Analysis of simulated functional diversity in tropical forests:

Differences between cultivated and naturally grown secondary forests in Cambodia

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Abstract

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Accelerated deforestation represents a major global environmental concern. Over the last decades Cambodia has experienced a drastic decrease in forest cover and measures to halt deforestation have not been as effective as planned. In order to support reforestation, as well as appropriate sustainable forest management practices, two aspects need to be taken into account: (a) the ecosystem functioning of the forest, thus its ability to promote productivity and resist disturbances, and (b) the influence of harvest measures on the forest dynamics.

For this study the dynamic vegetation model LPJ-GUESS was applied to simulate specific scenarios of the forests in four study sites in Cambodia, representing evergreen, semi-evergreen and deciduous forest covers. The functional diversity, expressed by the community-weighted mean of the analyzed plant functional traits, represents a suitable indicator to describe the performance of plant growth and the dynamics between the species within a forest ecosystem. Based on this model analysis, a difference in functional diversity between the old-growth, cultivated and naturally regrown forest ecosystems could be detected. In relation to the establishment and composition of the modelled group-specific plant functional types, the results suggest an overall dominance of shade tolerant and evergreen trees, emphasizing the advantage of longer leaf life-spans in hot and humid conditions. It is assumed that in three study sites (Koh Kong, Mondulkiri, and Takeo) the secondary forests show an overall higher ability to resist disturbances than the forests in Siem Reap. The extent of impacts of logging practices on biomass production depend on the interval and harvest intensity. Thinning processes of 10% conducted every 20 years tend to increase the forests' overall carbon stock, indicating a positive effect of minor disturbances on the forest's productivity. However, comparisons with self-derived measurements suggest an overestimation of the simulated plant growth, which requires further research to allow for specific recommendations on forest management practices.

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List of Abbreviations

C	Carbon
Cmass	Carbon biomass
CUL	Cultivated forest ecosystem
CWM	Community-weighted mean
CWM_a	Community-weighted mean weighted by abundance
CWM_b	Community-weighted mean weighted by biomass
C:N	Carbon to nitrogen ratio
DGVM	Dynamic global vegetation model
DBH	Diameter at breast height
EF	Ecosystem functioning
FD	Functional diversity
KK, KK_{se}	Study site in Koh Kong (semi-evergreen forest cover)
LAI	Leaf area index
LA:SA	Leaf area to sapwood area ratio
LES	Leaf economics spectrum
MK, MK_{se}	Study site in Mondulkiri (semi-evergreen forest cover)
N	Nitrogen
NPP	Net primary production
NRG	Naturally regrown forest ecosystem
NUE	Nitrogen use efficiency
OGF	Old-growth forest
PFT	Plant functional type
RQ	Research question
SLA	Specific leaf area
SR, SR_e	Study site in Siem Reap (evergreen forest cover)
TK, TK_d	Study site in Takeo (deciduous forest cover)
TrBDx	Tropical broadleaved deciduous shade tolerant PFT
TrBEx	Tropical broadleaved evergreen shade tolerant PFT
TrDDi	Deciduous PFT representing tree species (e.g. *Dipterocarpus intricatus*)
TrEAg	Evergreen PFT representing tree species (e.g. *Anisoptera glabra*)
TrIBDx	Tropical broadleaved deciduous shade intolerant PFT
TrIBEx	Tropical broadleaved evergreen shade intolerant PFT

1 Introduction

Effective ecosystem functioning is vital for life on Earth. Mankind depends on ecosystem processes such as water and air purification, pollination and soil formation that provide drinking water, oxygen, food and other supplies – societal benefits that are commonly known as ecosystem services (Díaz & Cabido 2001). Due to the massive rise of the global population, natural resources have become over-exploited and ecosystems have experienced modifications that in many cases have resulted in irreversible adverse consequences (Orlandi Laureto et al. 2015). As Naeem et al. (2009) express it "the minute humanity began to manipulate nature beyond what is common for ecosystem engineers like beavers or termites, ... humans began a path that would lead to extraordinary success, but at an extraordinary price".

Indiscriminate deforestation, often due to agricultural expansion (Geist & Lambin 2002), is considered one of the major causes of global climate change (Bologna & Aquino 2020). Forests, and particularly tropical forests, provide numerous ecosystem goods and services that encompass not only the capacity to stabilize the climate, but also to promote overall human-wellbeing (Seymour & Busch 2016). In order to support proper and adequate forest conservation, this study focuses on functional diversity within tropical forests and aims to improve the understanding of the complex forest dynamics.

1.1 Importance of forest ecosystems

The importance of tropical forests is explained by various social, cultural, and particularly economic as well as environmental functions (Montagnini & Jordan 2005). Next to wood fuels and non-timber forest products (food, fibers, medical plants, and seeds for handicraft such as souvenirs or other products) that generate on average over 20% of the household income of rural communities, timber production represents the biggest economic use of forests (Montagnini & Jordan 2005, Seymour & Busch 2016). Ecotourism attracted additional global attention during the last decades, as a profitable and still environmentally-friendly practice (Li & Han 2001). However, even properly managed ecotourism requires developed infrastructure to enable access for non-consumptive recreational activities (Montagnini & Jordan 2005) and thus promotes fragmented landscapes rather than a

continuous area of old-growth forests. Although most economic activities also involve smaller local stakeholders, the impact on forests is severe and results in unsustainable resource use that ultimately endangers the livelihood of local communities.

The environmental functions of a forest ecosystem can be summarized as ecosystem services. Tropical forests play an essential role by regulating the local as well as regional climate (Nobre et al. 1991, Gullison et al. 2007). Lower temperatures and higher relative humidity close to tropical forests support local agricultural productivity. On a global perspective forests are also known as the Earth's green lungs. By taking up atmospheric carbon dioxide (CO_2) through photosynthesis, forests store carbon (C) and release oxygen. Dead plant material either decomposes, which consequently leads to a production of CO_2, or remains in the soil as soil organic matter. Tropical forests are estimated to account for the largest global C stock in vegetation with approximately 212 gigatons (Gt) C and an additional 216 Gt C in soils (IPCC 2000). In comparison, cropland, that covers almost the same area as tropical forests, only contains around 3 Gt C in vegetation, and 128 Gt C in soils. A forest therefore represents a major C sink that only effectively releases CO_2 when deforested or burnt. Throughout the 1990s, for instance, tropical deforestation accounted for almost 20% of greenhouse gas emissions due to an annual release of approximately 1.5 Gt C (Gullison et al. 2007). Deforestation further reduces resilience to impacts of extreme weather events (Seymour & Busch 2016), prevents soil formation and its water holding capacity which results in increased surface runoff and decreased infiltration of water, that ultimately leads to floods and deterioration of water quality (Nasi et al. 2002). Additionally to these essential environmental services, estimations suggest that tropical forests represent a habitat for more than 50% of the species worldwide (Montagnini & Jordan 2005), in which angiosperm species alone account for more than 300,000 species of the tropical flora (Prance et al. 2000).

1.2   Deforestation in Cambodia

Despite the knowledge of irreversible consequences, systematic deforestation in the tropics, mainly driven by population pressure and need for agricultural land, has become a defining environmental challenge of our time (Geist & Lambin 2002, Montagnini & Jordan 2005, Bologna & Aquino 2020). The UNDP ranks Cambodia as one of the richest countries in forest resources in Asia (UNDP 2011). The forest types include, next to the dominating lowland evergreen, semi-evergreen and deciduous forests, as well as coastal mangrove forests. The tropical forest and wooded land area, however, experienced a drastic decrease from 73% of the total land area in 1990 to 53% in 2015 (with a forest area of around 95,000 km^2) (see Figure 1.1) (FAO 2015).

**Changes in forest and wooded land cover in % of total land area
in Cambodia from 1990 to 2015**
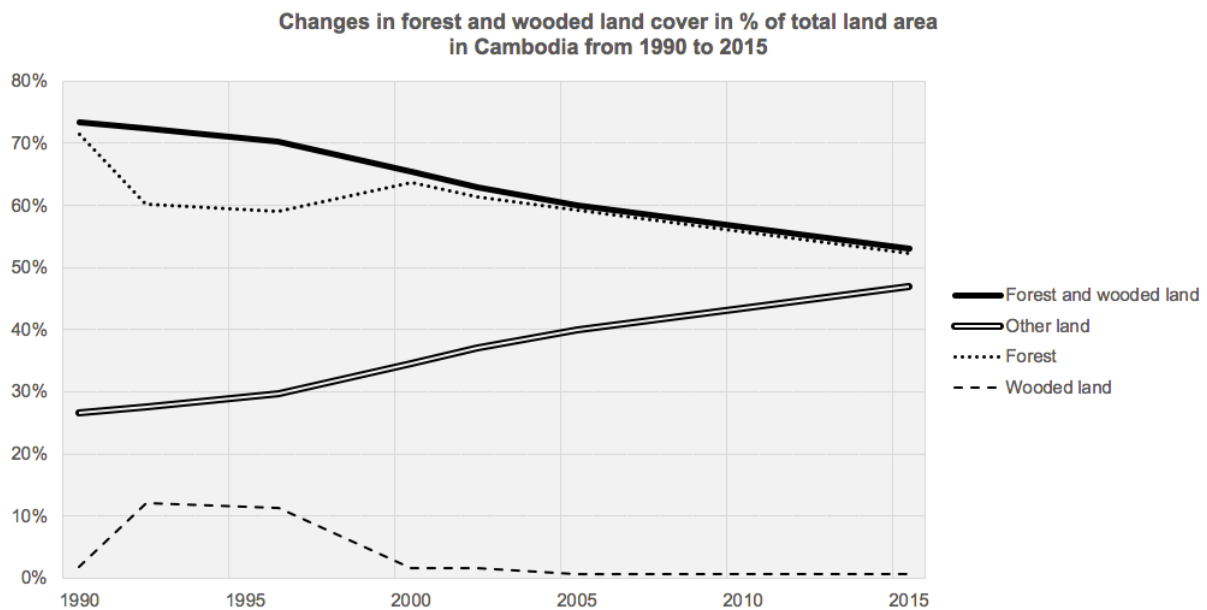
Figure 1.1: Changes in forest and wooded land cover in % of total land area in Cambodia from 1990 to 2015. Data source: FAO (2015). *Forest land*: Land spanning more than 0.5 ha with trees higher than 5 m. *Wooded land*: Land not classified as 'forest', with combined cover of shrubs, bushes and trees. *Other land*: Land that is predominantly under agricultural or urban land use. Inland water bodies (2.5% of total land area) is integrated into the category of 'other land'.

According to the National Strategic Development Plan 2006-2010, implemented by the Royal Government of Cambodia (RGC), a forest cover of at least 60% of the total land area was considered to be a central Cambodian Millennium Development Goal by 2015 (RGC 2006). The Food and Agriculture Organization of the UN (FAO) has been monitoring the global forest area and its changes since 1946 (FAO 2018). Although the FAO assessment for Cambodia should be interpreted with caution as the estimations are based on remote sensing data and forestry statistics with broad forest definitions (Hansen & Top 2006), the UNDP Cambodia highlights that the actual area of dense forest is even smaller than anticipated. More than 75% of the forest area is termed either as disturbed evergreen, mixed, or mosaic (UNDP 2007). The ongoing forest depletion is visible and acknowledged by the RGC, which already stated in 2006 that the deforestation process has not been reduced as planned (RGC 2006).

The reasons for the rapid land conversion can be summarized as (a) encroachment by local communities and (b) land concessions by domestic and foreign investors (Hansen & Top 2006). A total population of 16 million people in 2017, at a growth rate of 1.5% per year (WorldBank 2009), eventually results in an increase of rural communities, exacerbating the current population pressure. Rural people strongly rely on the forest and its supplies, but farming and raising livestock give them a better security to maintain their livelihood (UNDP 2011). Forest areas around settlements of local communities slowly degrade and give way to agricultural use (Hansen & Top 2006). The conversion due to land concessions on the other hand, happens on a much larger scale. Land acquisition by foreign and domestic investors

are often approved due to the promised rural and economic development facilitated by job creation and improved infrastructure. The ongoing investments in agricultural land, particularly in developing countries, often results, however, in accelerated deforestation and detrimental consequences for the rural population, such as eviction and loss of livelihoods (Davis et al. 2015). As Keating (2012) criticizes, "carried out in the name of development, these concessions are effectively nontransparent business exchanges of wealth and power for natural resources, contracted between the private sector and the state". Despite the social conflicts, Davis et al. (2015) demonstrate, that land concessions in particular contribute to annual deforestation rates approximately 29% to 105% higher than in non-leased areas. Forests are removed for productive use such as rubber-tree plantations and crops, or degraded areas are merely kept empty for speculative reasons (Davis et al. 2015).

1.3   Project aim and research questions

Besides the necessity of effective nature conservation and mitigation of current climate change to minimize the impacts on ecosystems, research is undertaken to identify efficient measures to assess ecosystem functioning (Orlandi Laureto et al. 2015). The complexity and dynamics of the interactions between biotic and abiotic components in an ecosystem make it particularly difficult to estimate ecosystem efficiency. As Garnier et al. (2016) indicate "if we wish to understand the functioning of ecological systems, and ultimately that of our planet, taking into account the functional approach of organisms is essential". This approach defines functions as specific activities carried out by organisms that inhabit an ecological system. In other words, ecosystem processes are more affected by the function of a species' trait than by the taxonomic unit the species is categorized to (Goswami et al. 2017). Studies on so-called *functional traits* result in enhanced estimations of ecosystem functioning, and based on the ranges and values of these traits, *functional diversity* can be defined (Tilman 2001). Functional diversity determines ecosystem stability, dynamics and productivity, and expressed as an index it is considered a crucial measure to quantify as well as to simplify ecosystem functioning (Tilman 2001, Lohbeck et al. 2012).

Following the urge for prevention measures to halt deforestation and promote reforestation of tropical forests in Cambodia, the present study aims for an improved understanding of functional diversity within secondary forest ecosystems. Tropical secondary forests are forests resulting from man-made disturbances (Brown & Lugo 1990). Following the notion of Corlett (1994) that "there is no logical reason to distinguish between the results of human and natural impacts", secondary forests are hereafter defined as regenerated forests that have been disturbed by natural processes or human-induced activities. Regeneration of forests can either be planned or occur naturally (FAO 2019), which results in a cultivated or naturally regrown forest ecosystem, respectively. As the index of functional diversity offers

a tool to analyze ecosystem functioning, the following research question (RQ) motivates the study:

> **RQ:** Does the simulated functional diversity differ between cultivated and naturally regrown tropical forest ecosystems?

The dynamic vegetation model Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) will be used for the model simulations. In order to relate the model output to the environmental conditions of the tropical forests in Cambodia, four traits as well as the leaf area index resulting from the model analysis will be compared with self-derived measurements. Further data was gained by the efforts of the Forest Restoration and Water Availability for Smart Agriculture (FRAWASA) research team and supplemented by the global TRY Plant Trait Database[1]. The field measurements were conducted in ten study plots, located across four provinces in Cambodia. Specific model input settings are defined to represent the two secondary forest ecosystems. These are then subsequently compared to the control simulation of a modelled old-growth forest, which is herein considered as the ideal state.

Based on the assumption that reforestation measures will only be implemented if financial benefits are guaranteed or expected, the study further focuses on sustainable forest management practices. As has been stated by Montagnini & Jordan (2005), "understanding the variety of ecosystem products and services of forests is therefore essential for the design of adequate conservation and management strategies, as well as for the development and maintenance of the policies that sustain them". In order to answer the following two tangentially related questions, varying harvest intensities will be simulated and evaluated by analyzing the functional diversity of these managed forest ecosystems.

> **RQ-a:** Do varying harvest intensities enhance or decelerate the forest dynamics towards the stage of an old-growth forest? How do the forest dynamics differ between the regenerated forest ecosystems?

> **RQ-b:** Which forest management practices could be implemented to enable sustainable harvesting within the regenerated forest ecosystems?

Considering the accelerated deforestation rate in Cambodia, and its impact on the social as well as natural environment, enhanced understanding of the dynamics of managed tropical forests is urgently required. Functional diversity, as a practical tool to determine ecosystem functioning, shall indicate (a) whether cultivated or naturally regrown forest ecosystems offer a higher forest productivity, and (b) how varying harvest intensities influ-

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[1]The TRY Plant Trait Database is organized as a network of vegetation scientists and represents a research platform that provides free and open access to global plant trait data (Boenisch & Kattge 2022).

ence regenerated forest ecosystems. Once secondary forest dynamics are well understood, implemented management practices, such as sustainable harvesting, can be evaluated and further compared. By comparing the model results with self-derived measured data, it allows for more realistic recommendations for appropriate reforestation approaches and suitable forest management practices, to ensure the needs of the local communities are met without further compromising the environment.

2 Theoretical Background

2.1 Ecosystem functioning

Ecosystem functioning (EF) implies various properties and scales which makes it particularly difficult to conclude a standard definition (Song et al. 2014). EF is commonly described as the rate and dynamics of productivity, such as primary production, total plant biomass or nutrient concentration, that represent relatively simple measurable features of ecosystems (Tilman 2001). EF can also be defined by the material cycle, energy fluxes, stability of stocks and rates of ecosystems (Song et al. 2014). Díaz & Cabido (2001) summarize two components of EF: ecosystem resource dynamics and ecosystem stability. The first focuses on key resources (C, water, nutrients) and analyzes the magnitude and rate of their in- and output and internal cycling. The latter describes the ability of a system to persist in the case of a disturbance (ecosystem resistance) as well as the ability to remain in the same state after a disturbance, thus adapting and reorganizing without converting to a new system state (ecosystem resilience).

The significance of EF is best described by the unified natural-social framework of the Millennium Ecosystem Assessment. This concept demonstrates the linkages between biodiversity and EF to human wellbeing, by acknowledging the dependence of mankind on ecosystem services (MEA 2003):

$$
\begin{array}{c}
\text{Biodiversity} \\
\Downarrow \\
\text{Ecosystem Functioning} \\
\Downarrow \\
\text{Ecosystem Services} \\
\Downarrow \\
\text{Human Wellbeing}
\end{array}
$$
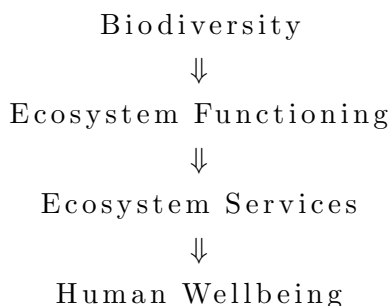
Ecosystem services are provided by ecosystem functions and encompass *goods*, such as water, food and raw materials, as well as *services*, that include soil formation, pollination, biological control, recreation and so forth (Díaz & Cabido 2001). An ecosystem function refers to the properties and processes of an ecosystem, such as regulating hydrological flows, storing C and nutrients, providing extractable food, etc. (Costanza et al. 1997).

Apart from a general interdependence, in most cases one ecosystem service is the result of two or more ecosystem functions and consequently one function often contributes to several services.

The dependence of EF on biodiversity can be described by the biodiversity and ecosystem function (BEF). The BEF framework implies an asymptotic relationship between species diversity and ecosystem stability (MEA 2003). In other words, as Hector & Bagchi (2007) put it, "individual ecosystem functions generally show a positive asymptotic relationship with increasing biodiversity, suggesting that some species are redundant". As biodiversity is commonly represented as species richness, ergo the number of taxonomic identifications (Song et al. 2014), the validity of the BEF concept remains uncertain (Griffin et al. 2009). The assumption that EF is less likely to be affected by potential species losses if sufficient species are present to compensate for lost ecosystem properties, is yet well established. Hooper et al. (2005), however, question the actual effect of species richness on EF and emphasize the importance of dominant and keystone species, as they strongly influence EF. Keystone species describe species that fulfill critical functions within an ecosystem, and with their removal significant alterations of species composition may be caused (Zhao-Hua et al. 2001). Not all species contribute to EF to the same extent, and a higher number of species merely increases the likelihood that the so-called keystone species are present (Hooper et al. 2005).

The BEF framework should thus not be based on species richness, but on the diversity of functions. As Malaterre et al. (2019) put it, "functional diversity can therefore be thought of as providing a novel vantage point of biodiversity, apprehending the diversity of life in terms of a diversity of organismal functional traits". The functional approach simplifies the complexity of ecological systems and gives information on the species' influence on the ecosystem and response to environmental change (Orlandi Laureto et al. 2015). This concept therefore gained great attention and is claimed to be an effective tool to determine ecosystem processes as well as to describe the effect on short-term ecosystem resource dynamics and long-term ecosystem stability (Díaz & Cabido 2001).

2.2 Functional diversity

Although functional diversity (FD) is nowadays considered an important concept and tool for general ecological research, it remains unclear what FD exactly is, how it should be measured, and how its performance should be assessed (Mason et al. 2003, Mouillot et al. 2005, Petchey & Gaston 2006). Tilman (2001) provides the most cited definition of FD, which he defines as "the range and value of those species and organismal traits that influence ecosystem functioning". The focus on the individual species is significant, as adaptive strategies regarding resource use, reproduction, competition, and defences against

natural disturbances happen at this level (Garnier et al. 2016). Individuals therefore have an essential effect on the dynamics of populations, communities, and consequently on ecosystems. Despite the importance of the individual level, EF is further influenced by the presence of other species and the dynamics between them. Petchey et al. (2009) define FD at the community level as "a measure of diversity that implicitly incorporates some mechanisms of ecological interactions between species". This approach focuses on the effect on FD when particular species are added to or removed from the community. As it relates to the dynamics between the same species (intraspecific) and between different species (interspecific) (Garnier et al. 2016), the complementarity and redundancy of co-occurring species is embedded in FD (Schleuter et al. 2010). This idea is based on trait similarity or trait dissimilarity, respectively (Petchey et al. 2009). The loss of one species among species with similar traits will not significantly affect FD. However, when a species with rather dissimilar traits is lost, FD reduces as a result of a potential resource-use decline.

Due to the lack of a standard definition of FD, Song et al. (2014) suggest putting the common delineations into two categories: (a) diversity of functional traits (see section 2.2.1) and (b) diversity of functional groups (see section 2.2.2). Although the major attention of this study is on trait diversity, both categories are briefly explained to understand the methods to calculate FD (see section 2.2.3).

2.2.1 Functional traits

Functional traits relate either to plant species, or information on animals (Petchey & Gaston 2006). Since ecological systems predominately consist of plant species, and this study focuses on tropical forests, this section only relates to plant functional traits. There are ample definitions and delineations of the concept of functional traits, and traits in general. Violle et al. (2007) therefore suggest a certain terminology of, and relationship between, traits to allow for a profound functional trait-based approach. By following the selection paradigm as defined by Arnold (1983), which describes how morphological features influence a species' performance, which eventually determines its fitness, Violle et al. (2007) develop a hierarchical order of traits dependent on their direct and indirect impact on plant performance (see Figure 2.1).

As can be seen in Figure 2.1, Violle et al. (2007) distinguish between (a) *functional traits* and (b) *performance traits*. A functional trait is considered as a measurable morphological, physiological, or phenological (M-P-P) feature of an individual plant species. In some cases the quantification of M-P-P traits is likely not precise enough, or extremely expensive and time-consuming, which necessitates *attributes* as surrogates (Violle et al. 2007). Attributes or functional traits either describe quantitative (e.g. specific leaf area, leaf lifespan), or qualitative characteristics, such as life forms as defined by Raunkiaer, or nutrient uptake
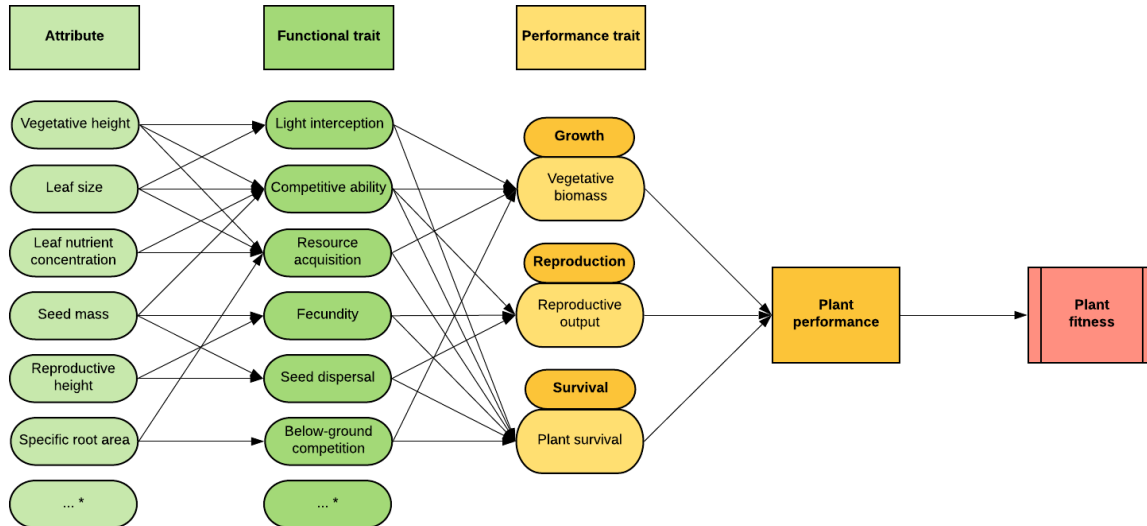
Figure 2.1: Schematic illustration of the hierarchical order of plant traits, generated by applying the three components of the selection theory: morphology, performance and fitness. *Green boxes:* Morphological features; traits that indirectly influence plant performance. *Yellow boxes:* Performance features; traits that directly influence plant performance. *Red box:* Plant fitness. *Given attributes and functional traits represent solely a selection of various variables.

strategies (Garnier et al. 2016). Quantitative values usually correspond to an average of a set of individuals or a population. Performance traits are categorized by the three components of fitness: (i) growth, (ii) reproduction, and (iii) survival, and result in *vegetative biomass*, *reproductive output* and *plant survival*, respectively (Garnier et al. 2016, Violle et al. 2007). Similar to the pattern of the interaction between ecosystem functions and ecosystem services (see section 2.1), traits can be the result of two or more attributes, and one attribute can contribute to more than one trait. The same accounts for the relationship between functional and performance traits.

This trait concept of functional and performance traits allows for an assessment of the functions performed by plant species at the individual level (Garnier et al. 2016). However, plant species do not usually exist in isolation, but are subject to ongoing biotic and abiotic factors that impact their performance. Traits associated with the response to, or effect on, these specific environmental conditions are called *response traits* and *effect traits*, respectively (Lavorel & Garnier 2002, Díaz et al. 2013). Since these traits are commonly categorized into functional groups, they will be further discussed in the following section.

2.2.2 Functional groups

Tilman (2001) states that each species consists of vast M-P-P traits, and in order to deal with this complexity, it is recommended to classify similar traits into one category or group. Consequently, functional groups represent a set of species with similar traits (Schleuter et al. 2010). Since there is no universal standardized identification mechanism of functional

groups, the classification depends on the process of interest, spatial and temporal scales, as well as on the type of organisms or ecosystems (Díaz & Cabido 2001, Hooper et al. 2002). They are usually associated with adaptation to environmental challenges, such as the response to, or effect on, ecosystem processes, as mentioned in section 2.2.1. As its name implies, a *functional response group* encompasses plant species with similar response traits in relation to biotic or abiotic factors. A typical example is the distinction between species that are tolerant or intolerant to shade, drought, fire, frost or other disturbances (Díaz & Cabido 2001). In contrast, *functional effect groups* focus on effect traits, thus on plant species that have a similar impact on ecosystem processes or the ecosystem itself (Hooper et al. 2002). Díaz & Cabido (2001) name: nutrient fixers, ecosystem engineers, or fire-promoting species as examples of functional effect groups. Besides the attempt to distinguish between these two functional groups, Hooper et al. (2002) emphasize the importance of merging both concepts to allow for an enhanced understanding of ecosystem properties. The groups also often coincide and influence each other (Díaz & Cabido 2001, Suding et al. 2008). For instance, species with high stress tolerance to natural disturbances (response) have a lower impact on decomposition or nutrient cycling (effect).

The concept of functional groups is popular because of the "perceived ease of assigning species groups" (Petchey et al. 2009). Despite the arbitrariness of objective and subjective classifications, the major critique is the issue of species similarity or dissimilarity (Petchey & Gaston 2002). In order to be assigned to the same functional group, how similar do species need to be? To what extent can interspecific differences be ignored? This decision determines the number of species within a group, and consequently the number of functional groups in total (Petchey et al. 2009). Next to a general different contribution of plant species to EF dependent on their M-P-P features (Hooper et al. 2005), Mason et al. (2003) further criticize the missing consideration of species abundance. Due to a greater abundance, some species may influence ecosystem processes more than others, assuming that the species' influence has a proportional relationship to its abundance. Functional group richness therefore represents a rather imprecise and vague measure of FD (Mason et al. 2003, Petchey et al. 2009).

2.2.3 Index of functional diversity

Indices are used to quantify and describe functional diversity to simplify and further compare its aspects (Tilman 2001). Despite ample research on FD and its measurement, issues regarding the statistical interpretation of results, experimental designs, or implementation of potential factors remain, and result in ongoing controversial debates regarding FD calculation (Díaz & Cabido 2001). Some functional traits are extremely difficult to quantify precisely (e.g. root growth, fecundity rates, seed dispersal) (Garnier et al. 2016) or to asses directly, especially if a vast number of species is required (Mason et al. 2003). In

relation to this impreciseness, Schleuter et al. (2010) describe FD as a "multi-dimensional cloud of points in trait space", where each coordinate represents a measured trait, and each point a species or an individual. A certain degree of approximation and simplification therefore needs to be accepted.

Following the notion of Mouillot et al. (2005), that it is neither likely or desirable to identify one single number to describe all aspects of FD, Mason et al. (2005) propose to apply the three components of species diversity (species richness, evenness, and divergence) to a functional approach to calculate different facets of FD. These components are based on niche differentiation, and thus on the abundances, dynamics, and interactions among species, which are dependent on their M-P-P traits (Tilman 2001). With a focus on species distribution and abundance in niche space[1], the functional components can be defined as follows (Mason et al. 2005): (a) *functional richness* (FRi) as the amount of niche space occupied by the species present (see section 2.2.3.1), (b) *functional evenness* (FEv) as the distribution of species abundance in occupied niche space (see section 2.2.3.2), and (c) *functional divergence* (FDi) as the degree to which abundance distribution maximizes the difference of the species' functional characters (see section 2.2.3.3). In simple terms, FRi gives information on *how much* niche space is filled, whereas FEv and FDi indicate *how* this space is filled. In contrast to FRi, FEv and FDi include species' abundance in their calculations (Schleuter et al. 2010).

2.2.3.1 Functional richness

FRi is commonly used as an indicator for productivity, resilience, or vulnerability of ecosystems, by focusing on the occupied or unoccupied niche space (Schleuter et al. 2010). Low FRi implies a low niche space coverage, and therefore a reduced productivity and lower resistance (Mason et al. 2005). Depending on the type of the corresponding functional traits, productivity decreases as potentially available resources remain unused. A lower resilience is caused by a lack of species that would provide a buffering effect against environmental disturbances, or fill in gaps in niche space that otherwise are likely to be exploited by invasive species. Contrary to common assumptions, a higher species richness does not necessarily correspond to a higher FRi, although a positive relationship between them is often observed (Díaz & Cabido 2001). Species richness can therefore be "an adequate surrogate for functional richness only if there is a linear increase in niche space 'coverage' as species richness increases" (Díaz & Cabido 2001). Since such conditions are uncommon in nature, FRi is either under- or overestimated if derived directly from species richness.

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[1]Niche space represents a multidimensional space encompassing biotic (e.g. food source, predators) as well as abiotic conditions (e.g. temperature) that impact species fitness and ultimately survival (Ashby et al. 2017). This notion provides a concept to understand the effects of ecological competition on species' coexistence.

2.2.3.2 Functional evenness

Similar to FRi, FEv gives information on productivity and vulnerability of ecosystems, by indicating under- or overutilization of resources (Schleuter et al. 2010). Under the assumption that resources are evenly distributed throughout niche space, low FEv signifies an utilization of only few parts of it (Mason et al. 2005). This untapped potential of resource availability decreases productivity and resilience as well, and may lead to similar consequences as mentioned in section 2.2.3.1. FEv can change without necessarily affecting FRi, and vice versa (Mason et al. 2005).

2.2.3.3 Functional divergence

In contrast to FRi and FEv, FDi is applied in studies on resource differentiation and competition (Schleuter et al. 2010). Low FDi indicates a low degree of niche differentiation, and thus the utilization of similar resources, which consequently results in high competition (Mason et al. 2005). Consequently, a high FDi implies a more efficient resource use that eventually leads to an increase in EF. Developed by Mason et al. (2003), the index FD_{var} is considered an appropriate measure to calculate FDi (Schleuter et al. 2010). It is based on the variance of trait values weighted by species abundance with those traits, and describes the distribution of species' individuals in niche space (Mason et al. 2005). Since FDi reflects niche complementarity it is considered a crucial measure, however as Lavorel et al. (2008) indicate, it has been little tested in the field. A widely used index to represent FD that is similar to FDi is the community-weighted mean (CWM). This measure is based on the mean trait values within a community weighted by the relative abundance of taxa exhibiting the trait (Lavorel et al. 2008, Miller et al. 2018). CWM of traits is commonly used to describe the trait-environment relationship and to assess the dynamics within a community. Often considered to be the dominant trait value, the CWM of traits is associated with the aboveground biomass, following the mass ratio hypothesis (Díaz et al. 2007, Ali et al. 2017). The mass ratio theory, as described by Grime (1998), emphasizes the influence of dominant plants and their functional traits to determine ecosystem processes within plant communities.

2.3 Leaf economics spectrum

The leaf economics spectrum (LES) represents a framework to investigate plant species strategies to sustain a population considering the environmental factors that impact the species survival (Reich 2014). The LES is based on the idea that plant species invest photosynthate (e.g. sugar) and mineral nutrients to grow leaves that in turn generate photosynthate which can be reinvested again to promote its growth - an inherently economic system (Wright et al. 2004). This ongoing biogeochemical cycle fundamentally enables

the functioning of terrestrial ecosystems. Depending on their strategy, plants either invest more or less in the construction of leaves (and other plant parts) to promote a quicker or slower growth (Wright et al. 2004, Reich 2014). For example, a plant needs to invest considerable resources to outcompete a neighboring plant to grow faster and higher to increase its light interception capacity. This approach might be advantageous as long as the return offsets the costs of the initial resource investment. In environments of low resources it might be more beneficial for plants to grow slower and therefore promote resource conservation to enhance survival. Such strategies eventually describe trade-offs between resource acquisition and striving for productivity (i.e. growth) or persistence (i.e. survival), respectively (Reich 2014).

Coordinated variations of functional traits provide clues to understand the underlying trade-offs and can therefore be considered valuable indicators for ecological strategies (Garnier et al. 2004, Wright et al. 2004, Reich 2014). The four most relevant functional traits for this study, namely specific leaf area, carbon to nitrogen ratio in leaves, leaf area to sapwood area ratio, and wood density will be briefly described in the following sections.

2.3.1   Specific leaf area

The specific leaf area (SLA) represents the ratio of leaf area to leaf dry mass (cm^2/g). SLA[2] is a widely measured and reported leaf trait that, in conjunction with leaf dry matter content, can be applied to estimate leaf thickness (Vile et al. 2005). Leaf thickness in turn indicates resource acquisition and use, that ultimately give information on the ecological performance and strategy (Westoby et al. 2002, Vile et al. 2005). As Wright et al. (2004) indicate, the leaf area and surface are fundamental traits to describe the ability to capture light, gain C and transpire water. In relation to the LES framework, there is a trade-off between SLA and leaf longevity (Osnas et al. 2013, Reich 2014). A low SLA refers to a slower and more expensive leaf production that allows for a better protection (i.e. higher stress tolerance due to improved leaf structure) and increases the leaf lifespan (Westoby 1998). The prolonged leaf longevity is crucial to offset the initial construction costs. As opposed to this, a high SLA is associated with less resource conservation that results in faster growth of simpler structured leaves. This strategy compensates the decreased protection and resilience against disturbances with its high competitive advantage on a short term basis.

2.3.2   C:N ratio in leaves

Growth and development of plants are significantly influenced by primary elements, such as C and nitrogen (N) (Westoby et al. 2002, Reich 2014, Zhang et al. 2019). The ratio

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[2]In literature SLA is also expressed and described as its inverse leaf mass per area (g/cm^2).

between the C to N concentration (mg/g) in leaves (C:N ratio) reflects the trade-off between the nitrogen use efficiency (NUE) and production rates of plants (Zhang et al. 2019). A low C:N ratio, thus a high N concentration in leaves, is associated with increased growth rates (Ågren 2004, Zhang et al. 2019). According to Reich (2014), plants with low C:N ratios in leaves are positioned on the faster end of the LES, which refers to productivity and growth rather than persistence. Plants that exhibit higher C:N ratios in leaves are generally less competitive in the short term but overall more persistent as a result of greater NUE in the long term (Zhang et al. 2019). C:N ratios in leaves do not only depend on plants and their strategy, but also on the environment (Zhang et al. 2019). In nutrient-rich environments, plants generally show lower C:N ratios in leaves as a result of resource availability. The competition then shifts towards other resources, such as light and water. In addition to this, N availability is not only influenced by topography, temperature, and precipitation, but also adversely affected by increasing atmospheric CO_2 concentration and longer growing season (Craine et al. 2018). Considering the importance of C as well as N pools for the overall biogeochemical cycles within an ecosystem, the C:N ratio in leaves represents an essential indicator for ecosystem analyses, and should thus be included in dynamic ecosystem models (Kucharik et al. 2000).

2.3.3   LA:SA ratio

Leaf area (LA) as well as sapwood area (SA) represent two crucial functional traits of trees that link photosynthesis to transpiration (Togashi et al. 2015). As the projected surface area of leaves, LA determines the leaf energy and water balance (Cornelissen et al. 2003). Similar to SLA, the LA is related to the plant's light harvesting strategy (Venn et al. 2011). Bigger leaves and wider crowns increase light interception and therefore the rate of photosynthesis, which in turn promotes plant growth. SA refers to the hydraulic capacity of a tree, hence determines the water supply of the leaves (Togashi et al. 2015). A low LA:SA ratio indicates a higher investment in sapwood area than in leaf area, and can therefore generally be related to survival strategies. It is further suggested that with increasing tree height the LA:SA ratio decreases (McDowell et al. 2002). Trees with a high LA:SA ratio tend to have more widely spreading crowns that provides them a competitive edge (Togashi et al. 2015).

2.3.4   Wood density

Wood density as a functional trait indicates the structural strength of a tree to support its own weight (Cornelissen et al. 2003). A higher tissue density increases the mechanical support and reduces the risk to any physical damage, such as stem breakage due to wind (Swenson & Enquist 2007). It further reduces the risk of implosion or rupture of the xylem conduit by negative water pressure (Hacke et al. 2001). In contrast to these protective

measures, a low wood density indicates a less conserving and therefore higher vertical growth rate that in turn allows for a competitive advantage (Swenson & Enquist 2007).

2.4 Ecosystem modelling

A model, as a simplified picture of reality, represents a tool to analyze a specific problem by incorporating the main components, features, and interactions that are relevant to solve it (Jørgensen & Bendoricchio 2001). The complexity of ecosystems, however, creates an exceptional challenge for ecological modelling approaches, due to their ability of self-organization, and numerous feedback mechanisms. Despite the extensive research and improving computer modelling capacities during the last decades, which generated effective and enhanced ecological models, environmental modelling still has to cope with predictive uncertainties (Beven 2009). However, without the use of models as a synthesis tool, the functions and properties of an ecosystem cannot be understood, nor explained (Jørgensen & Bendoricchio 2001). Ecological models are therefore used to test scientific hypotheses.

In order to represent the complex ecosystem processes so-called dynamic global vegetation models (DGVM) are applied (Quillet et al. 2010). The latest developments of DGVMs show promising results to adequately represent biogeochemical mechanisms (e.g. photosynthesis, respiration) (Quillet et al. 2010), and vegetation dynamics (e.g. interspecific competition, feedbacks on resource acquisition, reproduction, and survival) (Smith et al. 2001). The specific properties of the regional vegetation are usually encompassed by assigning plant functional types (PFTs) (Smith et al. 2001). A PFT is defined as a vegetation stand based on woody plant individuals and a herbaceous understorey, in which each individual represents the average properties of the population. PFTs are typical for patch or gap models that were initially developed for forest ecosystems to simulate nutrient cycling as well as the establishment, growth, competition, and mortality of trees (Quillet et al. 2010).

However, as indicated before, models are mere simplifications of reality and the output needs to be interpreted carefully. Particularly representations of ecosystem processes entail a high degree of uncertainty due to the complex biosphere-atmosphere interactions and significant effects of local drivers that are not captured in global-scale modelling, but may strongly influence ecosystems at a regional level (Quillet et al. 2010, Smith et al. 2014).

2.5 Sustainable forest management

In relation to the current situation of the accelerated deforestation rate in Cambodia and the accompanying loss in forest area, the implementation of sustainable forest management practices is urgently required. In order to measure and further assess the success of sustainable forest management, seven criteria are developed (Siry et al. 2005): (1) Conservation

of biodiversity, (2) maintenance of productivity of ecosystems, (3) maintenance of forest ecosystem health and vitality, (4) conservation of water and soil resources, (5) maintenance of forest contribution to carbon cycle, (6) enhancement of long-term socioeconomic benefits to meet societal needs, and (7) development of legal, institutional and economic framework for forest conservation and sustainable management.

The proper and sustainable tending of growing as well as of established forests is commonly referred to as silviculture (Stovall 2023). Adams et al. (2019) define silviculture as "the art and science of controlling the establishment, growth, composition, health, and quality of forests and woodlands to meet the diverse needs and values of landowners and society on a sustainable basis". It therefore encompasses management actions that are ecologically feasible, conducted within all economic constraints and that consider the context of the governing society (Stovall 2023). The intensity of silvicultural treatments and choice of applied measures depend on the management objectives as for instance forest and biodiversity preservation or enhanced timber production (Stovall 2023) (see Figure 2.2).

Extensive silviculture		Intensive silviculture	
Natural forest preserves	Managed naturally regenerating forests	Plantation forests	Agrosystem forests
Biodiversity Ecological complexity Rotation length			Productivity Cultural inputs Economic returns
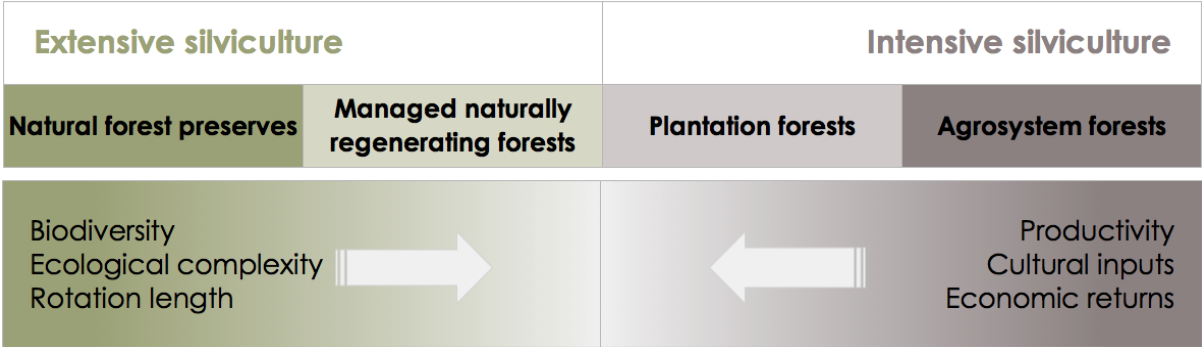
Figure 2.2: Differences between approaches of extensive silviculture (e.g. natural forest preserves or managed naturally regenerating forests) and intensive silviculture (e.g. plantation forests or agrosystem forests). Modified from the original picture by Stovall (2023).

As timber production represents the biggest economic use of forests (Montagnini & Jordan 2005), the socioeconomic component of sustainable forest management is particularly of importance in countries such as Cambodia. In order to allow for a sustainable and profitable logging, silvicultural treatments are often accompanied with the approach of reduced impact logging. The FAO (2002) defines reduced impact logging as "the use of scientific and engineering principles, in combination with education and training, to improve the application of labour, equipment and operating methods in the harvesting of industrial timber". This technique aims for a proper control of logging damages (Peña-Claros et al. 2008), entails aspects of climate mitigation measures (Griscom et al. 2019), and has shown beneficial post-logging effects in regards to forest recovery (e.g. carbon stock, timber stock) (Bedrij et al. 2022).

Considering the study's focus on the differences between cultivated and naturally grown secondary forest ecosystems, the following sections will briefly introduce two specific

restoration practices. Restoration of forest area gained great importance and became an essential part in numerous national, regional and global targets to promote reforestation (FAO 2019). Restoration of forests can either be managed or occur naturally, thus through cultivation (see section 2.5.1) or natural regeneration processes (see section 2.5.2).

2.5.1 Cultivation of forests

Cultivation describes the process of seeding or planting of tree species to artificially regenerate forests (Carnus et al. 2006). This approach represents a common, but more expensive restoration strategy (FAO 2019). Depending on the purpose, planted forests are distinguished between industrial and nonindustrial plantations (Carnus et al. 2006). Industrial plantations usually serve as highly managed forest stands of a single tree species (monoculture) with short rotations to allow for maximized wood biomass production. Nonindustrial plantations on the other hand, are established to provide essential ecosystem services (e.g. soil and water conservation). Similar to the inconsistent results of whether single- or mixed-species plantations permit an increased biomass production, there is no clear answer of whether planted forests promote or impede biodiversity as it depends on various factors (Carnus et al. 2006).

2.5.2 Natural regeneration of forests

Natural regeneration occurs on formerly disturbed forest areas when native species reestablish on their own (FAO 2019). These species are adapted to the prevailing bioclimatic conditions and can therefore be considered most adequate. This biological process can be additionally managed to enhance plant growth and increase forest cover by following the approach of assisted natural regeneration (FAO 2019). Assisted natural regeneration represents a set of measures that reduce or remove barriers to accelerate natural succession (Shono et al. 2007). These measures include reduction of weed competition, prevention of disturbances (e.g. fire, grazing livestock), establishment of pioneers to speed up enhanced microclimatic conditions, and more (Shono et al. 2007). Ecological restoration through assisted natural regeneration goes along with conserving biodiversity, promoting carbon sequestration and watershed protection as well as enhanced ecosystem resilience (FAO 2019).

3 Methodology

This study is based on a model analysis of simulated biomass production to understand the differences in functional diversity between cultivated and naturally regrown forests. The applied PFTs varied in their input parameters to simulate the processes of succession and competition of the forest ecosystems depending on the PFTs' phenology, shade tolerance, etc. that ultimately determines the overall productivity of the forests. To allow for more realistic results the input parameters were partly determined by self-derived measurements (see section 3.2). These measurements were further used to validate the model results, thus to get an insight into the model's over- or underestimation of the overall forests' productivity. In order to understand the impact of varying climatic and geographic conditions as well as specific scenarios to provide recommendations of potential sustainable forest management practices, the study included the analysis of four study sites (see section 3.1) and varying land cover and harvest settings (see section 3.3.3).

3.1 Study area

The study focuses on tropical forests in Cambodia in Southeast Asia and follows an ongoing ecosystem ecology project conducted by the department of Physical Geography and Ecosystem Science at Lund University in cooperation with the FRAWASA project team, situated in Phnom Penh in Cambodia. The same study sites, that were already selected for previous and ongoing measurements for the leaf turnover rate, were used for the data collection of this study. These sites are located in four provinces in Cambodia: Koh Kong, Mondulkiri, Takeo, and Siem Reap (see map in Figure 3.1).

Typical of the tropics, the climate in Cambodia can generally be described as hot and humid throughout the year (WorldAtlas 2019). The two seasons, a rainy and a dry season, are dominated by the monsoon winds which lead to heavy rainfalls between May and October, especially in the northern and western parts of Cambodia. As illustrated in the climate charts in Figure 3.2, the annual precipitation is around 1400 mm and the average temperature ranges between 25°C to 30°C with a peak by the end of the dry season in April. In general the humidity varies between 70% and 85% in Phnom Penh and lies around 10% lower in Siem Reap (DWD 2019).
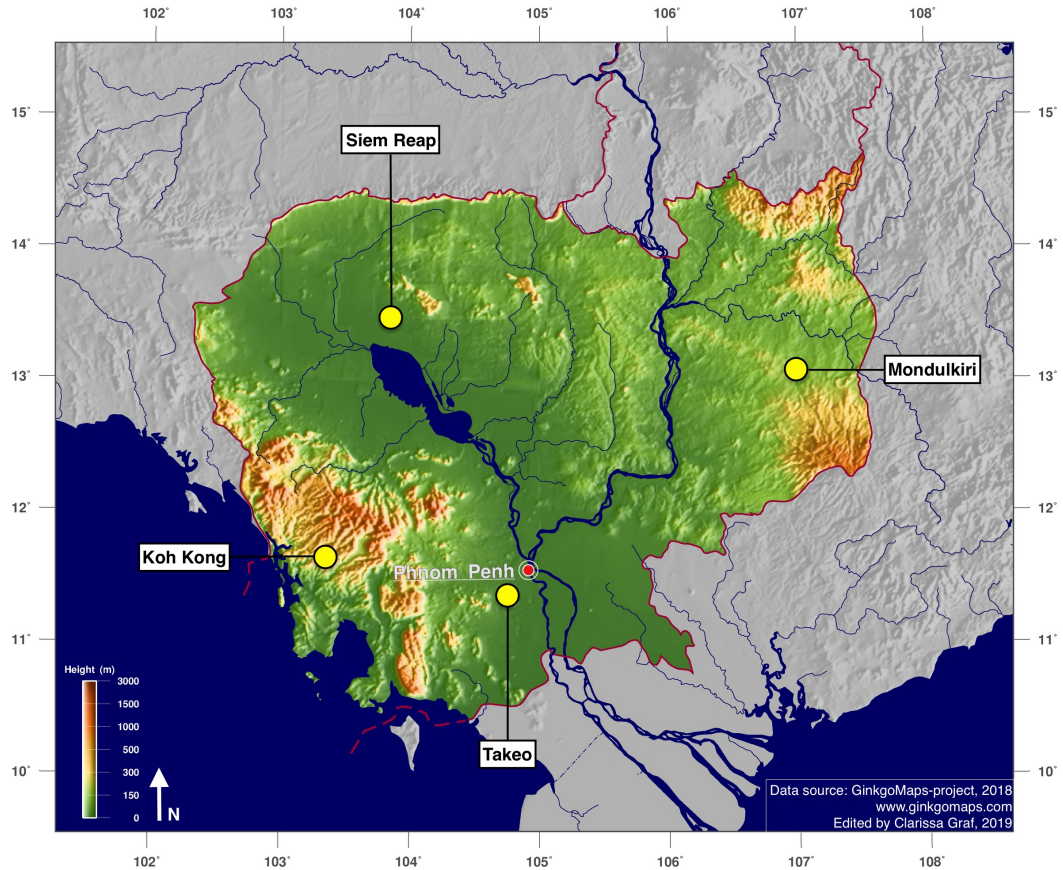
Figure 3.1: A relief map of Cambodia. Yellow dots indicate geographic location for each study site: Koh Kong, Mondulkiri, Takeo, and Siem Reap (Map source: Ginkgo Maps, 2018).
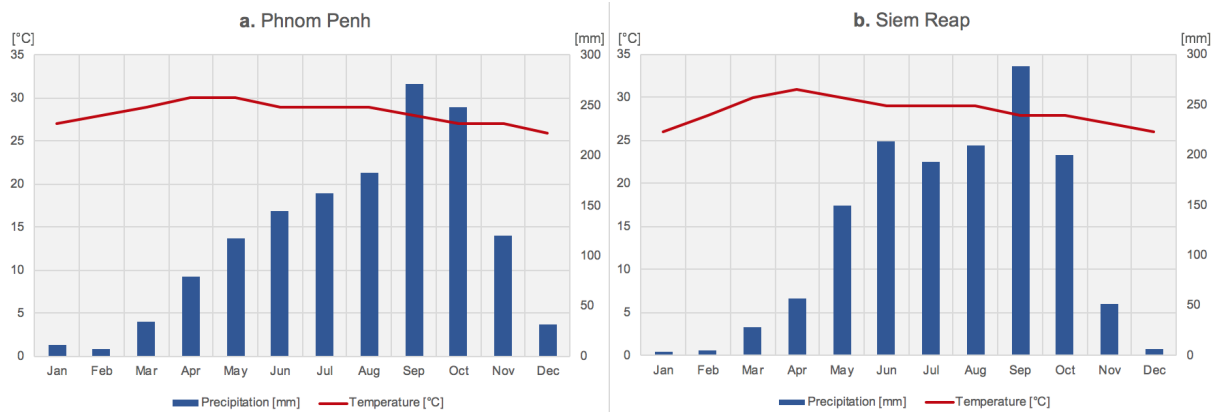
Figure 3.2: Climate charts showing monthly average temperatures (°C) and precipitation rates (mm) in (**a.**) Phnom Penh and (**b.**) Siem Reap. Temperature averages are based on data from 1988 to 2013 for Phnom Penh and from 1997 to 2010 for Siem Reap. Precipitation rates are based on data from 1985 to 2014 for Phnom Penh and from 1981 to 2009 for Siem Reap (DWD 2019).

Despite the impression that the climate in Cambodia is fairly homogeneous, the distinct relief (see map in Figure 3.1), such as the Cardamom Mountains in the southwest (mountain range around the study site in Koh Kong) or the Cambodian basin around the Tonle Sap

Lake (lake south of the study site in Siem Reap), as well as the vicinity or distance to the sea respectively, cause regional differences. In conjunction with varying soil types across the country, these specific climatic conditions lead to heterogeneous forest areas in Cambodia. The four study sites therefore cover three different forest types: deciduous, semi-evergreen, and evergreen tropical forests (see Table 3.1).

Table 3.1: Overview of sample plots of four study sites in Cambodia, including plot number, geographic location (long. E and lat. N), plot size, forest type, and average canopy height.

Study site	Plot no.	Long. E	Lat. N	Plot size	Forest type	Canopy height
Koh Kong	P1	103.3991	11.6603	30 x 50 m	Semi-evergreen	35 - 40 m
	P2	103.4007	11.6603	30 x 50 m	Semi-evergreen	35 - 40 m
Mondulkiri	P1	107.0938	13.0276	30 x 50 m	Deciduous	35 - 40 m
	P2	107.1006	13.0234	30 x 50 m	Deciduous	35 - 40 m
	P3	107.0976	13.0215	30 x 50 m	Semi-evergreen	35 - 40 m
	P4	107.0967	13.0214	30 x 50 m	Semi-evergreen	35 - 40 m
Takeo	P1	104.8030	11.3055	30 x 50 m	Deciduous	10 - 15 m
	P2	104.8030	11.2969	30 x 50 m	Deciduous	10 - 15 m
Siem Reap	P1	103.8699	13.4423	50 x 50 m	Evergreen	50 - 55 m
	P2	103.8699	13.4329	50 x 50 m	Evergreen	50 - 55 m

3.2   Data collection

In order to facilitate the understanding of the data collection as well as the following comprehensive model input preparation, Table 3.2 outlines the information that is required to determine the specific input parameters for this model analysis, and the data sources.

Table 3.2: Overview of the data required for specific input parameters, including information on the data source and the application for the model validation process. The traits *leaf longevity* and *turnover of leaves* are directly based on SLA.

Collected information	Input parameter
Leaf area index [1] Diameter at breast height [2]	**LA:SA ratio**
Chlorophyll content TRY data on N:C and SLA	**C:N ratio in leaves**
Leaf area [2] Leaf dry weight [2] TRY data on leaf mass per area	**SLA** – *Leaf longevity* – *Turnover of leaves*
Wood density [2]	**Wood density**

[1] Data applied for model validation.

[2] Data provided by FRAWASA team.

The data collection of the leaf area index (see section 3.2.1) and chlorophyll (see section 3.2.2) took place in Cambodia in cooperation with the FRAWASA team in July 2018, thus during the peak of the growing season. Due to restrictions related to the ongoing election at that time, only chlorophyll measurements were taken in Siem Reap. The missing data on the leaf area in Siem Reap was therefore gathered and provided by the FRAWASA team three months later, in October 2018. In addition to the in-situ measurements, more trait data was retrieved from the global Plant Trait Database named TRY (see section 3.2.4). The remaining data that has been worked with in this model analysis was provided by the FRAWASA team and partly prepared by Stefan Olin.

3.2.1 Leaf area index

The leaf area index (LAI) was measured with the LAI-2000 Plant Canopy Analyzer, an instrument that captures the attenuation of diffuse sky radiation with five detectors arranged in concentric rings. Each ring measures the radiation at one specific zenith angle simultaneously (Li-Cor 1992). The LAI measurements are based on the remote sensing mode. The sensors' calibration values corresponded to the values from the calibration certificate as suggested in the instruction sheet for using the LAI-2000 (Eklundh 2000):

Sensor A: PCH1445: 4024, 1254, 1007, 1000, 1275
Sensor B: PCH1446: 4055, 1258, 1002, 1000, 1361

As for the sensitivity to light, the sensors' resolutions were set to high, following the general rule recommended in the LAI-2000 manual (Li-Cor 1992). Sensor A was located outside the forest in an open spot to represent the incoming radiation above the canopy. If possible, the sensor was stationed as close as possible to the sample plots but with a minimum distance of at least 3.5 times the height of the surrounding trees, as suggested in the instruction sheet (Eklundh 2000). For the sensors' calibration, a relative difference of the x and y values of lower then 5% was achieved. For each measurement sensor A was leveled by using a tripod and set to capture the radiation at an interval of 15 seconds. Sensor B measured the incoming radiation below the canopy as point measurements inside the forests. These point measurements of each sample plot followed the exact location of the given litter fall nets that were used for the leaf turnover measurements conducted by the FRAWASA team. These nets were positioned along the north-south transect in the middle of the sample plot. Due to the varying net sizes (0.5 x 0.5 m or 1 x 1 m) the plot length of 50 m allowed for 9 or 10 set ups, thus 9 or 10 point measurements every 5 m. Following that, each point measurement should cover an area of at least 150 m^2 corresponding to the plot width of 30 m (see illustration in Figure 3.3).
According to the formula $A = f \cdot \pi \cdot H^2$ (where A represents the ground area by the sample, f the view fraction (0.5 for 180°), and H the canopy height) the coverage for each point
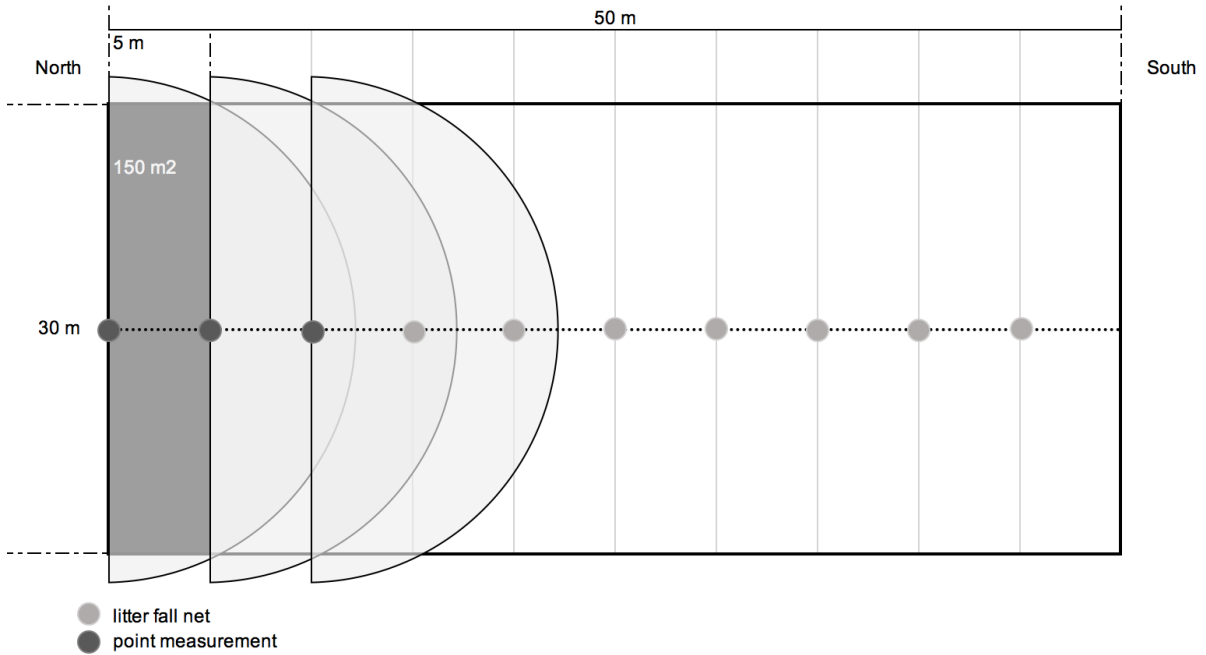
Figure 3.3: Illustration of covered area of each LAI point measurement by using the 180° view cap and following the position of the given litter fall nets in the sample plots.

measurement was dependent on the canopy height that represented the radius of the captured semicircle area, as well as on the density of the forest (Li-Cor 1992). For a better comparison the 180° view cap was used for all sample plots, even in the forests with the lowest canopy height of around 10 to 15 m in Takeo province. In this case, one point measurement still covered an area of at least 157 m^2 at 10 m canopy height, however due to the semicircle shape of the sensor's capture the outer corners of the rectangle could not be covered. Nonetheless, this neglect was accepted due to the low density of these forests.

In order to correlate the data from both sensors, the 180° view caps were always orientated in the same compass direction. In this case either north or south to ensure the coverage of the complete sample plot area by following the locations of the litter fall nets in the middle of the plots. After the data collection, the data from both sensors was transferred via the LAI-2000 File Viewer 1.11. By importing the records the two individual data sets could be combined by replacing the ? with the A records closest in time, and thus the average LAI was calculated. The output text file gave information about the statistics of the LAI results and summarized the statistics of each ring of the sensors. The resulting average LAI values were used to determine the parameter tree leaf area to sapwood ratio, which will be further described in section 3.3.1.1. In addition, the measured LAI also allowed for a comparison between the results of the simulated LAI and the in-situ measurements for each study site.

3.2.2 Chlorophyll

The chlorophyll content of the dominant species, which were represented by the dominant trees within the sample plots, was measured with the Chlorophyll Meter SPAD-502Plus. The Chlorophyll Meter SPAD-502Plus calculates the amount of chlorophyll in a plant leaf by measuring the transmitted light in the red and infrared wavelength ranges, which are characteristic for a high (at approx. 650 nm) and low (at approx. 940 nm) absorbance of chlorophyll (Minolta 1989). The output is given in SPAD values, expressed in arbitrary units, that represent an approximate absolute concentration of chlorophyll in $\mu g/cm^2$.

The number of the measured species within the sample plots varied from 2 to 5 between the study plots. As the major trees were too high (15 m and above) leaves could not be collected from all of them. For this reason, the leaves of the younger and thus smaller trees of the same species were gathered and measured instead. For a better representation 10 leaves per tree species were collected and each leaf was measured 5 times to calculate the leaf's average chlorophyll content. The mean of each tree's chlorophyll content was thus calculated out of 50 measurements, respectively. As 4 species were found in two study plots, 1 species in 4 and 1 in 5 study plots (see Table 6.1 in the appendix), these average values were based on 100, 200 and 250 measurements. The tree species that were considered the major trees within the sample plots, were identified by the local guides and whenever possible translated to the scientific names by the students of the FRAWASA team. The average chlorophyll values were further used to determine the minimum C:N ratio of leaves, representing an important model parameter (see section 3.3.1.2).

3.2.3 Specific leaf area

The SLA data, based on the measurements of the leaf area (cm^2) as well as the dry mass of leaves (g), was collected and provided by the FRAWASA team. The leaf area was calculated by using the ImageJ Software that measures the area of leaves by analyzing digital photos. The dry mass of leaves was weighted after a drying process in the oven at a temperature of 100°C. The measurements were based on a sample size of 100 leaves per tree species. The SLA values were then converted from cm^2/g to m^2/kgC following the model input requirements.

3.2.4 TRY data

Additionally to the measured LAI, chlorophyll and SLA data, comprehensive data sets of specific trait values from the TRY Plant Trait Database were obtained. These data sets encompass traits of SLA, chlorophyll, stem sapwood cross-sectional area and wood density. By using a simple script in Terminal, these data sets were searched for trait information on 30 species (see list of species in Table 6.1 in the appendix). 21 species were identified

during the chlorophyll data collection and an additional 9 species were identified during already conducted fieldwork by the FRAWASA team.

While information on SLA traits could be found for 10 species, chlorophyll data existed merely for 4 species and no information could be obtained for stem sapwood or wood density. Although the searching process led to a couple of hits, data of most of these species was comprised of solely one measurement and were consequently considered inapplicable. Instead of searching for the species names, the geographical location was taken into account by using longitude and latitude. Since too little data was available for the Cambodian region, the entire tropical area was searched through by limiting the latitude to -23° and +23°. The comprehensive output was again filtered and only information on chlorophyll a + b, SLA and N:C ratios, that were measured within the same observation was included. As a result, the final data set contained measurements that were undertaken entirely in French Guiana. Since data from similar individuals or stands were required to be referred to in this analysis, this information was considered appropriate for this study.

3.3   Model analysis

For the study analysis the ecosystem model LPJ-GUESS was applied. The model outcome gives information on the succession development within an entire population of a plant functional type (see section 2.4) as well as on biogeochemical cycles. Essential processes, such as photosynthesis, respiration, stomatal conductance and phenology determine the net primary production (NPP)[1], that further results in biomass growth. Competition for soil resources, space and light and population dynamics in terms of establishment and mortality are accounted for as well (Smith et al. 2014). Four geographical locations (see Table 3.3) were defined to cover all four study sites, namely Koh Kong (KK), Mondulkiri (MK), Takeo (TK), and Siem Reap (SR).

Table 3.3: Geographical coordinates of grid cells (0.5° x 0.5°) used for the model analysis. Each location represents the center of a grid cell.

Study site	Long. E	Lat. N
KK: Koh Kong	103.25	11.75
MK: Mondulkiri	107.25	13.25
TK: Takeo	104.75	11.25
SR: Siem Reap	103.75	13.25

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[1]NPP represents a valuable measure of plant growth by describing the rate of biomass production within an ecosystem, excluding the energy invested due to the process of respiration (Field et al. 1995).

3.3.1 Model input

The general model input encompassed climate data (i.e. temperature, precipitation, radiation, and atmospheric CO_2 concentration) that covered an area of 0.5° x 0.5°, as well as N deposition. The applied global climate and N deposition data sets were provided by Stefan Olin. In order to enable simulations suitable to the conditions of the tropical forest types in Cambodia, 13 Cambodian species-specific PFTs were defined in cooperation with the FRAWASA team (see Table 3.4).

Table 3.4: List of Cambodian PFTs representing the most characteristic tree species. 5 PFTs represent an evergreen, 3 a semi-evergreen, and 5 a deciduous forest type. PFT abbreviations derive from tropical forest (Tr); evergreen (E), semi-evergreen (SE) or deciduous (D) forest, and the initials of the species' names.

PFT name	Forest	Tree	Phenology	Species representative
PFT 1: **TrEAg**	Tropical	Broadleaved	Evergreen	*Anisoptera glabra*
PFT 2: **TrEDa**	Tropical	Broadleaved	Evergreen	*Dipterocarpus alatus*
PFT 3: **TrEHo**	Tropical	Broadleaved	Evergreen	*Hopea odorata*
PFT 4: **TrESr**	Tropical	Broadleaved	Evergreen	*Shorea roxburghii*
PFT 5: **TrEPi**	Tropical	Broadleaved	Evergreen	*Pterocarpus indicus*
PFT 6: **TrSEXx**	Tropical	Broadleaved	Semi-evergreen	*Xylia xylocarpa roxb.*
PFT 7: **TrSELc**	Tropical	Broadleaved	Semi-evergreen	*Lagerstroemia calyculata*
PFT 8: **TrSESs**	Tropical	Broadleaved	Semi-evergreen	*Syzygium sp.*
PFT 9: **TrDDi**	Tropical	Broadleaved	Deciduous	*Dipterocarpus intricatus*
PFT 10: **TrDDo**	Tropical	Broadleaved	Deciduous	*Dipterocarpus obtusifolius*
PFT 11: **TrDSo**	Tropical	Broadleaved	Deciduous	*Shorea obtusa*
PFT 12: **TrDTa**	Tropical	Broadleaved	Deciduous	*Terminalia alata*
PFT 13: **TrDDt**	Tropical	Broadleaved	Deciduous	*Dipterocarpus tuberculatus*

Due to the hierarchical organization of the model, the species-specific PFTs inherited the given parameters from the general settings. As for life form and leaf physiognomy, all PFTs were identified as *tree*, *tropical* and *broadleaved*, respectively. In order to simulate species-specific PFTs that represent common characteristics of the tropical forests in Cambodia, 16 parameters were applied accordingly (see Table 3.5). The parameters 11 to 15 were directly and indirectly derived from in-situ measurements and partly complemented by TRY data. Due to the complex model input preparation, the flow chart (see Figure 6.1 in the appendix) provides a detailed overview of the numerous interlinked steps to determine the relevant input parameters.

Table 3.5: Overview of applied parameters to allow for a simulation of species-specific PFTs representing the tropical forests in Cambodia, including the units and value ranges: *0 or 1*: 0 = is not; 1 = is. *0 - 1*: Floating value between 0 and 1.

No.	Parameter	Unit	Value	Parameter description
1	*evergreen*	-	0 or 1	Tree retains foliage throughout the year
2	*summergreen*	-	0 or 1	Tree loses foliage once a year; deciduous
3	*shade_tolerant*	-	0 or 1	Tree tolerates low light conditions
4	*shade_intolerant*	-	0 or 1	Tree does not tolerate low light conditions
5	*interm._shade_tol.*	-	0 or 1	Tree partly tolerates low light conditions
6	*drought_tolerance*	-	0 - 1	Tree is/ is not tolerant to droughts (0 = v. tol.; 1 = not tol.)
7	*fireresist*	-	0 - 1	Tree is/ is not tolerant to fire (0 = v. sensitive; 1 = resistant)
8	*k_allom2*	-	not lim.	Constant in allometry equation (size and shape relationship)
9	*k_allom3*	-	not lim.	Constant in allometry equation (size and shape relationship)
10	*longevity*	yr	not lim.	Tree lifespan under non-stressed condition
11	*k_latosa*	-	not lim.	Ratio of tree leaf area to sapwood area
12	*SLA*	m^2/kgC	not lim.	Specific leaf area, ratio of leaf area to leaf dry mass
13	*leaflong*	yr	not lim.	Longevity of the tree's leaves
14	*turnover_leaf*	fraction/yr	not lim.	Relationship between leaf production and leaf senescence
15	*cton_leaf_min*	-	not lim.	Minimum leaf C:N ratio, max. N concentration in leaves
16	*wooddens*	kgC/m^3	not lim.	Density of sapwood and heartwood

3.3.1.1 LAI input

The measured LAI, in conjunction with the diameter at breast height (DBH)[2] measurements conducted by the FRAWASA team, were further used to modify the input parameter tree leaf area to sapwood ratio (*k_latosa*). Since the LAI measurements represented mean values for each study plot (see Table 6.2 in appendix), these values needed to be adjusted for each PFT. Seven species were present on site and could directly be related to the given LAI values (see Table 3.6). In case a species was represented in more than one study plot (see Table 6.1 in the appendix), the average LAI of these plots was calculated and used for the PFT's parameter settings. The assigned LAI values for the remaining PFTs were based on the average LAI of all plots with a similar phenology. This resulted in values of 2.11 for deciduous, 3.65 for semi-evergreen, and 3.55 for evergreen PFTs.

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[2]DBH represents a common measure to reference the diameter of trees at breast height, that usually varies between 1.25 m to 1.37 m above the ground level, depending on the applied system in the country (Chhetri & Fowler 1996).

Table 3.6: Assigned LAI for PFTs based on measured and averaged LAI values dependent on PFT's phenology and presence in study plots.

PFT name	LAI	Description
PFT 1: **TrEAg**	3.55	Based on averaged LAI for evergreen forests.
PFT 2: **TrEDa**	3.55	Based on averaged LAI, PFT in more than 1 study plot present.
PFT 3: **TrEHo**	3.55	Based on averaged LAI for evergreen forests.
PFT 4: **TrESr**	3.55	Based on averaged LAI for evergreen forests.
PFT 5: **TrEPi**	3.55	Based on averaged LAI for evergreen forests.
PFT 6: **TrSEXx**	2.39	Based on averaged LAI, PFT in more than 1 study plot present.
PFT 7: **TrSELc**	3.40	Based on measured LAI, PFT in only 1 study plot present.
PFT 8: **TrSESs**	3.65	Based on averaged LAI for semi-evergreen forests.
PFT 9: **TrDDi**	2.11	Based on averaged LAI for deciduous forests.
PFT 10: **TrDDo**	1.98	Based on measured LAI, PFT in only 1 study plot present.
PFT 11: **TrDSo**	2.22	Based on averaged LAI, PFT in more than 1 study plot present.
PFT 12: **TrDTa**	1.75	Based on averaged LAI, PFT in more than 1 study plot present.
PFT 13: **TrDDt**	1.75	Based on averaged LAI, PFT in more than 1 study plot present.

3.3.1.2 Chlorophyll input

The output of the chlorophyll measurements was given in SPAD values. Following the recommendation of Süß et al. (2015) to calibrate SPAD to gain a more accurate chlorophyll content, the calibration model of Coste et al. (2010) was applied. Since it was based on 13 tropical forest species, this regression equation was considered the best possible relationship between SPAD and chlorophyll. The chlorophyll values were further converted from $\mu g/cm^2$ to mg/g by using the given SLA values. In order to derive the C:N ratios for the *cton_leaf_min* parameter from chlorophyll measurements, TRY data was applied. Based on the linear regressions between chlorophyll and N:C ratio ($R^2 = 0.32$) as well as between SLA and N:C ($R^2 = 0.33$) (see Figure 6.2 in the appendix), the N:C ratios were calculated and further converted to C:N. Missing values within the measured chlorophyll data were filled with TRY data by applying the modelled C:N ratio relationship. The resulting average C:N ratios needed to be changed correctly to the minimum concentration in leaves as model input. As a result, apart from the linear regressions based on TRY data, the C:N ratio of leaves of 7 PFTs were directly related to chlorophyll measurements, and of the remaining 6 PFTs to SLA measurements.

3.3.1.3 Parameter settings

This specific data preparation for the parameter setting allowed for a simulation as species-specific as possible. Table 3.7 gives an overview of the resulting parameter values for each PFT. The settings for the parameter describing foliage, shade, drought and fire tolerance (parameters 1 to 7) were based on the species description prepared by the FRAWASA team. The values for the parameters 8, 9, and 10 were inherited from previous model settings and partly adapted by Stefan Olin. Parameter 11 (*k_latosa*) was based on the LAI as well as in-situ DBH measurements. Parameter 12 (*SLA*) was derived from the measured data

on leaf area and dry leaf mass (see section 3.2.3). *SLA* was further applied to calculate parameter 13 (*leaflong*) that in turn was used to determine parameter 14 (*turnover_leaf*). Parameter 15 (*cton_leaf_min*) was partly based on measurements where missing values were complemented with measured SLA data. The information on parameter 16 (*wooddens*) was provided again by the FRAWASA team and completed by adopting the average values within the same PFT group.

Table 3.7: Overview of the parameter settings for each PFT as model input based on the species-specific information. *Green:* Data based on measurements. *Yellow:* Data complemented by measured variable. *Blue:* Data estimated and based on averages within the same PFT group. *Blank:* Data based on species description conducted by the FRAWASA team or on preset model settings.

Parameter	TrEAg	TrEDa	TrEHo	TrESr	TrEPi	TrSEXx	TrSELc	TrSESs	TrDDi	TrDDo	TrDSo	TrDTa	TrDDt
1: *evergreen*	1	1	1	1	1	0	0	0	0	0	0	0	0
2: *summergreen*	0	0	0	0	0	1	1	1	1	1	1	1	1
3: *shade_tol.*	0	1	0	1	0	0	0	0	1	0	0	0	0
4: *shade_intol.*	0	0	1	0	1	1	0	0	0	0	0	0	0
5: *int._shade_tol.*	1	0	0	0	0	0	1	1	0	1	1	1	1
6: *drought_tol.*	0.5	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.5	0.0
7: *fireresist*	0.5	0.0	0.5	0.5	0.0	0.5	0.5	0.5	0.5	1.0	0.5	0.5	1
8: *k_allom2*	50.0	23.3	23.6	50.0	48.0	12.6	17.7	20.7	24.7	50.0	48.0	48.0	16.3
9: *k_allom3*	0.60	0.67	0.59	0.60	0.58	0.57	0.48	0.60	0.67	0.60	0.58	0.58	0.28
10: *longevity*	500	500	500	500	500	500	500	500	500	500	500	500	500
11: *k_latosa*	1310	1410	1960	2610	2450	1310	3350	2520	1930	1810	3050	530	2390
12: *SLA*	11.9	13.8	16.7	26.1	16.8	14.9	15.7	26.6	13.0	15.3	16.5	12.4	16.8
13: *leaflong*	3.94	2.64	1.61	0.49	1.58	2.18	1.88	0.47	3.09	2.04	1.66	3.52	1.58
14: *turnover_leaf*	0.25	0.38	0.62	2.02	0.63	0.46	0.53	2.11	0.32	0.49	0.60	0.28	0.63
15: *cton_leaf_min*	30.3	29.5	27.0	22.4	27.0	30.3	30.5	22.2	29.4	29.4	31.6	29.8	29.7
16: *wooddens*	200	320	370	330	370	360	360	360	390	430	420	490	430

3.3.2 Model adjustment

Despite the comprehensive data preparation to allow for PFT parameter settings as species-specific as possible, the model results remained inconclusive. By analyzing the development of biomass production (based on *Cmass* output) of all PFTs in all four study sites, 1 PFT, namely TrESr, represented the most dominant PFT that outcompeted all other PFTs in MK, TK, and SR. Merely in KK TrEAg showed an overall higher biomass production than TrESr, and represented the second most dominant PFT in the other sites. Figure 6.3 in the appendix illustrates the skewed simulation results where semi-evergreen and deciduous PFTs were not present due to their low or non-existing biomass production (< 1% of total biomass).

Due to the poor representation of the actual forest types in the investigated study plots, the model input needed to be adjusted to allow for more conclusive results. As part of a model sensitivity analysis numerous new input files were created with slight adjustments in the parameter settings. Parameters such as *k_latosa* were increased or decreased to promote or reduce the competitive advantage of PFTs respectively; standard settings, like water uptake mechanisms, occurrence of natural disturbances, etc. were modified,

activated or deactivated; differences in input data were minimized by using average levels for each PFT group (i.e. evergreen, semi-evergreen, deciduous) - countless attempts to improve the model simulations, unfortunately without success. With time the model development as well as the ongoing project made progress when it was decided to overthrow the idea of using 13 species-specific PFTs and to adapt to a new approach. As a result the parameters were once more modified to describe 8 specific PFTs that represent functional groups rather than individual species (see Table 3.8 and for more detailed information on their specific characteristics Table 6.3 in the appendix).

Table 3.8: List of 8 group-specific PFTs used for the adjusted model analysis. PFT 1 to PFT 4 represent evergreen, and PFT 5 to PFT 8 deciduous forest types.

PFT name	Forest	Tree	Foliage	Shade tolerance
PFT 1: **TrBE1**	Tropical	Broadleaved	Evergreen	Shade tolerant
PFT 2: **TrBE2** *	Tropical	Broadleaved	Evergreen	Shade tolerant
PFT 3: **TrIBE1**	Tropical	Broadleaved	Evergreen	Shade intolerant
PFT 4: **TrIBE2**	Tropical	Broadleaved	Evergreen	Intermediate shade tolerant
PFT 5: **TrBD1**	Tropical	Broadleaved	Deciduous	Shade tolerant
PFT 6: **TrBD2** *	Tropical	Broadleaved	Deciduous	Shade tolerant
PFT 7: **TrIBD1**	Tropical	Broadleaved	Deciduous	Shade intolerant
PFT 8: **TrIBD2**	Tropical	Broadleaved	Deciduous	Intermediate shade tolerant

* TrBE2 and TrBD2 differ from TrBE1 and TrBD1 in two parameters (SLA, $cton\_leaf\_min$).

This optimized parameterization process, performed by Stefan Olin, included the measured LAI as well as the composition between evergreen and deciduous trees in each study plot. With respect to the application of a global model, this approach represented an enhanced analysis allowing for a more realistic forest cover simulation. The same parameters, as previously described in section 3.3.1, were adjusted to represent the specific functional groups based on the ability to tolerate shade. Merely one parameter, namely *drought_tolerance* (parameter 6 in Table 3.7) was not further included due to its redundant function. The water uptake setting, that was finally decided on for the model analysis (see section 3.3.3.1), did not incorporate this parameter, which reasoned its omission. Following the notion as mentioned in section 2.2.2, these PFTs refer to functional response groups.

Table 3.9 provides the information on the adjusted parameter values for the 8 group-specific PFTs. Apart from the obvious differences in *SLA*, *leaflong*, *turnover_leaf*, and *cton_leaf_min*, the remaining parameters resembled each other dependent on their categorization to the PFTs' shade tolerance (see Table 3.8). For example, shade intolerant PFTs were assigned to a lower tree longevity (*longevity*, 200 instead of 500 years), a lower wood density (*wooddens*) and a higher LA:SA ratio (*k_latosa*).

Table 3.9: Overview of adjusted parameter settings for each group-specific PFT as new model input based on the ability to tolerate shade.

No.	Parameter	TrBE1	TrBE2	TrIBE1	TrIBE2	TrBD1	TrBD2	TrIBD1	TrIBD2
1	*evergreen*	1	1	1	1	0	0	0	0
2	*summergreen*	0	0	0	0	1	1	1	1
3	*shade_tolerant*	1	1	0	0	1	1	0	0
4	*shade_intolerant*	0	0	1	0	0	0	1	0
5	*interm._shade_tol.*	0	0	0	1	0	0	0	1
6	*fireresist*	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
7	*k_allom2*	71.1	71.1	57.2	53.9	71.1	71.1	57.2	53.9
8	*k_allom3*	0.67	0.67	0.67	0.67	0.67	0.67	0.67	0.67
9	*longevity*	500	500	200	200	500	500	200	200
10	*k_latosa*	3890	3890	7730	6557	3890	3890	7730	6557
11	*SLA*	16.8	17.3	16.8	16.8	24.9	23.5	24.9	24.9
12	*leaflong*	2	2	2	2	0.9	0.9	0.9	0.9
13	*turnover_leaf*	0.67	0.67	0.67	0.67	1	1	1	1
14	*cton_leaf_min*	20.5	23.0	20.5	20.5	17.5	20.0	17.5	17.5
15	*wooddens*	200	200	180	190	200	200	180	190

3.3.3 Model configuration

3.3.3.1 Standard settings

For all simulations the vegetation mode was set to *cohort* to define each PFT cohort of an age class in a particular patch by the average properties of an individual. Each grid cell was represented by 20 patches, each with an area of 1000 m^2, where they differed due to varying stages of secondary succession and stochastic events (e.g. fire as a disturbance). For the model spin-up 500 years were considered appropriate, hence the period from 1400 to 1900. Since no data was available to project the future, the 20th century, from 1900 to 2015 to be exact, represented the study period. For the general water uptake mechanism the option *rootdist* was chosen. This setting describes that water is taken up proportionally from the soil according to a prescribed root distribution. As specific *cton_leaf_min* and *SLA* values were determined for the PFTs, the parameters for the C3 as well as C4 grass PFTs were set to 16 and 26, respectively.

As indicated in the introduction, the simulated old-growth forest (OGF) represents the reference for the general model analysis. This scenario was simulated by solely implementing the individual parameter settings for each PFT without any additional land cover changes.

3.3.3.2 Land cover settings

In order to simulate regenerated forest types, additional land cover input settings were generated. In contrast to the reference of the OGF, simulations of regenerated forest types were modified by a new start condition in the year 1900. This date was chosen to allow for an improved set up for the test period from 1900 onwards.

Cultivated forest types (CUL) were simulated by changing the land cover types from *cropland* to *forest* in 1900 and 1901, respectively. The representation of naturally regrown forest types (NRG) was defined by a land cover change from *natural* to *forest* for the

same years. These settings were based on the idea that cultivated forests are planted on formerly used agricultural land and naturally grown forests start reestablishing after a natural disturbance. By simply modifying the particular land cover settings, each regenerated forest type was dependent on different starting conditions, such as varying N content in the soils. In contrast to the OGF scenario, overall stress conditions, such as natural disturbances due to fire, were suppressed. Without including any additional harvest settings (see following section 3.3.3.3), this model configuration allowed for the simulations of the standard scenarios for CUL as well as NRG forest ecosystems.

3.3.3.3 Harvest settings

For an improved understanding of the effects of sustainable forest management, the standard land cover scenarios (CUL and NRG) were further modified with specific harvest settings. The overall harvest system was set to *continuous*, hence only in the first year of management the forest is cut clear. As for the thinning condition, it was merely indicated that big trees need to be cut first. In order to determine an adequate, thus sustainable harvest yield, the cutting intervals were set to every 10, 20 and 30 years with an intensity of 10% (low), 20% (medium) and 30% (high), resulting in 9 scenarios for both land cover settings. The following Figure 3.4 provides an overview of the resulting model scenarios.

Control simulation	Old-growth forest (OGF)			
Land cover simulation	**Cultivated forest (CUL)** *cropland → forest* high N concentration in the soil		**Naturally regrown forest (NRG)** *natural → forest*	
Harvest simulation	Interval 10 years 20 years 30 years	Intensity Low (10%) Medium (20%) High (30%)	Interval 10 years 20 years 30 years	Intensity Low (10%) Medium (20%) High (30%)

Figure 3.4: Overview of the applied model scenarios for the old-growth, cultivated and naturally regrown forests, including the 9 varying harvest settings related to changed intervals and intensities.

3.3.4 Model output

The output of the LPJ-GUESS model encompassed results for numerous parameters. For the given study, only the outputs of the C biomass (*Cmass*, as an indicator for NPP), the abundance (*density*), and the LAI (*LAI*) were further applied. The information on *Cmass* was used to demonstrate the overall biomass production and to calculate the community weighted mean of traits weighted by biomass (CWM_b). The modelled *density* was required to refer to the standard CWM of traits weighted by the abundance (CWM_a). The *LAI* output was compared with the actual LAI measurements. These results were considered to gain information on the dynamics between, and the presence as well as dominance of the different PFTs. The data was further processed and visualized in MATLAB 2017b.

4 Results

4.1 Results on functional traits and PFTs

The functional traits represented the centerpiece of this study and were therefore explicitly analyzed. With regard to the model validation process, the measured species-specific values (13 PFTs parameters) were compared with the assigned group-specific values (8 PFTs paramters) to understand if and to what extend the estimated functional traits were over- or underestimated, and hence influenced the model results accordingly. Figure 4.1 illustrates the differences between the measured and assigned values for LA:SA ratio, C:N ratio, wood density, SLA, leaf turnover, and leaf longevity dependent on the PFTs' phenology (i.e. evergreen, deciduous).
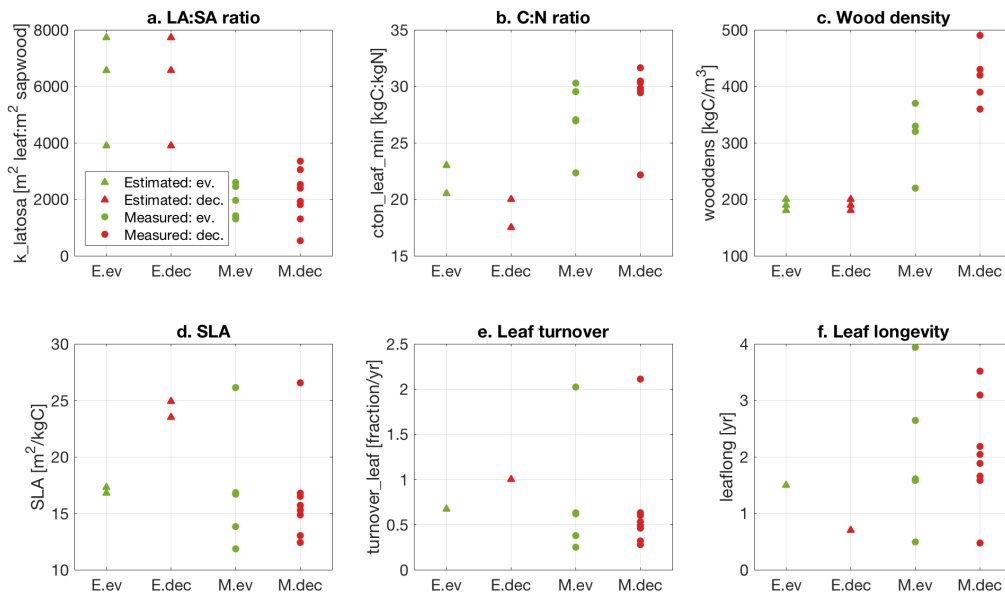
Figure 4.1: Comparison between estimated (8 group-specific PFTs) and measured (13 species-specific PFTs) parameter values for (**a.**) LA:SA ratio (*k_latosa* in m² leaf:m² sapwood), (**b.**) C:N ratio (*cton_leaf_min* in kgC:kgN), (**c.**) wood density (*wooddens* in kgC/m³), (**d.**) SLA (*SLA* in m²/kgC), (**e.**) leaf turnover (*turnover_leaf* in fraction/yr), and (**f.**) leaf longevity (*leaflong* in yr). Parameters are distinguished between estimated (triangle) and measured (dot) values, and evergreen (green) and deciduous (red) PFTs, respectively.

As can be seen in Figure 4.1 the assigned values for the LA:SA ratio parameter were overall higher than the measured values, that were directly based on the LAI measurements (see section 3.3.1.1). The estimated C:N ratio and wood density parameters were slightly lower, and the SLA, leaf turnover, and leaf longevity parameter values were basically within the range of the measured information. At this point it is essential to highlight that leaf turnover (*turnover_leaf*) as well as leaf longevity (*leaflong*) represented two traits that were based solely on SLA. This over- and underestimation of the applied PFT parameters need to be accounted for when describing and discussing the results on FD (see section 4.3 and chapter 5).

The new categorization of 4 group-specific PFTs to either evergreen or deciduous phenology further facilitated the comparison of the results. In order to understand the parameter settings, and thus to interpret the results correctly, the following Figure 4.2 gives an insight into the specific strategies (i.e. resistance/survival, productivity/growth) and expected performance in relation to the LES position. In order words, to understand how well PFTs were equipped to react to disturbances and competition.
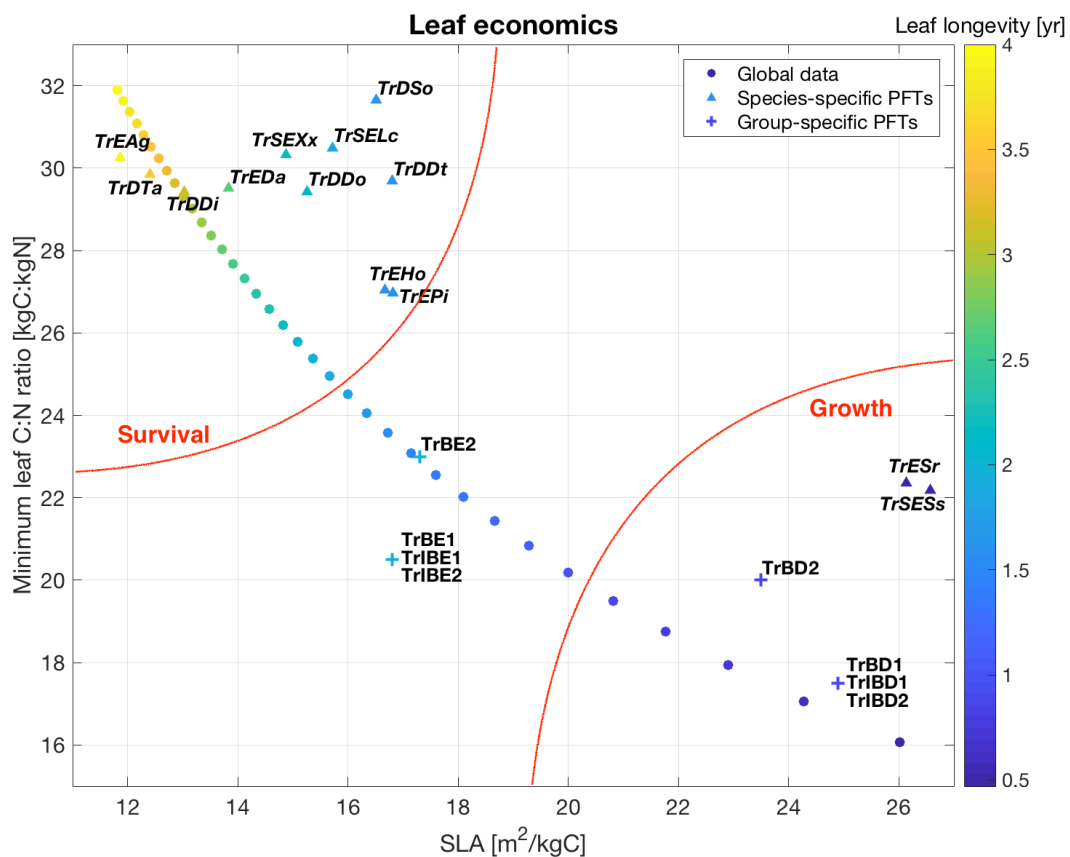
Figure 4.2: Illustration of leaf economics in relation to minimum C:N ratio in leaves (kgC:kgN), SLA (m²/kgC), and leaf longevity (years). Global data is based on Reich et al. (1992) (dot), the 13 species-specific PFTs refer to measured values (triangle), and the 8 group-specific PFTs represent the adjusted parameter settings (plus). Red lines indicate survival and growth strategy according to LES.

Based on the measured information (C:N ratio, SLA, and leaf longevity) that were initially applied for the species-specific parameter settings for the 13 PFTs, Figure 4.2 indicates that the majority of these PFTs were assumed to follow a slower approach (i.e. survival strategy) and only 2 PFTs, namely TrESr and TrSESs, were considered to invest more resources at a faster rate (i.e. growth strategy). Referring to the accumulated biomass production for each species-specific PFT (see Figure 6.3 in the appendix), it is noticeable that TrSESs was however significantly outcompeted by the evergreen PFTs, particularly by TrESr and TrEAg. The 8 PFTs, on the other hand, differed clearly as a result of their categorization to an evergreen or deciduous phenology. Following the LES notion, the growth rate of the deciduous PFTs was expected to be higher than that of the evergreen PFTs.

In comparison to the results of the model analysis based on 13 species-specific PFTs, the following Figure 4.3 indicates a more balanced presence of the 8 different group-specific PFTs, albeit the evergreen PFTs revealed much higher percentages of the overall biomass production than the deciduous PFTs. Only in SR were the deciduous PFTs comparatively more dominant.

Figure 4.3: Percentage of accumulated biomass production of OGF scenario from 1500 to 2015 for the study sites (**a.**) KK_{se}, (**b.**) MK_{se}, (**c.**) TK_d, and (**d.**) SR_e based on 8 group-specific PFTs.

In order to facilitate the understanding of the results due to the numerous relevant information, the study sites' forest cover is, when necessary, herein indicated as follows: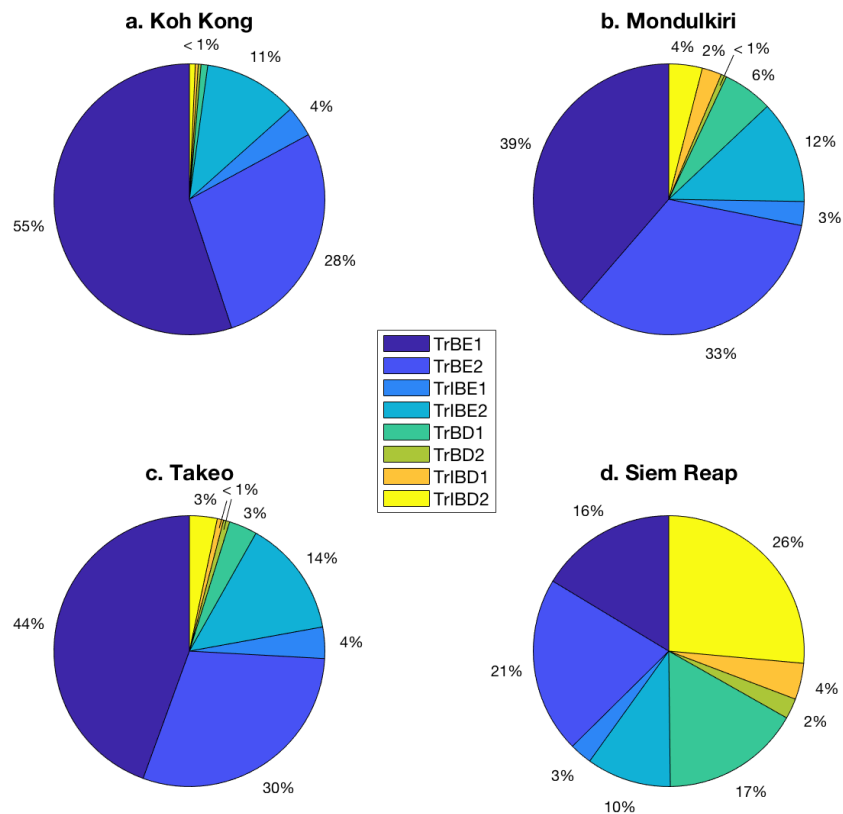 KK_{se} and MK_{se}[1] for semi-evergreen, TK_d for deciduous, and SR_e for evergreen forest covers. This addition further provides the information on whether the study sites tend to be dry or wet, and therefore support the establishment of deciduous and semi-evergreen or evergreen forests, respectively.

4.2   Results on LAI

The LAI represented the only collected data that could be directly related to the model output, and thus provided basic information on the model validation. In Figure 4.4 the measured LAI is compared to the simulated LAI output for each study site.
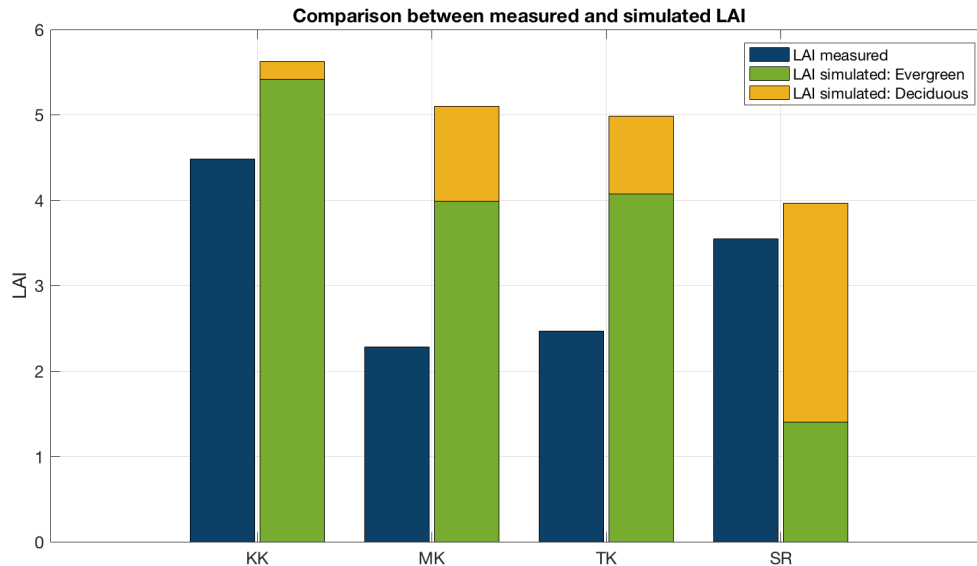
Figure 4.4: Comparison between measured and simulated LAI. Measured LAI is based on average values for each study site from data collection conducted in 2018. Simulated LAI is based on the average values of the last 5 years (2011 - 2015) of the LAI model outputs of the OGF scenario, as a total value and distinguished between evergreen (PFT 1 to PFT 4) and deciduous (PFT 5 to PFT 8) group-specific PFTs.

The simulated LAI for the study sites KK_{se} and particularly for SR_e was comparatively similar to the measured LAI. The modelled output for MK_{se} and TK_d, however, revealed an at least twice as high LAI than initially measured at these study sites. For KK_{se}, MK_{se}, and TK_d the simulated LAI indicated a dominance of the evergreen PFTs, whereas SR_e showed a more balanced but higher presence of deciduous PFTs. This result reflected the overall presence of evergreen and deciduous PFTs in accordance with the results on the biomass accumulation as indicated in Figure 4.3. However, the results did not necessarily represent the initial assignment of the forest types for each study site. For example, the

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[1]The two forest types in MK (deciduous and semi-evergreen) are combined for reasons of simplification.

forest type in TK was considered deciduous and in SR evergreen, which contrasted the simulated LAI results.

Overall the model results were considered sufficiently appropriate to proceed with the research project. The next sections describe the results on FD expressed by the CWM of traits (see section 4.3), and the different developments in biomass production dependent on varying harvest intensities (see section 4.4).

4.3   Results on functional diversity

In order to answer the overall RQ, whether the simulated functional diversity differs between cultivated and naturally regrown tropical forest ecosystems, FD was represented by the community-weighted mean of the selected traits (see section 2.2.3.3). As previously described, CWM of traits is weighted by the relative abundance of the species exhibiting the trait. For an improved understanding of the model results, the CWM of the selected traits was weighted by the abundance as well as the biomass (see Figure 4.5).
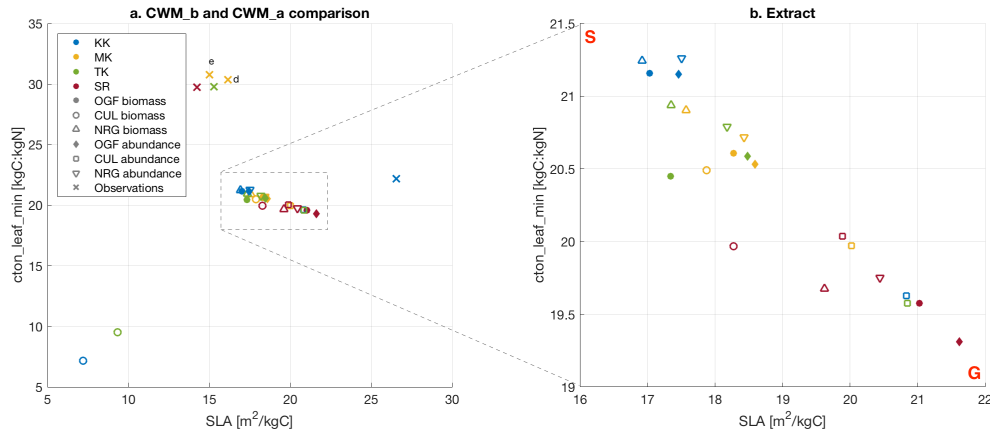
Figure 4.5: (**a.**) Comparison of CWM of SLA and C:N ratio weighted by biomass and abundance of OGF (dot and diamond), CUL (circle and square), NRG (upward-pointing and downward-pointing triangle) standard scenarios based on C:N ratio (*cton_leaf_min* in kgC:kgN) and SLA (*SLA* in m^2/kgC). CWM$_b$ of traits of OGF, CUL, and NRG is based on average values of modelled biomass (Cmass in kgC/m^2) and abundance (density in number of individuals/m^2) data from 2001 to 2015 for the standard scenarios. CWM$_a$ of observed traits is based on species abundance. Observed information on MK is distinguished between deciduous (*d*) and evergreen (*e*) forest types. (**b.**) Extract of the same results as presented in plot a. to provide enlarged scatter plot. Red letters S and G refer to survival and growth strategy according to LES.

The CWM$_a$ of the observed trait values, derived from the information on the species composition at each study site, did not overlap with the ranges of the modelled results, regardless of whether being compared with CWM of traits weighted by the abundance or biomass. In addition, the CWM$_b$ of traits of KK$_{se}$ and TK$_d$ for the CUL standard scenario revealed much lower values than the remaining CWM. The CWM$_a$ of the selected traits indicated an overall slightly higher production than the CWM$_b$ for the same traits

and scenarios (see plot b. in Figure 4.5). Due to the focus of this study on harvest management practices, the CWM_b of the selected traits was considered more relevant and was further analyzed. As mentioned above, the outlying data points (i.e. observed CWM_a, as well as CWM_b of traits of KK_{se} and TK_d CUL standard scenarios) remained to be apart also in comparison with the other functional traits like LA:SA ratio and wood density (see Figure 6.4 in the appendix). Figure 4.6 provides therefore an extract to allow for a more detailed overview of the remaining CWM_b of traits of the CUL and NRG standard scenarios (see section 3.3.3.2) in relation to the OGF as a reference. The simulated CWM_b of the considered traits was based on the average biomass results of the last 15 years and calculated by applying the current parameter settings of the 8 group-specific PFTs.
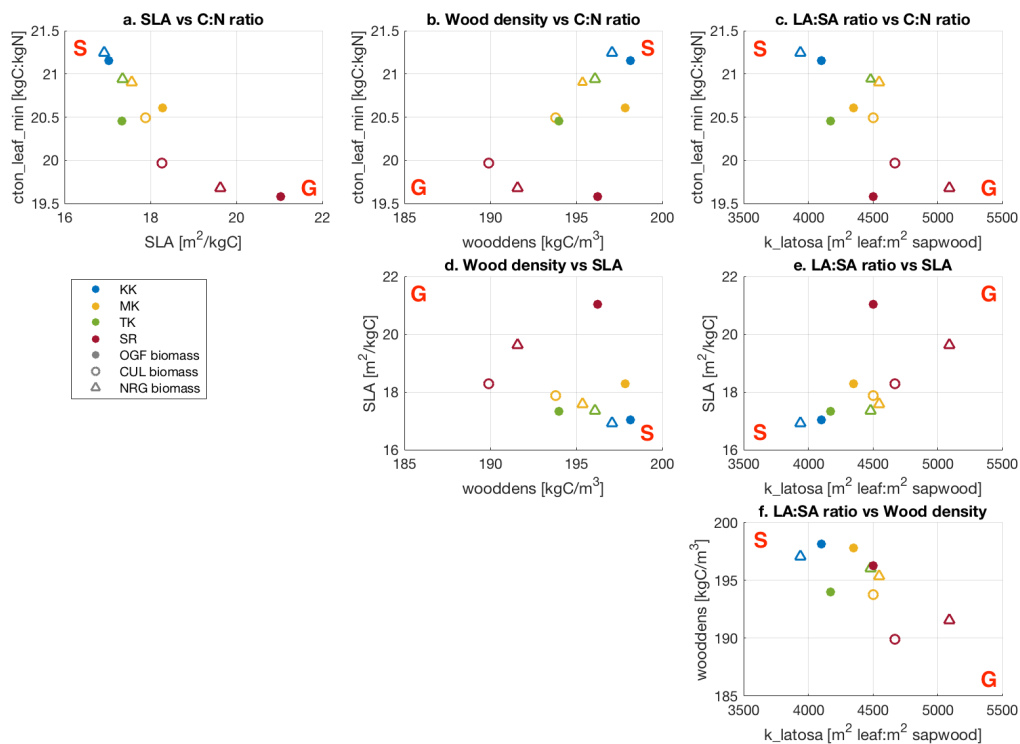
Figure 4.6: Extract of comparison of CWM_b of OGF, CUL, NRG standard scenarios based on C:N ratio (*cton_leaf_min* in kgC:kgN), SLA (*SLA* in m²/kgC), wood density (*wooddens* in kgC/m³), and LA:SA ratio (*k_latosa* in m² leaf:m² sapwood). CWM_b of selected traits OGF, CUL, and NRG are based on average values of modelled biomass (Cmass in kgC/m²) from 2001 to 2015 for the standard scenarios. Red letters S and G refer to survival and growth strategy according to LES. Outlying CWM_b of analyzed traits of the CUL scenario for KK_{se} and TK_d as well as observations are omitted.

Following the notion of the leaf economic spectrum as well as the concept of CWM_b representing the most dominant trait values, the overall presence of slow or fast growing PFTs can be determined by comparing the different CWM_b of traits of the modelled OGF, CUL, and NRG standard scenarios of each study plot. With a focus on KK_{se} it is interesting to point out that, in contrast to the outlying values of the CUL scenario, the OGF and NRG scenario revealed relatively similar results of being more dominated by

slower growing PFTs. The CWM_b of the traits in MK_{se} as well as TK_d resembled each other and fell within a similar range. In MK_{se}, the CWM_b of the considered traits of the CUL scenario indicated a promoted growth rather than survival strategy compared to the OGF and particularly to the NRG scenarios. In TK_d the results of the OGF CWM_b of traits suggested a faster growth than the CWM_b of the NRG simulations, except when compared with the CWM_b of LA:SA ratio traits (see plot c., e., and f. in Figure 4.6). The different scenarios in SR_e, however, revealed an overall dominance of faster growing PFTs. It is further noticeable that the results in SR_e differed more from each other than the results of the remaining study plots. The CWM_b of the considered traits of the NRG scenario suggested a higher production than that of the CUL scenario.

Focusing on the biomass production as a proxy of the ecosystem's productivity and the CWM_b of the selected traits as an indicator for FD, the model results revealed variations between the three scenarios (CUL, NRG, and OGF as the control simulation) (see Figure 4.6 and Figure 6.4 in the appendix). Based on this comprehensive model analysis it could therefore be concluded that the simulated FD differed between CUL and NRG tropical forest ecosystems.

4.4   Results on harvest scenarios

In order to understand the impact of harvest processes on the biomass production of the forests, thus to answer RQ-a and RQ-b (see section 1.3), the total biomass (related to *Cmass* output) of each study site was calculated based on the average values from the last 15 years (i.e. from 2001 until 2015) of all PFTs for the standard scenarios (OGF, NRG and CUL standard) and each harvest scenario (every 10, 20, and 30 years at low (10%), medium (20%) and high (30%) intensity). As RQ-b merely focuses on recommendations it will be further discussed in the following chapter 5.

Figure 4.7 provides an overview of the varying biomass production in NRG forest ecosystems for each study site and harvest scenario. Except for TK_d, in each site the overall biomass of the OGF was higher than the NRG standard scenario. In KK_{se} the values ranged between 6.3 and 14.9 kgC/m² (even slightly higher than the OGF reference), in MK_{se} between 6.6 and 13.4 kgC/m², in TK_d between 5.7 and 11.8 kgC/m², and in SR_e between 6.2 and 9.5 kgC/m². In KK_{se}, MK_{se}, and SR_e the largest biomass was resulted from a harvest setting of every 20 years and 10% intensity. In TK_d, on the other hand, a harvest of every 30 years with no significant differences regarding the intensity allowed for the highest production. Harvests conducted every 10 years or of high intensity of 30% generally lowered the total biomass.
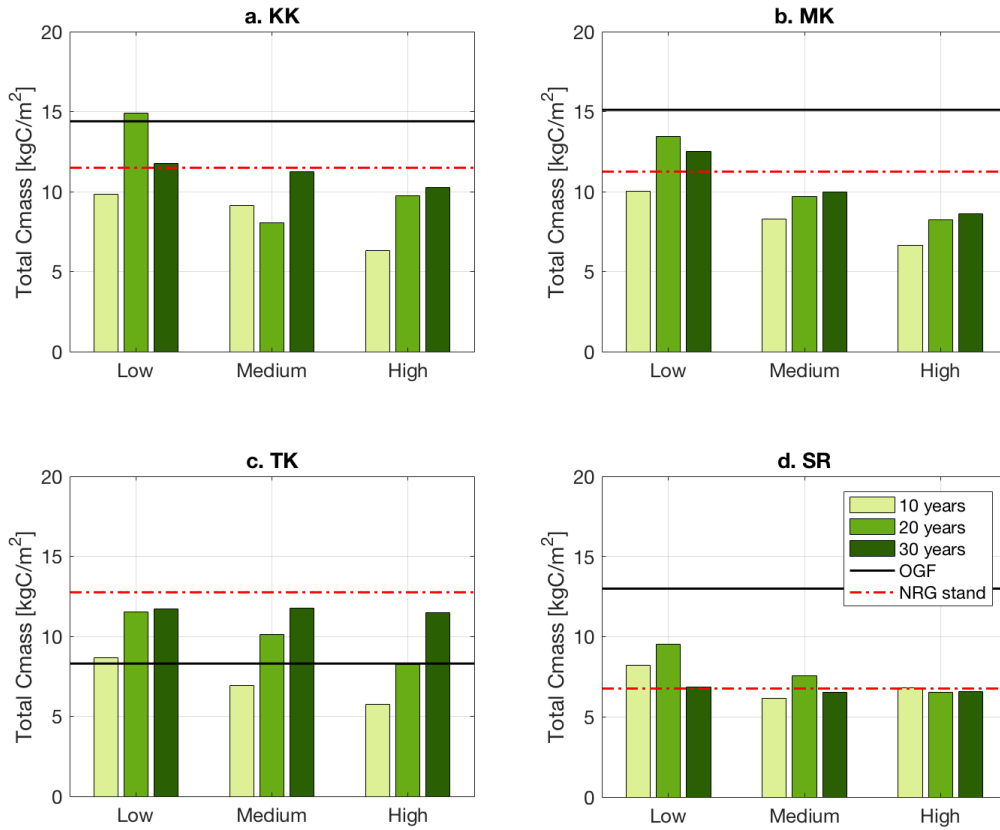
Figure 4.7: Total Cmass (kgC/m^2) for each harvest scenario (cutting interval of every 10, 20, and 30 years at low (10%), medium (20%), and high (30%) harvest intensity) for the study sites (**a.**) KK$_{se}$, (**b.**) MK$_{se}$, (**c.**) TK$_d$, and (**d.**) SR$_e$ for NRG. Total Cmass is based on average values from the last 15 years (2001 - 2015) of all PFTs. OGF (black horizontal line) and NRG (red dashed line) represent reference values of the ideal state (OGF) and standard NRG scenarios without harvest management, respectively.

In the case of the CUL scenario it is essential to note that the modelled biomass production in KK$_{se}$ and TK$_d$ was significantly low, as in both sites the grass PFTs C3 and C4 predominate (see Figure 6.5 in the appendix). At the study site MK$_{se}$, on the other hand, the biomass production showed values between 1.7 and 4.4 kgC/m^2, lower than the CUL standard scenario. In SR$_e$, the total biomass reached values between 4.9 and 7.5 kgC/m^2, that were mostly higher than the CUL standard values. The largest biomass in MK$_{se}$ was modelled with a harvest setting of every 20 years with an intensity of 10%, and in SR$_e$ of every 10 years with an intensity of 10%. The harvest scenario of every 10 years with the highest intensity of 30% caused the lowest biomass production in both sites. The overall biomass production of the CUL standard scenarios was significantly lower than that of the OGF in MK$_{se}$ as well as in SR$_e$. Regarding RQ-a, this model analysis revealed that varying harvest intensities both enhanced and decelerated the forest dynamics towards the stage of an OGF, depending on the site and exact settings for the harvest intensity.

The pattern of the outlying CWM_b of the selected traits of the CUL standard scenarios in KK_{se} and TK_d, as well as of the OGF scenarios in SR_e, could be detected in the simulated forests' production with and without harvest measures. The limited production of the CUL scenarios in KK_{se} and TK_d (see Figure 6.5 in the appendix) were either inconclusive or might be caused by the forests' inability to be particularly persistent or productive. It is further noticeable that SR_e revealed an overall lower biomass production, particularly for the NRG and harvest simulations in comparison with the remaining scenarios. TK_d, on the other hand, showed the lowest biomass production among the OGF scenarios, although its OGF CMW_b of traits was positioned within a similar range. Even its NRG biomass was higher than the production of its OGF.

5 Discussion

The simulated functional diversity, herein represented by the community-weighted mean of the selected traits weighted by the biomass, differed between the old-growth, cultivated, and naturally regrown forest ecosystems, as well as the observed data. With a focus on the measured and modelled LAI values (see Figure 4.4 in section 4.2), as well as CWM_a of the observed trait data, it is crucial to indicate that the model simulations seemed to underestimate the forests' ability to resist and survive any disturbances and overestimate their productivity in each study plot (see Figure 6.4 in the appendix). Considering the difference between the measured trait values (representing the 13 species-specific PFTs) and estimated trait values (representing the 8 group-specific PFTs) the modelled results were in fact expected to show a higher productivity (see Figures 4.1 and 4.2 in section 4.1). The group-specific PFTs were set to values indicative of faster growth rather than survival. This was due to their higher SLA and LA:SA ratio, and lower C:N ratio in leaves and wood density values compared to the measured information. This pattern of the model simulation's under- and overestimation of the growth rate was also found, and even marginally more significant, in the comparison with the modelled CWM_a of the selected traits weighted by the abundance (see Figure 4.5 in section 4.3). It is however interesting to note, that in relation to the assessment of the average C biomass in Cambodia of 121 tC/ha, thus 12,1 kgC/m^2 (FAO 2009), these results stayed within the limits, since the simulated biomass production of the OGF scenarios indicated values between approximately 8 and 15 kgC/m^2. Despite the divergent representation, the model results can be assumed to be valid. With respect to the actual representation of the forest covers in KK_{se}, MK_{se}, TK_d, and SR_e, it needs to be mentioned that no differences in soils could have been modelled. Considering the fairly homogeneous rainfall patterns, the actual varying demography of trees in the study sites are, however, most likely related to diverse soil conditions. Potential forest management recommendations should therefore be treated with caution.

5.1 Forest productivity

Based on the simulated biomass production as a proxy for the productivity of a forest ecosystem, it can be concluded that the OGF represents the overall ecosystem with the highest production, hence the scenario of the forest with the largest C stock (see Figure 4.7

in section 4.4 and Figure 6.5 in the appendix). This was accounted for in all study plots, except for in TK_d in comparison to the NRG standard simulation. The contrasting result in TK_d signifies a more productive forest growth due to the forest clearance in 1900, thus a possibility for a new and different PFT establishment in relation to the given climatic conditions. In fact, based on the accumulated biomass production from 1900 to 2015 of the OGF and NRG standard scenario, a distinct difference in the PFT variation could be detected. The two PFTs of the NRG simulation, namely TrIBE2 revealed a higher (+7%), and TrBE1 a notably lower (-15%) biomass production in comparison to the OGF scenario. Considering the trait similarity of these two PFTs, it can be concluded that the intermediate shade tolerant TrIBE2 could thrive due to the forest clearance, and thus increased light availability. It can further be hypothesized that at a longer simulation running time TrIBE2 might not necessarily prevail due to the overall dominance of shade tolerant PFTs.

The result of the overall high biomass production in the OGF scenarios of the remaining study plots reflects the expected C stocks of well established forests. It contradicts, however, the common understanding of the expected 'age-related' decline in productivity in OGFs. As Kutsch et al. (2009) indicate, older as well as taller trees only sustain at higher resource costs to compensate increased respiration rates and higher investments in stems for support. It is further assumed that the absolute as well as relative growth rates decline with age and height due to various reasons, such as decreasing photosynthesis as a result of hydraulic limitations (i.e. longer path lengths in higher trees lower leaf water potential), or an increasing risk to mechanical damages (e.g. windthrow will more likely adversely affect the tallest trees) and its corresponding cessation of growth (Kutsch et al. 2009).

Additionally, considering the notion that in the tropics the old-growth phase can be reached after approximately 80 years (Wirth et al. 2009), the model results of the NRG standard scenario revealed surprisingly low productivity levels, as the simulation encompassed a time period of 115 years (from 1900 to 2015). On top of this, disturbances, thus any stress conditions, were suppressed in the land cover settings (i.e. CUL and NRG simulations), which would allow for a proper establishment of the forest ecosystems without any major disruptions. As the overall biomass production of NRG forests was expected to resemble the production of an OGF system, it is assumed that an even longer simulated time period would reveal more realistic results.

The CUL scenarios represented the forest ecosystems with the lowest productivity in all four study sites. The relatively low biomass production was similarly unexpected due to the specific land cover settings for the CUL scenarios assuming a higher N content in the soils as a starting condition. A higher N content allows for an increased productivity considering that N supply determines plant growth (biomass production) as well as plant

development (development of organs and structure) (Lawlor et al. 2001). On the one hand, this result might be related to limitations in other key mineral elements that are essential for plant growth, such as macro elements like P or K. According to Boroomand & Grouh (2012), an enhanced plant production is achieved by applying N, P, and K nutrients combined rather than one major element by itself. On the other hand, it can be assumed that the increased N levels in fact hamper plant growth. An overabundance of N can alter underlying ecosystems processes (e.g. affecting ground waters), which may ultimately lead to adverse impacts on the environment (Lawlor et al. 2001). However, the current model set-up directly linked any additional N content to an increase in net primary production (i.e. biomass production), without limitation. The seemingly inconclusive results of the CUL simulations for KK_{se} and TK_d give reason to assume that the tree PFTs could not establish due to the overdominance of the grass PFTs, C3 and particularly C4 grass. This may be related to the effect of competition in the soil, particularly on shallow and lateral roots of trees and grass that compete for nutrients like N (Messenger 1976). It can further be inferred that a longer simulation running time may result in a more balanced representation of the tree PFTs.

The increased N concentration in soils also suggest a lower nitrogen use efficiency, and hence overall lower CWM_b of the C:N ratio in leaves for the CUL scenarios in comparison to the OGF and NRG simulations. This pattern was shown in KK_{se}, MK_{se}, and TK_d, but in SR_e the CWM_b of the C:N ratio in leaves indicated the opposite. This contrary outcome in SR_e can be interpreted as a result of the definite presence of deciduous PFTs and their highly productive leaf growth. With respect to the LES and the information on leaf longevity, a low C:N ratio in leaves correlates with a faster growth, but also with a shorter leaf life-span (see Figure 4.2 in section 4.1). In order to grow leaves, a considerable investment of C is required at the expense of protection and resilience. The abundance of N, and thus the expected lower C:N ratio in leaves, does therefore not necessarily represent an advantage.

5.2 Harvest impacts

Biomass production was further subject to the interval as well as intensity of timber harvest. Based on the model results it can be concluded that in NRG forest ecosystems thinning processes occurring every 10 years overall lower, and every 30 years increase the forest productivity, respectively. Harvest intensities of 20% and 30% tended to reduce the biomass production for every interval. It is however noticeable that logging processes conducted every 20 years at a low density of only 10% allowed for the highest biomass production. Except for the study site TK_d, it even exceeded the productivity of a NRG forest without any harvest measures. These results suggest that more regular disturbances,

such as reduced impact logging, in fact promote plant growth. This agrees with the notion that disturbances are key to maintain the functional potential of a forest ecosystem (Kuuluvainen et al. 2021). However, as indicated by Bedrij et al. (2022), reduced impact logging may not be the most sustainable approach for subtropical forests, as selective logging may promote the growth of understory plants, such as bamboo, instead of trees. The recovery of timber stocks depends on the type of growing species, as fast-growing plants may not necessarily represent marketable wood products (Bedrij et al. 2022). With respect to the improved wood-processing technologies however, wood resources that were formerly considered impractical became more valuable (FAO 2009). For instance, wood types with lower wood density are nowadays used for the production of shorter lasting furniture or medium-density fibreboards. Either way, alternative forest management practices are required to guarantee stand recovery, particularly in areas with a high rate of natural disturbance, in order to mitigate forest degradation.

5.3 Forest dynamics

In comparison with the varying CWM_b of the analyzed traits of the modelled OGF, CUL, and NRG standard scenarios, it can be concluded that the forests of the study sites vary in their ecosystem functioning due to different degrees of persistence and productivity. The results suggest a dominance of slower growing PFTs particularly in KK_{se}, but also in MK_{se} and TK_d, and faster growing PFTs in SR_e. This gives reason to assume that the different simulated forest ecosystems in KK_{se}, MK_{se}, and TK_d are slightly more resistant to disturbances than the forests in SR_e. In order to recommend adequate practices that promote sustainable forest management it is necessary to consider the study sites individually. In KK_{se}, MK_{se} and TK_d for instance, the evergreen PFTs were significantly more dominant than the deciduous PFTs, as indicated by the total biomass production (see Figure 4.3 in section 4.1) or simulated LAI (see Figure 4.4 in section 4.2). Shade tolerant evergreen PFTs, like TrBE1 and TrBE2, particularly thrived and accounted for around three-quarters of the forest's production in OGF systems. Based on the assumption that trait similarity refers to a low degree of niche differentiation, this result suggests an inefficient resource use and hence a high competition between the two PFTs. The forest's resistance can eventually be considered low and greater adverse effects of disturbances should be expected.

It is further interesting to note that TrBE1 was more dominant than its counterpart TrBE2. According to the parameter settings (see Table 3.9 in section 3.3.2) the higher SLA as well as lower C:N value for TrBE2 would suggest not only a faster growth but also a higher tolerance to disturbances than compared to TrBE1. The higher productivity of TrBE1 may therefore be explained by the differences between competitive effects of traits. A low

SLA, for instance, is correlated with a strong competitive effect on neighbors, but not with a high tolerance of competition from neighbors (Kunstler et al. 2016). High wood density, on the other hand, is correlated with an effect as well as tolerance of competition.

Concerning the remaining PFTs, it is noticeable that TrIBE2 represented the third most dominant PFT (biomass production between 11% and 14%). Considering the parameter settings, the counterpart TrIBE1 was expected to show a higher productivity than TrIBE2, as its wood density was set to a lower value and LA:SA ratio to a higher value (both settings promote growth). The major difference between them is the classification as shade tolerant. TrIBE1 was not tolerant to shade and therefore less competitive, whereas TrIBE2 was intermediate shade tolerant, that in turn reasoned its dominance. In regard to the deciduous PFTs, it is important to highlight that their parameter values were set to a lower C:N ratio in leaves and higher SLA compared to their counterparts among the evergreen PFTs, and were therefore expected to show a high productivity. Their comparatively low presence however, gives reason to assume the results are dependent on the leaf turnover rate (100% per year) and leaf longevity (under 1 year). Deciduous trees regrow their foliage annually, which requires significant resource investments. This strategy is generally beneficial if water resources are scarce, however, in tropical climates water tends to be abundant and no harsh climatic seasons have to be coped with. The competitive capacity of evergreen trees is therefore expected to be greater than that of deciduous trees.

The results for the study plot SR_e indicated a rather balanced dominance between evergreen as well as deciduous PFTs (approx. fifty-fifty) that differed strongly from the coverage of the remaining study sites, and also from the initial considered evergreen forest cover in SR. This might be due to the model's uncertainty and inaccuracy to adequately simulate regional conditions, such as the water uptake to represent the actual water availability in SR. At this point it is essential to mention that SR represents a rather wet study site. The installed irrigation system to maintain the temple complex Angkor Wat provides abundant water for the surrounding forests, that ultimately promotes the growth of evergreen trees. As previously described above, deciduous PFTs only prevail under conditions of water scarcity. The misrepresented model simulation may also be a consequence of the delayed LAI data collection in SR_e. With respect to the position of the CWM_b of the selected traits, the results for SR_e further suggest a higher degree of competition between the PFTs, particularly in relation to the presence of deciduous PFTs.

5.4   Study limitations

There are several reasons why this study's results can be considered inconclusive. The LPJ-GUESS model, as DGVMs in general, has its limitations to fully represent accurate

forest dynamics, particularly on a regional level. As already pointed out in section 2.4, ecological modelling entails a degree of uncertainty and the results need to be interpreted carefully. However, this study adds additional uncertainties to the model process due to inconsistencies in the data collection and data preparation, as well as necessary modifications to the model settings and model adjustments to allow for results that can be worked with.

Regarding the data collection, it is essential to point out that the LAI measurements in SR happened in October 2019, hence 3 months later than in MK, KK, and TK. Since July represents the peak of the growing season, the LAI values for SR seem to be underestimated. A higher assumed LAI value for SR would refer to higher LA:SA ratios and hence influence competition due to the advantage of presumable wider crowns. This inadequate representation of SR as an evergreen forest type is seen in the total biomass production (see Figure 4.3 in section 4.1), where the deciduous PFTs are comparatively dominant, particularly in relation to the other study sites. In addition, the information on the chlorophyll content is based on measurements of leaves of younger and older trees, and leaves that were found on the ground, as it was partly impossible to access fresh leaves from high trees. This inconsistency may cause inaccuracies as the chlorophyll content changes dependent on the age of the leaves (Šesták 1963). The corresponding parameter *cton_leaf_min* may therefore be skewed, which affects the simulation of the competitive performance of the PFTs.

The values of the measured input parameters are either based on cumbersome calculations or merely assigned with the mean values when data was missing. Despite the fact that this complex data preparation was a necessary step to enable a more realistic model simulation (and later on comparison), the results may be misrepresented considering the model's sensitivity to small parameter differences. The adjusted approach of applying group-specific PFTs enabled the model analysis, but represented nonetheless merely an approximation. For an improved representation of the observed data, its CWM of the considered traits could be based on Cmass instead of abundance. Cmass could be derived by referring to the measured DBH information as a rough estimate and applying allometric relationships, as well as considering the wood density of the given species.

Regarding the model settings, it is necessary to highlight that only for the CUL and NRG, including the harvest scenarios, stress conditions were suppressed. Natural disturbances, such as fire, influence forest dynamics strongly. In particular, deciduous forests are prone to fire. Such impacts were, however, not accounted for in the model simulations apart from the OGF scenario. The results therefore give only a limited insight into the forests' strategies on survival and growth (i.e. leaf economics spectrum), as this setting minimizes the competitive advantage of more persistent PFTs on a long-term basis. In addition, the difference between the CUL and NRG forest simulations was solely based on varying N

content in the soil. The assumption that forest regrows on land that was formerly used for agricultural activities remains valid. However, it does not reason the difference between CUL and NRG as described in sections 2.5.1 and 2.5.2. In fact, both simulated scenarios can solely be defined as naturally regenerated forests, as specific processes of seeding or planting tree species or removing any barriers can not be modelled.

Another model limitation that needs to be taken into account is the neglect of changes in traits over time (i.e. process of growth). With increased height or age, plants tend to adapt to new strategies and are regulated by different traits (Gibert et al. 2016). For instance, insufficient light resources may not be a limiting factor anymore for full-grown trees once they reach a position in the canopy. This approach is further supported by McDowell et al. (2002), who suggested that the LA:SA ratio decreases with increasing tree height. Varying biotic and abiotic conditions influence growth rates, which in turn determine the correlation with functional traits (Gibert et al. 2016). The current model set-up, however, considered the functional traits as constants and such variations over time were not simulated. In order to adequately determine the performance of trees, and thus the ecosystem functioning of a forest, the modified regulation of different traits due to changes in plant size and age has to be considered comprehensively.

6 Conclusion

It is of great importance to understand complex forest dynamics in order to develop and implement adequate forest management practices. Functional diversity, a crucial measure to assess ecosystem functioning, represents an approach to evaluate the state of an ecosystem in relation to its resilience, stability and resource dynamics. Considering the accelerated deforestation rates in Cambodia, this study focused on the differences between secondary tropical forests, that have been regenerated either through cultivation or were left on their own resources (i.e. naturally regrown). Based on the assumption that reforestation as well as proper forest management practices will only take place if financial benefits can be expected, the study further analyzed the impacts of varying harvest intensities on the forests' productivity. By applying the dynamic vegetation model LPJ-GUESS, the functional diversity, expressed as the community-weighted mean, was simulated for each standard scenario. The model result revealed differences in functional diversity for each scenario and also varying biomass production depending on the harvest intensity. The overall productivity was significantly higher in naturally regrown than in cultivated secondary forests. It is further notable that a thinning process at an interval of every 20 years and a harvest intensity of 10% allowed for the highest biomass production and generally promoted plant growth. However, in comparison with the observed information, the model analysis tended to overestimate the forests' productivity. With respect to the inconsistencies in the data collection and preparation as well as the overall model's uncertainties due to its sensitivity, it remains unclear whether this harvest setting represents the ideal strategy. Sustainable forest management practices can therefore not be recommended with confidence and further research needs to be done.

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Appendix

Table 6.1: List of identified species within the study sites based on chlorophyll (Chl.)and SLA measurements, including their assignment to PFTs. *Study plot of Chl. data* indicates plots where chlorophyll measurements of given species were taken (KK = Koh Kong, MK = Mondulkiri, TK = Takeo, SR = Siem Reap). There is no exact information available of study plot location of SLA measurements. Columns *TRY data* give information on existing data within searched TRY data sets for given species.

| No. | Species name | Measurements | | | TRY data | | PFT |
		Chl.	SLA	Study plot of Chl. data	Chl.	SLA	
01	*Anisoptera glabra*	-	√	-	-	-	TrEAg
02	*Anomianthus dulcis*	√	-	SR-P1	-	-	
03	*Aporosa ficifolia*	√	-	TK-P2	-	-	
04	*Argyreia obtecta*	√	-	KK*	-	-	
05	*Barringtonia acutangula*	-	√	-	-	√	
06	*Careya arborea*	√	-	TK-P1	-	-	
07	*Croton poilanei*	√	-	KK*	-	-	
08	*Diospyros bejaudii*	√	-	SR-P1, P2	-	-	
09	*Diospyros cambodiana*	-	√	-	-	-	
10	*Dipterocarpus alatus*	√	√	SR-P1, P2	√	√	TrEDa
11	*Dipterocarpus intricatus*	-	√	-	√	√	TrDDi
12	*Dipterocarpus obtusifolius*	√	√	TK-P2	-	-	TrDDo
13	*Dipterocarpus tuberculatus*	√	√	MK-P1, P2	√	√	TrDDt
14	*Dysoxylum loureiri*	√	-	KK*	-	-	
15	*Ellipanthus tomentosus*	√	-	TK-P2	-	-	
16	*Hopea odorata*	-	√	-	-	√	TrEHo
17	*Irvingia malayana*	√	-	TK-P1	-	-	
18	*Lagerstroemia calyculata*	√	√	SR-P2	√	√	TrSELc
19	*Lophopetalum wightianum*	√	-	TK-P1	-	-	
20	*Mallotus anisopodus*	-	√	-	-	-	
21	*Markhamia stipulata*	√	-	TK-P1	-	-	
22	*Pterocarpus indicus*	-	√	-	-	-	TrEPi
23	*Rhizophora apiculata*	√	√	KK*	-	√	
24	*Rhizophora mucronata*	√	√	KK*	-	√	
25	*Shorea obtusa*	√	√	MK-P1, P2, P3, P4; TK-P2	-	-	TrDSo
26	*Shorea roxburghii*	-	√	-	-	-	TrESr
27	*Syzygium sp./lineatum*	-	√	-	-	√	TrSESs
28	*Terminalia alata*	√	√	MK-P1, P2	-	√	TrDTa
29	*Vatica philastreana*	√	-	TK-P1	-	-	
30	*Xylia xylocarpa*	√	√	MK-P2, P3, P4; TK-P2	-	-	TrSEXx
		21	18		4	10	

* Chlorophyll measurements in Koh Kong show values for entire study site, not for each study plot.
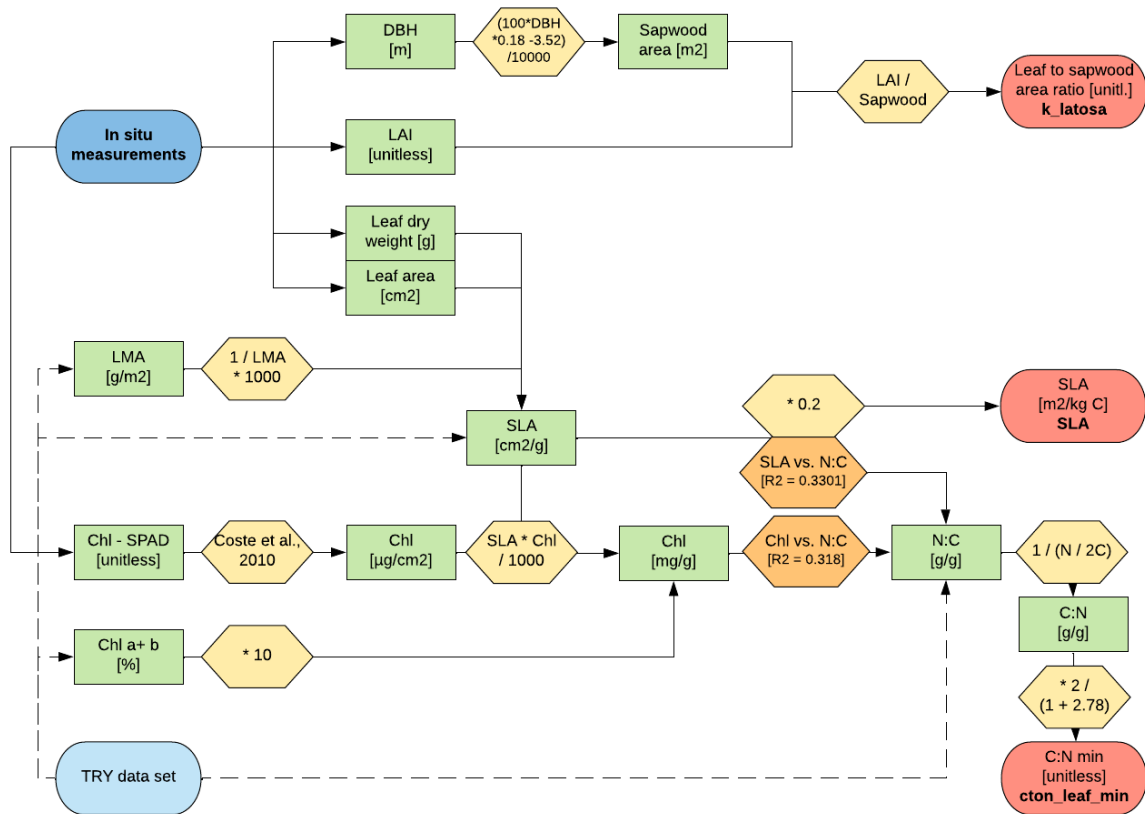
Figure 6.1: Flow chart of data preparation steps. *Blue boxes:* Data is based on in-situ measurements and TRY data sets. *Green boxes:* Applied and changed variables. *Yellow boxes:* Implemented conversions and calculations. *Orange boxes:* Conversion according to linear relationships based on TRY data. *Red boxes:* Final parameters used for model analysis.

Table 6.2: Average of measured LAI for each study plot based on 9 point measurements in KK and MK, and on 10 in TK and SR.

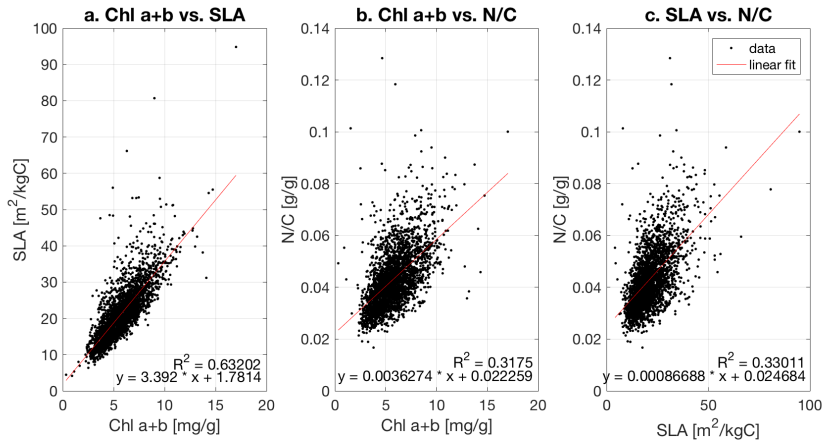| Study plot	Phenology	LAI
KK - P1	Semi-evergreen	4.54
KK - P2	Semi-evergreen	4.42
MK - P1	Deciduous	1.57
MK - P2	Deciduous	1.92
MK - P3	Semi-evergreen	2.88
MK - P4	Semi-evergreen	2.76
TK - P1	Deciduous	2.95
TK - P2	Deciduous	1.98
SR - P1	Evergreen	3.69
SR - P2	Evergreen	3.40

Figure 6.2: Graphs of linear relationships between chlorophyll a + b, (mg/g), SLA (m²/kgC) and N:C ratios (g/g) including R^2 values, slope and intercept. Data is based on TRY data sets and represents a data collection in French Guiana (n = 2827), where each observation give information on all three parameters. SLA values are converted from cm²/g or g/m² (as reciprocal leaf mass per area of SLA) to m²/kgC as used in the model. Chlorophyll a + b values are converted from % to mg/g and N:C ratios are given as a concentration in g/g. (**a.**) Relationship between chlorophyll a + b and SLA; (**b.**) relationship between chlorophyll a + b and N:C ratio and (**c.**) relationship between SLA and N:C ratio.
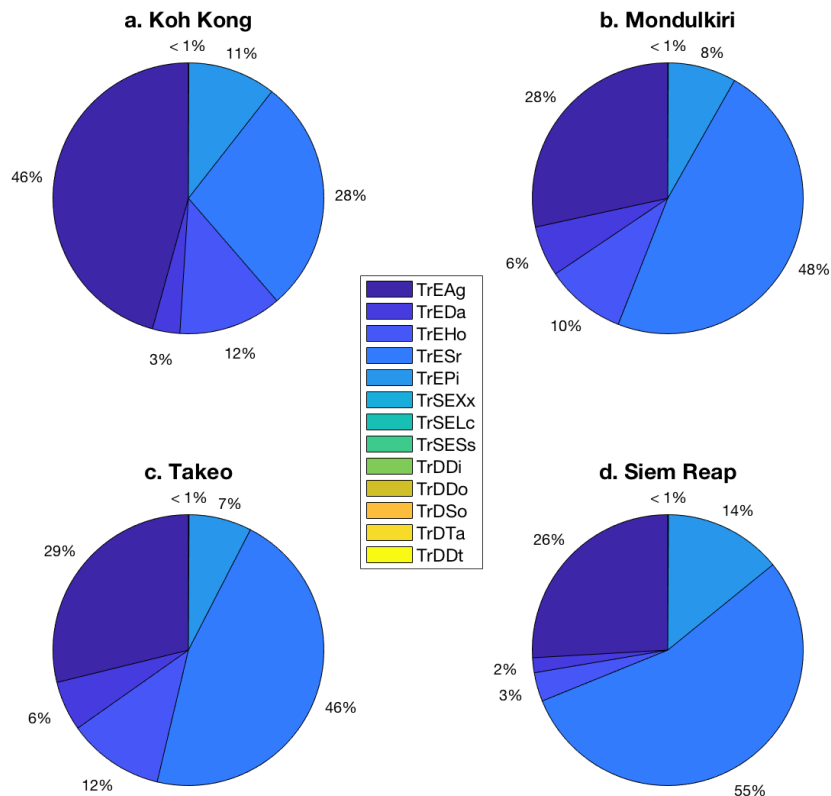

Figure 6.3: Percentage of accumulated biomass production of OGF scenario from 1500 to 2015 for the study sites (**a.**) KK_{se}, (**b.**) MK_{se}, (**c.**) TK_d, and (**d.**) SR_e based on 13 species-specific PFTs. Semi-evergreen and deciduous PFTs show values < 1%.

Table 6.3: List of identified species within the study sites, including their specific characteristics used for the assignment to PFTs. Species are identified to be evergreen (*ev.*), semi-evergreen (*semi-ev.*), or deciduous (*dec.*); to be tolerant (*tol.*), intermediate tolerant (*interm.*), or intolerant (*intol.*) to shade; and to be resistant (*res.*) or sensitive (*sens.*) to fire, droughts and floods/flooded soils. Information is based on plant species description provided by the FRAWASA team.

No.	Species name	Phenology	Shade	Fire	Drought	Flood	PFT
01	*Anisoptera glabra*	ev.	tol./interm.	res.	-	sens.	TrEAg, TrIBE2
02	*Anomianthus dulcis*	ev.	-	-	-	-	
03	*Aporosa ficifolia*	dec.	-	-	-	-	
04	*Argyreia obtecta*	-	-	-	-	-	
05	*Barringtonia acutangula*[1]	ev.	intol.	res.	-	res.	
06	*Careya arborea*	dec.	-	-	-	-	
07	*Croton poilanei*	dec.	-	-	-	-	
08	*Diospyros bejaudii*	dec.	-	-	-	-	
09	*Diospyros cambodiana*[1]	ev.	intol.	res.	-	res.	
10	*Dipterocarpus alatus*	ev.	tol./interm.	sens.	sens.	res.	TrEDa, TrIBE2
11	*Dipterocarpus intricatus*	dec.	tol./interm.	res.	res.	-	TrDDi, TrIBD2
12	*Dipterocarpus obtusifolius*	dec.	tol./interm.	res.	res.	-	TrDDo, TrIBD2
13	*Dipterocarpus tuberculatus*	dec.	tol./interm.	res.	res.	-	TrDDt, TrIBD2
14	*Dysoxylum loureiri*	semi-ev.	-	-	-	-	
15	*Ellipanthus tomentosus*	dec.	-	-	-	-	
16	*Hopea odorata*	ev.	tol./interm.	sens.	sens.	-	TrEHo, TrIBE2
17	*Irvingia malayana*	-	-	-	-	-	
18	*Lagerstroemia calyculata*	semi-ev.	intol.	res.	res.	sens.	TrSELc
19	*Lophopetalum wightianum*	dec.	-	-	-	-	
20	*Mallotus anisopodus*[1]	-	intol.	res.	-	res.	
21	*Markhamia stipulata*	dec.	-	-	-	-	
22	*Pterocarpus indicus*	ev.	intol.	res.	res.	-	TrEPi, TrIBE1
23	*Rhizophora apiculata*[2]	-	tol.	sens.	-	res.	
24	*Rhizophora mucronata*[2]	ev.	intol.	sens.	sens.	res.	
25	*Shorea obtusa*	dec.	intol.	res.	-	sens.	TrIBD1
26	*Shorea roxburghii*	ev.	tol.	res.	res.	-	TrDSo, TrBE1, TrBE2
27	*Syzygium sp./lineatum*	semi-ev.	intol.	res.	-	res.	TrSESs
28	*Terminalia alata*	dec.	tol.	res.	-	-	TrDTa, TrBD1, TrBD2
29	*Vatica philastreana*	dec.	-	-	-	-	
30	*Xylia xylocarpa*	semi-ev.	intol.	res.	-	sens.	TrSEXx

[1] Plant species commonly representative for flooded forests.
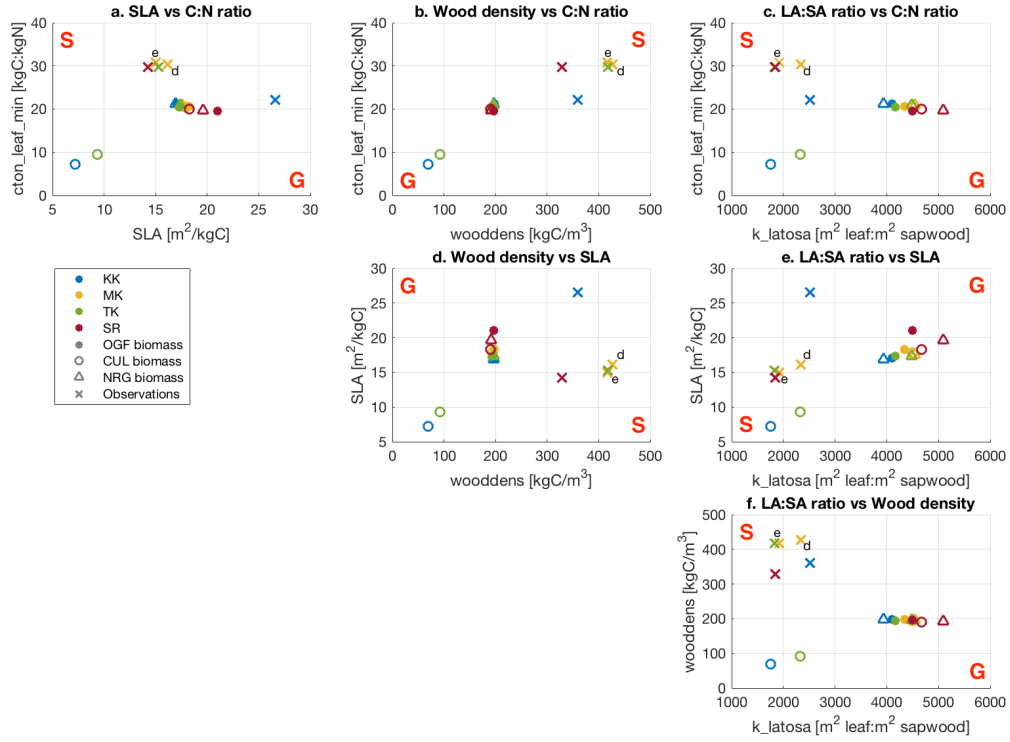[2] Plant species commonly representative for mangrove forests.

Figure 6.4: Comparison of CWM$_b$ between OGF, CUL, NRG standard scenarios, and observations based on C:N ratio (*cton_leaf_min* in kgC:kgN), SLA (*SLA* in m^2/kgC), wood density (*wooddens* in kgC/m^3), and LA:SA ratio (*k_latosa* in m^2 leaf:m^2 sapwood). CWM$_b$ of selected traits of OGF, CUL, and NRG are based on average values of biomass (Cmass in kgC/m^2) from 2001 to 2015 for the standard scenarios. CWM$_a$ of observed traits is based on species abundance. Red letters S and G refer to survival and growth strategy according to LES. Observed information on MK is distinguished between deciduous (*d*) and evergreen (*e*) forest types.
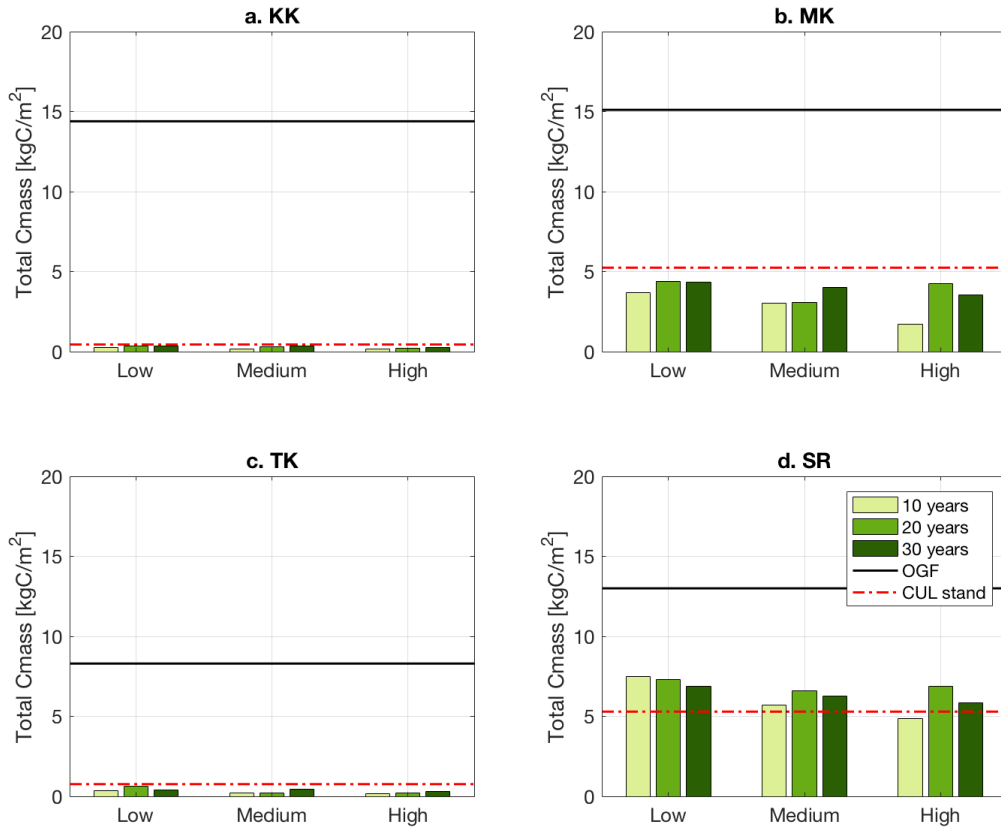
Figure 6.5: Total Cmass (kgC/m²/yr) for each harvest scenario (cutting interval of every 10, 20, and 30 years at low (10%), medium (20%), and high (30%) harvest intensity) for the study sites (**a.**) KK_{se}, (**b.**) MK_{se}, (**c.**) TK_d, and (**d.**) SR_e for CUL. Total Cmass is based on average values from the last 15 years (2001 - 2015) of all PFTs. OGF (black horizontal line) and CUL (red dashed line) represent reference values of the ideal state (OGF) and standard CUL scenarios without harvest management, respectively.