demanding species. Through the significant negative effect

of SLP trees in the plantation scheme on the  $BA_{pl}$ , it is shown that SLP are not successful in carbon sequestration through a failure in  $BA_{pl}$ .

The inclusion of N-fixers in the plantation scheme did not significantly contribute to the AGC, although it has been shown that the effect of N-fixers strongly depends on site conditions and complementarity with the other planted species (Forrester *et al.* 2006). Additionally, tropical old-growth forests are generally considered N-rich leading to a down-regulation of symbiotic N-fixation (Batterman *et al.* 2013). In the case of the Yangambi experiment, N-fixers may have been actively fixing in the early stand development, but its effect may have been masked by growth-effects in the long-term.

Including N-fixers in the plantation scheme was the only compositional parameter with a significant, positive effect on the SOC stock, which is known from other reforestation sites in the tropics (e.g. Resh, Binkley & Parrotta 2002). The plots with higher AGC were not associated with high SOC stocks. Although literature reports a positive correlation of aboveground productivity with root allocation (Raich, Clark, Schwendenmann, & Wood, 2014), total SOC stock development after land use change is more complex and less understood (Laganière, Angers, & Paré, 2010). Initial carbon content and tree species have been identified as key determinants for the soil carbon processes following afforestation (Laganière *et al.*, 2010; Shi, Zhang, Zhang, Yu, & Ding, 2013). As we have no baseline data on the initial SOC stocks, we cannot quantify actual changes in soil carbon stock. However, taking into account the relative importance of spontaneous ingrowth, we assume that in this case the effective species composition rather than the planted species determines the changes in this stock. This augments the complexity of disentangling the role of tree species composition in the SOC stock formation, as the effective species pool rises to 143 tree species in the total study area, rather than only considering the 23 planted species. For the long-term development of tropical plantations, we state that changes in the absolute SOC stock, following afforestation, are small compared to the sequestration in AGC. This observation, combined with the far higher variability of the AGC stock and the complexity of predicting the SOC changes when considering processes like spontaneous ingrowth, leads to the suggestion that plantation managers should focus on aboveground C sequestration.

$BA_{pl}$  is an important driver of carbon stocks in tropical plantations, and is linked to the functional identity of the planted species. This identity should thus be a primordial consideration for reforestation projects in the tropics, which aim at both the re-establishment of native forest and successful carbon sequestration. The species identity can be translated and generalized into very basic functional types, where low wood-density short-lived pioneers had a clear negative impact on both the  $BA_{pl}$  and carbon accrual in the long run. Given a high  $BA_{pl}$  of planted species, spontaneous ingrowth positively affects the carbon sequestration. In this study, we found no clear positive effect of admixing species (but not a negative one either). Including nitrogen fixers in the plantation did not lead to higher above ground carbon stocks, although these plots showed a higher soil carbon stock.

#### *Tree species effects*

The high sand concentration and the low amount of non-hydrolyzing, exchangeable cations in the soils imply that the cation exchange capacity (CEC) of the mineral soil is mainly controlled by soil organic matter. This also explains the strong positive correlation between C in the topsoil and exchangeable Al. Aluminium clearly dominated the cation exchange complex (Table 20).

The strong link between soil C and total N, available P and exchangeable K also follows from the fact that the mineral matrix of these acid, sandy soils is low in abiotic, mineral derived nutrients. Hence, nutrient availability is more likely determined by the amount of topsoil organic matter. In this study site, the contribution of the top 10 cm soil C stock to the total soil C stock (to 1 m depth) ranged from 11 to 30% (unpublished data), which highlights the importance of this thin layer for element cycling. The soil C concentration in this upper layer showed a more than three-fold in the experiment, which is perhaps the most striking result of this study. This soil C concentration was highly correlated with soil pH (fig 23c), which, in turn, enhanced Al availability (Chorover and Sposito 1995; Gruba and others 2013). In acidic conditions as in Oxisols, ligand exchange between OH groups of Fe- or Al-oxides and carboxyl or phenolic OH-groups on the OM is likely to play an important role in the OM stabilization (Gu et al., 1994; von Lützw et al., 2006). Additionally, there are important toxicity effects of acid pH and available Al on soil fauna and the microbial community, as well as increased and effective cation bridging between the trivalent Al and soil C, stabilizing the soil C and both lowering the decomposition processes (Hobbie et al., 2007; Mueller et al., 2012; Mulder et al., 2001).

No correlation between soil exchangeable Ca and pH, exchangeable acidity and Al concentration was found. Very acidic soils with low exchangeable cation concentrations are in the aluminium buffer range as shown by the dominance of exchangeable Al on the exchange complex (Table 20). The low concentrations of Ca or Mg on the cation exchange complex will thus have little effect on the soil pH.

The C and N stoichiometry of the canopy, litter and topsoil invoke the idea of a strong microbial control on the soil C in the upper 5 cm, as suggested by previous research (Hobbie et al., 2007; Russell et al., 2007). At least two observations from our study confirm this: (1) reduced variability in C:N ratios of the topsoil compared to canopy and litter (Table 20), caused by microbial processes narrowing the divergence of resource stoichiometry during the build-up of soil C, and (2) the lack of correlations between C and N concentration within the canopy and litter, along with the strong correlation in the topsoil (SI 2). However, further research on the soil microbial community in the different plots is needed to corroborate this hypothesis.

The randomized planting design of the experiment allows us to safely exclude that the species pool in the different plots was filtered by soil properties. Strongest multivariate relations between canopy and litter traits and soil variables were found for *soil pH*, explained by leaf C concentration, litter N and Ca. This suggests that tree species are primarily affecting soil conditions by changing the soil pH, in turn inducing the build-up of a higher soil C concentration via mechanisms discussed above. In the framework of previous work on tree-species effects, three mechanisms have been hypothesised to contribute to this link between functional composition and soil acidification: (1) increased input of organic acids, (2) increased soil respiration and (3) sequestration and redistribution of non-hydrolyzing cations by the vegetation, resulting in a net loss of cations from the soil, which is compensated by protons (Jobbágy & Jackson, 2003). The latter mechanism (3) invokes a species-specific strategy for non-hydrolyzing cation cycling. Although the mechanisms underlying species-specific Ca cycling are still not fully understood, it has been made clear that species-specific physiologic differences are indeed the main drivers for this chemical leaf trait (Dauer et al., 2007). In our case, the canopy Ca concentration correlated with both litter and soil Ca concentration, but no link was present between litter and soil Ca. The positive link between soil pH and canopy Ca (fig 23) and Mg, corroborates with observations in temperate forest (Finzi et al., 1998; Reich et al., 2005). As no

direct correlation between pH and Ca or Mg on the exchange complex in the mineral soil was found, the input and fluxes of these cations through litter decomposition is probably not the main mechanism for decreases in soil pH values. Instead, both mechanism (1) and (2) are more likely to cause acidification; (1) high C concentration and low non-hydrolyzing cation concentration of foliage and litter of the species on more acid topsoils are linked to low leaf and litter pH and high organic acid concentrations (Cornelissen et al., 2006), and (2) the high cation concentration in litter is predominantly balanced by organic anions, and the decarboxylation of these organic anions during microbial decomposition is a proton-consuming process, hence causing a pH increase (Xu et al., 2006).

Additionally, N fixation is known to be a soil acidifying process. Bonnier (1957) reported that he only found nodules on potential fixers in very recently disturbed forest soils during his two years of research at Yangambi, and that nodules were absent in all other forest sites, as also observed in a nearby site (Bauters et al., 2016). This suggests that symbiotic N-fixation would no longer be actively influencing soil pH in this nearly 80-year-old experiment, although we do not have data on this. However, in the original experiment three potential N-fixing legumes were planted and we cannot exclude that this had no significant effects on soil in the early development stages of the experiments.

Our results suggest that the community-level leaf and litter chemistry have altered important topsoil characteristics (C, total N, available P, exchangeable K and Al; fig 23, c to f) predominantly via an effect on soil pH (fig 23, a to b), which corroborates with what we know from temperate forests (Hobbie et al., 2007; Mueller et al., 2012), and from other shorter-term tropical experiments (Fisher, 1995; Russell et al., 2007). However, our data does not allow to fully determining the underlying mechanism. We've provided information on the above ground carbon (AGC) stocks in fig 23 (Bauters et al., 2015). From this graph it is clear that the effects of the community-level leaf chemistry on mineral topsoil are also strongly linked to our previous results from this setup. The more soil-acidifying communities, with clear effects on other topsoil chemical characteristics, gave rise to higher aboveground carbon stocks, compared to the less acidifying communities in fig 23a. The functional identity of tree species is thus of vital importance for biogeochemistry in our study sites.

In our analysis of pH and C concentration in different soil layers, we found evidence that the effects of the tree communities extend to deeper soil layers on the timescale of this experiment. For both C concentration and pH, we show that links between the functional composition of the tree community and the soil characteristics are to be found until at least 30 cm depth. Overall, pH variability was better explained than the soil C concentration. This confirms our findings from the topsoil layer, i.e. that trees control soil C and nutrient concentrations primarily via effects on soil pH. Furthermore, the tree communities' effects on pH in deeper soil layers seem also more consistent than on soil carbon (Table 3). As Dawud et al. (2016) have shown, both tree diversity and functional identity affect the distribution of C in deeper soil layers. It is likely that these diversity effects are also important in this experiment. Additionally, we did not sample roots in this experiment, although it is known that they contribute considerably to soil C stocks (e.g. Schmidt and others 2011). The limited and varying  $R^2_{adj}$  values might thus (partly) be caused by these important root contributions. Recent work, however, has shown that root chemistry is closely linked to the species-level leaf chemistry and (Valverde-Barrantes et al., 2015), in which case the discussed effects of nutrient concentrations and stoichiometry of the input material remain valid.

### Consequences for biodiversity conservation

The effects of carbon conservation programs such as REDD+ on diversity of forest species can be ambiguous. Both win-win situations (highest diversity in high carbon forests) and trade-offs (or leakage; highest diversity in low carbon forests) occur within a region when considering multiple rainforest taxa. However, apart for the differences in the number (and abundance) of species, it is important to consider the identity of species in a community. Forests that have similar biodiversity may be compositionally distinct, depending on the number of species that are specialized for living in particular habitat types. Our results show that for most taxa, communities are less compositionally similar when the forests have larger differences in carbon stock, suggesting that conservation of high carbon forest is necessary, but that effective conservation of regional biotas will require strategies that also conserve low carbon stock habitats. Although these low carbon forests are less valuable in terms of species diversity for most taxa, they maintain other species communities than old growth forests. Furthermore, although regrowth forests have a lower carbon stock, they do have high rates of carbon sequestration (net carbon uptake) and therefore a large potential for storing more carbon in the future (Chazdon, Broadbent, Rozendaal, Bongers, & Al., 2016). The regrowth forests in our study area are the result of logging, we can also argue that logging followed by natural regeneration close to old growth forests, might be an extraction strategy that can still preserve regional biodiversity.

A second implication of the lack of general shapes in the observed diversity – carbon relationships findings for REDD+ is that when biodiversity is explicitly considered in REDD+ programs, monitoring the diversity will not always show increases. We propose that conservation planners should carefully consider which taxa and which aspect of their diversity to monitor as the overall (taxonomic) diversity of a forest, measured as a broad range of taxa, is unlikely to increase.

Lastly, the aim of the classification into specialist and generalist species was to identify species that could be impacted disproportionately by the disappearance of regrowth or old growth forests. It is important to stress that species (whether generalist or specialist) can have a small range (endemism) and are therefore worth conserving. It is known that speciation and variation in forest-dependent species is strongly influenced by the evolution of the forests (Bryja et al., in press). However, we were not able use the literature or to consider the IUCN status of species to distinguish specialists and generalists as many of the taxa in this study are new to science, understudied, so that their ecological attributes are poorly known at best (de Kesel et al., 2016; e.g. Grootaert & Shamshev, 2014). We therefore highlight the need for more research in the understudied region of Central Africa (Gibson et al., 2011; Yadvinder Malhi, Adu-bredu, Asare, Lewis, & Mayaux, 2013).

## 6. FUTURE PROSPECTS AND PLANNING

### 6.1 WP2 Baseline C inventory

#### Carbon storage

In the next few months, the data from the reinventory of the 21 PSP will be encoded and the dynamics of tree growth and carbon sequestration will be assessed.

#### Sampling in the edge setup

A full study of the relationships between Diameter, height and wood specific gravity of 5 dominant species in edge and core area will be conducted before the end of 2015. In the eventuality of an impact on carbon stocks, some recommendations will be formulated.

#### Time lapse study of the fragmentation of Yangambi Reserve

Aerial photography of Yangambi reserve from 1957 will be used, in addition to images already obtained by the project (Landsat, GeoEye ...) to conduct a time lapse study of the fragmentation of the forest in the reserve landscape.

#### Djolu

Currently, the project partners are collaborating with the local INERA agents trained by COBIMFO. During the final stages of the project, 15 new hectare plots were delineated and inventoried on a forest succession gradient in Djolu (Equateur). This work will add up to the core-findings of the carbon stock findings from COBIMFO.

### 6.2 WP3 Biodiversity monitoring

#### Small mammals

Currently, a master student from the UA is analysing rodent and shrew samples from three PSP's that were not yet inventoried. These samples will be identified using DNA barcoding later this year. We will use the dataset of Yangambi together with the data we assembled on rodent and shrew collections in the region to compare the diversity of small mammals in different localities of the Congo basin.

#### Diptera

During the end of 2015 we will describe the larger hybotid flies of the subfamily Hybotinae. These are flies that hunt insect by interception in flight. Beside the descriptions we will photograph all species using our recently obtained stacking device.

An analysis of the bees and fungus gnats is pending.

### 6.3 WP4 Integration of carbon and biodiversity data

So far, we calculated taxonomic diversity measures for each species group. However, our goal is to address 'biodiversity' as a multidimensional measure. For this task, we collaborated with prof dr. Michael Willig of the University of Connecticut. To this end, we started collecting additional information from the COBIMFO partners, such as phylogenetic trees and functional traits for their studied taxon.

As phylogenetic trees were not readily available for all taxa, we started DNA-barcoding for all species. At this point, most specimens have been barcoded and we are in the stage of constructing phylogenetic trees for each taxon.

Based on the BD data obtained from the COBIMFO study plots, we will generate area-wide predictions of BD using Ecological Niche Modelling techniques (ENMs, which are statistical techniques that relate species occurrences to aspects of the environment) and MacroEcological Modelling (MEM). ENM generates predictions of individual species ranges and by stacking species-specific ENMs, estimates of species richness and community composition can be obtained. MEMs rely on macroecological diversity theory to directly model relationships between environmental conditions and species richness patterns. For this project, MEMs have the advantage that their output directly extrapolates other diversity measures as well (for example Hill numbers).

The resulting BD maps will be compared with the Saatchi et al. (Saatchi et al., 2011) map as these estimates found by remote sensing were found to be in accordance with the field data. The spatial extrapolation results will allow us to (1) plot the amount of C, and value of each BD parameter for each grid cell and (2) analyse these data the same way as described above (cf. 'Statistical analysis').

Furthermore, we are currently investigating the possibility to sample soil fungi in the PSP's in Yangambi. Soil fungi play an important role in the C cycle, but have so far not been addressed in the COBIMFO project. For this task, we will collaborate with prof dr Erik Verbruggen of the Plant and Soil lab (UA).

#### Djolu

Currently, the project partners are collaborating with the local INERA agents trained by COBIMFO. During the final stages of the project, 15 new hectare plots were delineated and inventoried on a forest succession gradient in Djolu (Equateur). This work will add up to the core-findings of the carbon stock – functional diversity link findings from COBIMFO.

### **6.4 WP5 Sustainable policies**

In previous networking meetings experts with links to policy (REDD+) were invited (Inge Jonckheere and JP Kibamba). Kelly Hertenweg from FPS Health, Food Chain Safety and Environment of Belgium also presented the Belgian policy concerning REDD+ during the Xylaredd symposium. Therefore we are up to date on policy making and requirements within this context for carbon reporting.

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## 8. SCIENTIFIC OUTPUT

### 9.1 Publications of the teams

#### 9.1.1 Peer review

##### WP2 Baseline C inventory

Doetterl, S., Kearsley, E., Bauters, M., Hufkens, K., Lisingo, J., Baert, G., Verbeeck, H., and Boeckx, P. 2015. Aboveground vs. Belowground Carbon Stocks in African Tropical Lowland Rainforest: Drivers and Implications. *Plos One* 10.

Kearsley, E. et al. Conventional tree height-diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. *Nature Communications*. 4, 2269 (2013).

Verbeeck, H., Betehndoh, E., Maes, W.H. Hubau, W., Kearsley, E., Buggenhout, L. Hufkens, K., Huygens, D., Van Acker, J., Beeckman, H., Maté Mweru, J.-P., Boeckx, P. and Steppe, K. Functional leaf trait diversity of ten tree species in Congolese secondary tropical forest. *Journal of Tropical Forest Science* 26, 409-419 (2014).

Bauters, M., Verbeeck, H., Doetterl, S., Ampoorter, E., Baert, G., Vermeir, P., ... Boeckx, P. 2016. Functional Composition of Tree Communities Changed Topsoil Properties in an Old Experimental Tropical Plantation. *Ecosystems*, *in press* (2016).

Kearsley, E., Moonen, P.C.J., Hufkens, K., Doetterl, S., Lisingo, J., Boyemba Bosela, F., Boeckx, P., Beeckman, H., Verbeeck, H. Model performance of tree height-diameter relationships in the central Congo Basin. *Annals of Forest Science* (Accepted 2016)

##### WP3 Biodiversity monitoring

Grootaert, P. & I. Shamshev (2014). New Tachydromiinae (Diptera: Empidoidea, Hybotidae) from different types of forests near Yangambi. *Belgian Journal of Entomology* 18: 1-34.

Lücking R., Johnston M.K., Aptroot A., Kraichak E., Lendemer J.C., Boonpragob K., Cáceres M.E.S., Ertz D., Ferraro L.I., Jia Z., Kalb K., Mangold A., Manoch L., Mercado-Díaz J.A., Moncada B., Mongkolsuk P., Pamong K.B., Parnmen S., Peláez R.N., Poengsungnoen V., Rivas Plata E., Saipunkaew W., Sipman H.J.M., Sutjaritturakan J., Van den Broeck D., Von Konrat M., Weerakoon G. & Lumbsch H.T. (2014) One hundred and seventy-five new species of Graphidaceae: closing the gap or a drop in the bucket? - *Phytotaxa* 189: 7–38

Lumbsch H.T., Kraichak E., Parnmen S., Rivas Plata E., Aptroot A., Cáceres M.E.S., Ertz D., Feuerstein S.C., Mercado-Díaz J.A., Staiger B., Van den Broeck D. & Lücking R. (2014) New higher taxa in the lichen family Graphidaceae (lichenized Ascomycota: Ostropales) based on a three-gene skeleton phylogeny - *Phytotaxa* 189: 39–51

Kraichak E., Parmen S., Lücking R., Rivas Plata E., Aptroot A., Cáceres M.E.S., Ertz D., Mangold A., Mercado-Díaz J.A., Papong K., Van den Broeck D., Weerakoon G. & Lumbsch H.T. (2014) Revisiting the phylogeny of Ocellularieae, the second largest tribe within Graphidaceae (lichenized Ascomycota: Ostropales) - *Phytotaxa* 189: 52–81

Van den Broeck D., Lücking R. & Ertz D. (2014) Three new species of Graphidaceae from tropical Africa - *Phytotaxa* 189: 325–330

Van den Broeck D., Lücking R. & Ertz D. (2014) The foliicolous lichen biota of the Democratic Republic of the Congo with the description of six new species - *Lichenologist* 46(2): 141-158.

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Grootaert, P; & Shamshev I.V. (2013). The flies of the family Hybotidae (Diptera, Empidoidea) collected during the Boyekoli Ebale Congo 2010 Expedition in Democratic Republic of Congo. *Zootaxa* 3603: 61 pp. <http://dx.doi.org/10.11646/zootaxa.3603.1.1>

Grootaert, P; & Shamshev I.V. (2013, in press). New Tachydromiinae (Diptera: Empidoidea, Hybotidae) from different types of forests near Yangambi. *Belgian Journal of Entomology* 18.

Grootaert, P; & Shamshev I.V. (2013, in press). First record of a “whitish yellow” terrestrial *Chersodromia* (Diptera: Hybotidae) in the Afrotropical region (D.R. of the Congo). *Bulletin K.B.V.E.*

Grootaert, P; & Shamshev I.V. (2014, to submit). New species of *Platypalpus* (Diptera: Hybotidae) from the D. R. of the Congo. *European Journal of Taxonomy*

Grootaert, P., Sonet, G., Mortelmans, J., Vandewinkel, C. & Z. Nagy (2013). Using DNA barcodes for diversity assessment in Hybotidae (Diptera : Empidoidea). Abstracts Entomologische Studiedag, KBVE (23 Nov. 2012): p. 8.

Nagy, Z., Sonet, G., Mortelmans, J., Vandewinkel, C. & Grootaert, P. (in press). Using DNA barcodes for diversity assessment in Hybotidae (Diptera, Empidoidea). *ZooKeys*  
WP4 Integration of carbon and biodiversity data

Bauters, M., Ampoorter, E., Huygens, D., Kearsley, E., De Haulleville, T., Sellan, G., Verbeeck, H., Boeckx, P., and Verheyen, K. 2015. Functional identity explains carbon sequestration in a 77-year-old experimental tropical plantation. *Ecosphere* 6, 1–11.

Van de Perre, F., Willig, M.R., Presley, S.J., Boeckx, P., Cooleman, S., De Haan, M., De Kesel, A., Desein, S., Grootaert, P., Janssens, S., Kearsley, E., Lachenaud, O. Leponce, M., Van den

Broack, D., Verbeeck, H., Würsten, B., Leirs, H. & Verheyen, E. No general patterns in the relationship between carbon storage and taxonomic diversity: a multi-taxon assessment (submitted)

Kearsley, E., Verbeeck, H., Hufkens, K., Van de Perre, F., Doetterl, S., Baert, G., Beeckman, H., Boeckx, P., Huygens, D. Functional community structure of African monodominant Gilbertiodendron dewevrei forest influenced by local environmental filtering. Ecology and Evolution (Accepted October 11, 2016)

## 9.1.2 Others

Poster at 1<sup>st</sup> International Conference on Biodiversity in the Congo Basin, Kisangani, DR Congo, 6-10 June 2014: Van de Perre, F., Dessein, S., Verheyen, E., Van den Broeck, D., Kearsley, E., Leirs, H. *the COBIMFO project: An assessment of the relation between carbon storage and biodiversity in the Yangambi biosphere reserve (DR Congo).*

Poster at 21th Benelux Congress of Zoology, Liège, Belgium, 12-13 December 2014: Van de Perre, F., Dessein, S., Verheyen, E., Leirs, H. *Diversity of rodents and shrews in the Yangambi biosphere reserve, DR Congo.*

Lecture at the 12<sup>th</sup> African Small Mammal Symposium, Mantasoa, Madagascar, 13 April 2015: Van de Perre, F., Verheyen, E., Dessein, S., Leirs, H. *Diversity of rodents and shrews in the Yangambi biosphere reserve, DR Congo.*

Grootaert, P. & I. Shamshev (2014). Taxonomy and diversity of hybotids (Diptera: Hybotidae) in various types of forest in the Congo Basin near Yangambi (D. R. of the Congo). *8<sup>th</sup> International Congress of Dipterology*, Potsdam, 10-15 August 2014. Abstract

Grootaert, P. (2014). Diversity of insects in various types of forest near Yangambi with special attention to the hybotids flies (Diptera: Hybotidae). *First International Conference of Biodiversity in the Congo Basin*, 6-10 June, Kisangani, R.D. Congo. Abstracts 263, p.220. Oral presentation.

Wetsi Lofete, J.L. & P. Grootaert (2014). Atlas des chenilles comestibles de la région de Kisangani: diversité, utilisation et avenir. *First International Conference of Biodiversity in the Congo Basin*, 6-10 June, Kisangani, R.D. Congo. Abstracts 198, p.176. Poster.

Oral presentation at EGU General Assembly, Vienna, Austria, 18-22 April 2016: Bauters, M., Verheyen, K., Verbeeck, H., Ampoorter, E., Doetterl, S., Baert, G., Boeckx, P. *Tree species effects on topsoil properties in an old tropical plantation.*

## 9.2 Co-publications

### 9.2.1. Peer review

#### WP2 Baseline C inventory

Slik, J. W. F., Arroyo-Rodríguez, V., Aiba, S. I., Alvarez-Loayza, P., Alves, L. F., Ashton, P., Balvanera, P., Bastian, M., Bellingham, P. J., van den Berg, E., et al. How many tree species are there in the world's tropical forests. PNAS, Accepted (2015).

Lewis, S. L. et al. Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society London, B. Biological Sciences* 368, 20120295 (2013).

Bastin, J.-F., Barbier, N., Réjou-Méchain, M., Fayolle, a., Gourlet-Fleury, S., Maniatis, D., de Haulleville, T., Baya, F., Beeckman, H., Beina, D., et al. 2015. Seeing Central African forests through their largest trees. *Scientific Reports* 5, 13156.

Avitabile, V., Herold, M., Heuvelink, G.B.M., Lewis, S.L., Phillips, O.L., Asner, G.P., Armston, J., Asthon, P., Banin, L.F., Bayol, N., et al. 2015. An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology* n/a – n/a.

Alongo S., Visser M., Drouet T., Kombele F., Colinet G., Bogaert J. (2013) Effets de la fragmentation des forêts par l'agriculture itinérante sur la dégradation de quelques propriétés physiques d'un Ferralsol échantillonné à Yangambi, R.D. Congo. *Tropicultura*, 31, 1, 36-43

Bastin J.F., Djibu J.P., Havyarimana F., Alongo S., Kumba S., Shalukoma C., Motondo A., Joiris V., Stévigny C., Duez P., De Cannière C., Bogaert J. (2011) Multiscalar analysis of the spatial pattern of forest ecosystems in Central Africa justified by the pattern/process paradigm; two case studies. *Forestry: Research, Ecology and Policies*. Nova Science Publishers. Editor: D.A.Boehm, pp. 79-98

### WP3 Biodiversity monitoring

Stanley W.T., Robbins L.W., Malekani J.M., Gambalemoke S.M., Dudu A.M., Mukinzi J.C., Hulselmans J., Prévot V., Verheyen E., Hutterer R., Doty J.B., Monroe B.P., Nakazawa Y.S., Braden Z., Carroll D., Kerbis Peterhans J.C., Bates J.M. & Esselstyn J.A. (2013). A new hero emerges: another exceptional mammalian spine and its potential adaptive significance. *Biological letters* 9: 20130486.

Ilyongo L.W.M., De Cannière C., Ulyel J., Dudu B.A., Bukasa K., Verheyen E., Bogaert J. (2013). Effets de lisière et sex ratio de rongeurs forestiers dans un écosystème fragmenté en République Démocratique du Congo (Réserve de Masako, Kisangani). *Tropicultura* 31(1): 3-10

Gembu Tungaluna G.C., Van Cakenberghe V., Musaba Akawa P., Dudu Akaiibe M., Verheyen E., De Vree F., Fahr J. (2013). Rediscovery of *Glauconycteris superba* Hayman, 1939 (Chiroptera: Vespertilionidae) after 40 years at Mbiye Island, Democratic Republic of the Congo. *European Journal of Taxonomy* 42: 1-18

Colangelo P., Verheyen E., Leirs H., Tatar C., Denys C., Dobigny G., Duplantier J.M., Brouat C., Granjon L., Lecompte E. (2013). A mitochondrial phylogeographic scenario for the most widespread African rodent, *Mastomys natalensis*. *Biological Journal of the Linnean Society*; 108(4):901-916

Bryja J., Mikula O., Patzenhauerová H., Oguge N., Šumbera R., Verheyen E. (2013). The role of dispersal and vicariance in Pleistocene history of an East African mountain rodent, *Praomys delectorum*. *Journal of Biogeography*

Sonet G., Colyn M., Verheyen E., Nagy Z.T., Wendelen W., Van Rompaey H., Hulselmans J. (accepted). Craniometry and mitochondrial DNA uncover intraspecific diversity of Afrotropical forest-dwelling mongooses (Mammalia: Herpestidae: *Crossarchus*). *Journal of Zoological Systematics and Evolutionary Research*

Jacquet F, Denys C, Verheyen E, Couloux A, Colyn M, Nicolas V (submitted) Phylogeography and evolutionary history of the *Crocidura olivieri* complex (Mammalia, Soricomorpha): from a forest-dwelling origin to a wide expansion throughout Africa. *Journal of Biogeography*

Kumba S., Nshimba H., Ndjele L., De Cannière C., Visser M., Bogaert J. (2013) Structure spatiale des trois espèces les plus abondantes dans la Réserve Forestière de la Yoko, Ubundu, République Démocratique du Congo. *Tropicultura*; 31, 1, 53-61

Vranken I, Djibu Kabulu J.P., Munyemba Kankumbi F., Mama A., Iyongo Waya Mongo L., Bamba I., Laghmouch M., Bogaert J. (2011) Ecological impact of habitat loss on African landscapes and biodiversity. *Advances in Environmental Research*; 14, 365-388

Barima YSS, Djibu JP, Alongo S, Ndayishimiye J, Bomolo O, Kumba S, Iyongo L, Bamba I, Mama A, Toyi M, Kasongo E, Masharabu T, Visser M, Bogaert J. (2011) Deforestation in Central and West Africa: landscape dynamics, anthropogenic effects and ecological consequences. *Advances in Environmental Research*, 7, 95-120