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# Modelling the terrestrial carbon cycle – drivers, benchmarks, and model-data fusion

Zhendong Wu



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DOCTORAL DISSERTATION

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<p>Abstract</p> <p>The terrestrial ecosystem sequesters about one-third of anthropogenic emissions each year, thereby providing a critical ecosystem service that slows the rate of increase of atmospheric carbon dioxide and helps mitigate climate change. Observed atmospheric carbon dioxide concentrations exhibit a large inter-annual variability which is considered to be caused primarily by the response of the terrestrial ecosystem to climate change and anthropogenic activity. A better understanding of the functioning of the terrestrial ecosystem is therefore required to improve our ability to predict the global carbon cycle and climate change.</p> <p>Ecosystem models integrate and apply knowledge of ecological processes (e.g. photosynthesis, respiration, allocation, and other plant physiological and microbial processes) to simulate net primary production, biomass accumulation, litterfall and soil carbon amongst others, in terrestrial ecosystems worldwide. These models are widely applied to explore, analyze and further our understanding of the complex interactions among biomes as well as the flows of carbon, nutrients and water through ecosystems over time in response to climate change and disturbances. Ecosystem models also allow the projection of the evolution of the carbon cycle under different scenarios of future possible carbon dioxide concentrations. However, current studies have demonstrated large uncertainties in predictions of past and present terrestrial carbon dynamics which limits our confidence in projections of future changes. These uncertainties, originating from model structure, parameters and data that drives the model, greatly limits our ability to accurately assess the performance of ecosystem models as well as our understanding of the response of ecosystems to environmental changes.</p> <p>This thesis aims to analyze these caveats by disentangling the causes of uncertainties in modeling terrestrial carbon dynamics to inform future model improvement. A state-of-the-art ecosystem model LPJ-GUESS is employed as the model platform for this study. Climate data induced uncertainty in model-based estimations of terrestrial primary productivity are analyzed and quantified for different ecosystems. Also, different climate variables are identified as the main contributors to total climate induced uncertainty in different regions. In addition, this thesis assesses the suitability of contemporary climate datasets with respect to a given research purpose and study area, and quantifies the effect of land use and land cover changes on the terrestrial carbon sink. Moreover, a matrix approach, which reorganizes the carbon balance equations of the ecosystem models into one matrix equation while preserving dynamically modeled carbon cycle processes and mechanisms, is applied to identify which ecological processes contribute most strongly to model-data disagreement in term of terrestrial carbon storage and flux.</p> <p>Identifying and reducing uncertainty in estimations of the terrestrial carbon cycle via a modeling approach enables us better understand, quantify, and forecast the effects of climate change and anthropogenic activity on the terrestrial ecosystem, but is also of increasing relevance in the context of climate change mitigation policies.</p>			
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# Modelling the terrestrial carbon cycle – drivers, benchmarks, and model-data fusion

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*The world is a fine place, and worth fighting for.*

*---- Ernest Miller Hemingway*

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- IV. Wu, Z., Hugelius, G., Luo, Y., Smith, B., Xia, J., Fensholt, R., Lehsten, V. and Ahlström, A. (2018). Approaching the potential of model-data comparisons of global land carbon storage. *In the second revision for Scientific Reports*.

## List of contributions

- I. Zhendong Wu led the study design, performed all simulations and data analysis, interpreted the results together with the co-authors and led the writing.
- II. Zhendong Wu led the study design, performed all simulations and data analysis, interpreted the results together with the co-authors and led the writing.
- III. Zhendong Wu joined data analysis, discussed and commented on the draft paper.
- IV. Zhendong Wu led the study design, performed all simulations and data analysis, interpreted the results together with the co-authors and led the writing.

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# Abstract

The terrestrial ecosystem sequesters about one-third of anthropogenic emissions each year, thereby providing a critical ecosystem service that slows the rate of increase of atmospheric carbon dioxide and helps mitigate climate change. Observed atmospheric carbon dioxide concentrations exhibit a large inter-annual variability which is considered to be caused primarily by the response of the terrestrial ecosystem to climate change and anthropogenic activity. A better understanding of the functioning of the terrestrial ecosystem is therefore required to improve our ability to predict the global carbon cycle and climate change.

Ecosystem models integrate and apply knowledge of ecological processes (e.g. photosynthesis, respiration, allocation, and other plant physiological and microbial processes) to simulate net primary production, biomass accumulation, litterfall and soil carbon amongst others, in terrestrial ecosystems worldwide. These models are widely applied to explore, analyze and further our understanding of the complex interactions among biomes as well as the flows of carbon, nutrients and water through ecosystems over time in response to climate change and disturbances. Ecosystem models also allow the projection of the evolution of the carbon cycle under different scenarios of future possible carbon dioxide concentrations. However, current studies have demonstrated large uncertainties in predictions of past and present terrestrial carbon dynamics which limits our confidence in projections of future changes. These uncertainties, originating from model structure, parameters and data that drives the model, greatly limits our ability to accurately assess the performance of ecosystem models as well as our understanding of the response of ecosystems to environmental changes.

This thesis aims to analyze these caveats by disentangling the causes of uncertainties in modeling terrestrial carbon dynamics to inform future model improvement. A state-of-the-art ecosystem model LPJ-GUESS is employed as the model platform for this study. Climate data induced uncertainty in model-based estimations of terrestrial primary productivity are analyzed and quantified for different ecosystems. Also, different climate variables are identified as the main contributors to total climate induced uncertainty in different regions. In addition, this thesis assesses the suitability of contemporary climate datasets with respect to a given research purpose and study area, and quantifies the effect of land use and land cover changes on the terrestrial carbon sink. Moreover, a matrix approach, which

reorganizes the carbon balance equations of the ecosystem models into one matrix equation while preserving dynamically modeled carbon cycle processes and mechanisms, is applied to identify which ecological processes contribute most strongly to model-data disagreement in term of terrestrial carbon storage and flux.

Identifying and reducing uncertainty in estimations of the terrestrial carbon cycle via a modeling approach enables us better understand, quantify, and forecast the effects of climate change and anthropogenic activity on the terrestrial ecosystem, but is also of increasing relevance in the context of climate change mitigation policies.

# Sammanfattning

Det terrestra ekosystemet absorberar cirka en tredjedel av de antropogena utsläppen varje år, vilket är en avgörande ekosystemtjänst som minskar ökningstakten av atmosfärisk koldioxid och bidrar till att mildra klimatförändringen. Observerade koncentrationer av atmosfäriskt koldioxid uppvisar en stor årlig variabilitet som främst anses vara orsakad av det terrestra ekosystemets respons på klimatförändringar och antropogen aktivitet. En bättre förståelse för det terrestra ekosystemets funktion ger därför inblick i den globala koldioxidcykeln och klimatförändringen.

Ekosystemmodeller tillämpar kunskap om ekologiska processer (e.g. fotosyntes, respiration, kolallokering och andra växtfysiologiska och mikrobiella processer) för att simulera nettoprimärproduktion, ackumulering av biomassa, dött organiskt material och markkol i markbundna ekosystem världen över. Dessa modeller används i stor utsträckning för att undersöka möjligheter och ge ökad förståelse för de komplexa interaktionerna mellan biom och flöden av kol, näringsämnen och vatten genom ekosystem över tiden som svar på klimatförändringar och störningar. Ekosystemmodeller möjliggör också att projicera utvecklingen av kolcykeln under olika scenarier av framtida potentiell koldioxidkoncentration. Nuvarande studier har dock visat på stor osäkerhet vid förutsägelser av tidigare och nuvarande markbunden koldynamik och även stor osäkerhet i framtida prognoser. Dessa osäkerheter, som här är från modellstruktur, parametrar och indata, begränsar vår förmåga att korrekt bedöma ekosystemmodellernas prestanda samt vår förståelse av ekosystemens svar på miljöförändringar.

Denna avhandling avser att utreda osäkerheter i modellering av markbunden koldynamik, vilket hjälper till med förbättring av modeller. En modern ekosystemmodell, LPJ-GUESS, har använts som modelleringsplattform för denna studie. Osäkerhet orsakad av klimatdata vid modellbaserade uppskattningar av markbunden primärproduktion analyseras och kvantifieras för olika ekosystem. Olika klimatvariabler identifieras som de främsta bidragsgivarna till den totala klimatinducerade osäkerheten. Denna avhandling utvärderar också lämpligheten hos nuvarande klimatdataset med avseende på specifikt forskningssyfte och studieområde. Dessutom tillämpas en matrismetod som omorganiserar ekosystemmodellernas ekvationssystem till en matrisekvation och bibehåller alla ursprungliga mekanismer och processer relaterade till kolcykeln. Matrismetoden

tillämpas för att identifiera vilka ekologiska processer som bidrar mest till avvikelser mellan modellresultat och data med hänsyn till markbaserade flöden och lagring av kol.

Att identifiera och minska osäkerheten vid uppskattningar av den markbundna kolcykeln via ett modelleringsförfarande gör att vi bättre kan förstå, kvantifiera och förutspå effekterna av klimatförändringar och antropogen aktivitet på det markbundna ekosystemet, men det är också av ökande relevans i samband med klimatpolitik.

# 摘要

陆地生态系统每年吸收约三分之一的人为二氧化碳排放量，从而提供关键的生态系统服务即减缓大气二氧化碳的增加速度，并有助于缓解气候变化。观测到的大气二氧化碳浓度表现出剧烈的年际变化，被认为主要是由陆地生态系统对气候变化和人类活动的响应引起的。因此，加深对陆地生态系统的功能理解有助于提高我们预测全球碳循环和气候变化的能力。

生态系统模型整合并应用生态过程的知识（例如光合作用，呼吸作用，分配和其他植物生理和微生物过程）来模拟全球陆地生态系统的净初级生产量，生物量积累，凋落物和土壤碳含量等。这些模型广泛地用于探索在应对气候变化和干扰下生物群落之间复杂的相互作用，以及生态系统中碳，养分和水分的变化。生态系统模型还允许在未来不同二氧化碳浓度的情景下预测碳循环的演变。然而，目前的研究表明，对过去和当前陆地碳动态的模拟存在很大的不确定性，这限制了我们的预测其未来变化的能力。这些不确定性源自模型结构，参数和驱动模型的数据，并极大地限制了我们对生态系统模型性能的准确评估以及我们对生态系统对环境变化的响应的理解。

本论文旨在研究分析陆地碳动态建模中不确定性的因素，以便为未来的模型改进提供信息。这里采用了最先进的生态系统模型 LPJ-GUESS 作为本研究的模型平台。本论文分析和量化气候数据在模拟不同生态系统的初级生产力中引起的不确定性，并在空间上识别对引起的不确定性贡献最大的气候变量。本论文还评估了当前气候数据集在特定研究目的和研究领域的适用性，量化了土地利用和土地覆盖变化对陆地碳汇的影响。此外，论文中采用了一种矩阵方法，该方法将生态系统模型的碳平衡方程重组为一个矩阵方程并保留原始模型的碳循环过程和机制，用于识别哪些生态过程主导模型与观测数据间的差异（在陆地碳存储和通量方面）。

通过识别和降低模拟陆地碳循环的不确定性，使我们能够更好地理解，量化和预测气候变化和人类活动对陆地生态系统的影响，同时对气候变化减缓政策具有越来越重要的意义。

# Abbreviations

AGB	Above Ground Biomass
C	Carbon
CMIP5	Coupled Model Intercomparison Project Phase 5
DGVM	Dynamic Global Vegetation Model
ESM	Earth System Model
GCB	Global Carbon Budget
GCM	General Circulation Model
GPP	Gross Primary Production
IPCC	Intergovernmental Panel on Climate Change
LPJ-GUESS	Lund-Potsdam-Jena General Ecosystem Simulator
LUE	Light-Use Efficiency
LULCC	Land Use and Land Cover Change
MODIS	Moderate Resolution Imaging Spectroradiometer
MTE	Model Tree Ensembles
N	Nitrogen
NBP	Net Biome Production
NEE	Net Ecosystem Exchange
NPP	Net Primary Production
TF	Traceability Framework
VOD	Vegetation Optical Depth

# 1. Introduction

## 1.1. Global carbon cycle

The global carbon cycle can be viewed as an exchange of fluxes of carbon within a series of reservoirs of carbon in the earth system (atmosphere, ocean, land and lithosphere). Conceptually, the global carbon cycle has two domains, the fast and slow domains (Ciais et al., 2014). The fast domain consists of carbon in the atmosphere, the ocean surface, ocean sediments and on land in vegetation, soils and freshwater, where carbon turnover is relatively fast (from a few years to decades). In the slow domain, which consists of the huge carbon stores in rocks and sediments, carbon turnover is slow (up to millennia or longer). Since 1750, the beginning of the Industrial Era, fossil fuel extraction from geological reservoirs, and their combustion, has resulted in the transfer of a significant amount of fossil carbon from the slow domain into the fast domain, thus causing a major anthropogenic perturbation in the carbon cycle and further in the climate system (Ciais et al., 2014).

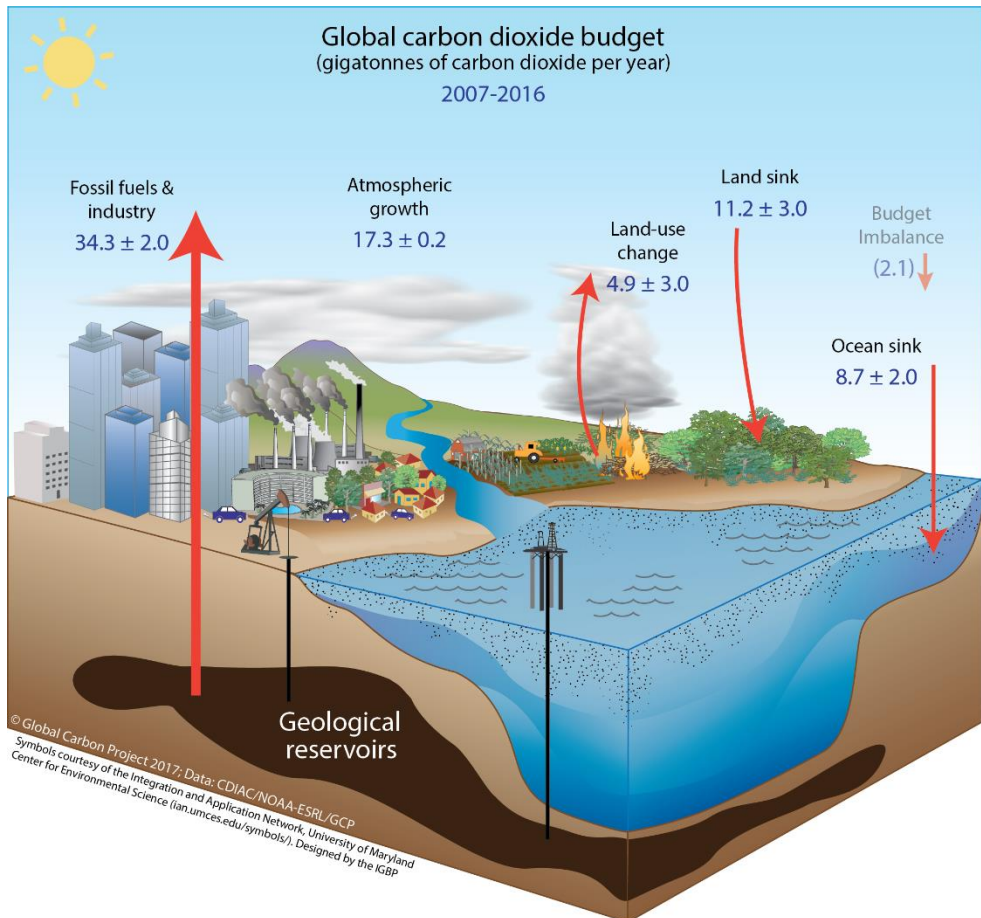
The global carbon budget (Le Quéré et al., 2018), a key indicator of the anthropogenic influence of the global carbon cycle, provides an assessment of anthropogenic carbon emissions and their redistribution among the atmosphere, ocean, and terrestrial biosphere (Figure 1). Le Quéré et al. (2018) reported that human-induced perturbation (e.g. combustion of fossil fuels and land-use change) during 2007-2016 resulted in an input of  $39.2 \pm 5.0$  PgC yr<sup>-1</sup> carbon dioxide (CO<sub>2</sub>) into the atmosphere, of which 51% was taken up by land ( $11.2 \pm 3.0$  PgC yr<sup>-1</sup>) and ocean ( $8.7 \pm 2.0$  PgC yr<sup>-1</sup>) reservoirs and 44% remained in the atmosphere ( $17.3 \pm 0.2$  PgC yr<sup>-1</sup>) leaving a remaining unattributed budget imbalance of 5%. Therefore, oceanic and terrestrial ecosystems represent a critical ecosystem service which slows the rise in atmospheric CO<sub>2</sub> concentration, and reduces the influence of anthropogenic carbon emissions on global climate change (Ballantyne et al., 2012).

## 1.2. The terrestrial ecosystem in the global carbon cycle

Ballantyne et al. (2012) showed that the uptake of carbon by oceanic and terrestrial ecosystems increased with accelerating CO<sub>2</sub> emissions, while atmospheric CO<sub>2</sub>



concentrations exhibited a large inter-annual variability (Le Quéré et al., 2018). Such inter-annual variability is considered to be caused primarily by terrestrial ecosystem processes, e.g. increased carbon uptake in semi-arid regions with increased precipitation (Poulter et al., 2014, Ahlström et al., 2015a) or the large amount of CO<sub>2</sub> released from tropical forests to atmosphere with warming



**Figure 1.** Schematic representation of the overall perturbation of the global carbon cycle caused by anthropogenic activities, averaged globally for the decade 2007-2016. The arrows represent emissions from fossil fuels and industry, emissions from deforestation and other land-use changes, the growth rate in atmospheric CO<sub>2</sub> concentration, and the uptake of carbon by the sinks in the ocean and land reservoirs. The budget imbalance is also shown. All fluxes are in units of PgC yr<sup>-1</sup>, with uncertainties reported as ±1σ (68% confidence that the real value lies within the given interval) as described in the text. (Le Quéré et al., 2018)

temperatures (Cox et al., 2013). The carbon uptake by terrestrial ecosystems varies markedly between years and has a strong response to climate variations, in comparison with the relatively stable carbon uptake by the ocean reservoir (e.g.

Lovenduski and Bonan, 2017, Le Quéré et al., 2018). Terrestrial ecosystems have the capacity to be a sink or a source of carbon depending on the balance between carbon uptake by vegetation and the return of vegetation and soil carbon to the atmosphere through respiration, biomass burning and other minor release fluxes (Luo et al., 2003). The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR5) reported that there are large uncertainties in projecting future carbon storage by Earth System Models (ESMs): the majority of ESMs projected continued net carbon uptake (sink) under all future CO<sub>2</sub> emission scenarios, yet some models simulated a net carbon emission from the land (source) due to the combined effect of climate change and land use change (Ciais et al., 2014). Therefore, reducing uncertainty in estimations of the terrestrial carbon sink or source and its response to global changes is of great importance to the global carbon budget, and enables us to better understand, quantify, and forecast the effects of climate change and anthropogenic activities on terrestrial ecosystems, thus further assisting policy makers to make informed decisions for mitigating human-driven climate change.

### 1.3. Methods for quantifying terrestrial carbon dynamics

Typically, there are three methods for quantifying the carbon dynamics of terrestrial ecosystems: (i) ground-based measurements, (ii) satellite-based measurements and (iii) model simulations (Prentice et al., 2007). Ground-based measurements, such as biomass inventories, community descriptions and eddy covariance flux measurements are made at single sites or across networks, but remain a challenge to scale up. Satellite-based measurements provide comprehensive coverage and averages over landscapes, which enables understanding of the large-scale processes of carbon dynamics. With advances in techniques and sensors, satellite-based measurements are expanding the scope of observations, improving spatial resolution from the scale of kilometers to meters and reducing temporal sampling intervals from weeks to hours. However, one of the major limitations of available satellite observations is their short record length providing continuous global coverage only since the 1970's. Moreover, satellite-based measurements provide limited information with regards to biodiversity and belowground processes.

Therefore, there is a need for ecosystem models (Prentice et al., 2000), which integrate the knowledge of the representative ecological processes (e.g. photosynthesis, respiration, allocation, and other plant physiological and microbial processes) from field measurements and satellite observations, to simulate net primary production, biomass accumulation, litter fall and soil carbon amongst others in terrestrial ecosystems worldwide. These models aid our understanding of the complex interactions among biomes under rapidly changing environmental

conditions, e.g. climate change and land use change. Ecosystem models complement observation-based methods such as remote sensing and field measurements by explicitly accounting for the process interactions and feedbacks linking climate and other drivers to ecosystem dynamics. Furthermore, ecosystem models can be used to predict future carbon budgets under different scenarios describing future possible CO<sub>2</sub> conditions.

One type of ecosystem model is known as dynamic global vegetation models (DGVMs) (Cramer et al., 2001), and nowadays these models are widely applied to represent transient aspects of ecosystem response (e.g. plant geography, plant physiology and biogeochemistry, vegetation dynamics, and biophysics) to climate change and certain other aspects of global change. DGVMs have been developed since the 1990s and examples include BIOME (Prentice et al., 1992), IBIS (Foley et al., 1996), HYBRID (Friend et al., 1997), LPJ-GUESS (Smith et al., 2001), TRIFFID (Cox, 2001), LPJ-DGVM (Sitch et al., 2003), ORCHIDEE (Krinner et al., 2005) to name a few. These models are usually driven by external drivers (e.g. CO<sub>2</sub> concentration, land use and climate data) and simulate changes in community composition, biomass, and productivity as result of the birth, growth, and death of vegetation, as well as the decomposition of dead organic matter associated with the carbon cycle and other biogeochemical cycles (Cox, 2001, Smith et al., 2001, Sitch et al., 2003, Krinner et al., 2005, Prentice et al., 2007, Zaehle and Friend, 2010). DGVMs are often considered the primary approach for mapping future regional to global terrestrial carbon storage and fluxes under climate change.

## 1.4. Ecological terms for quantifying terrestrial carbon exchange

There are four commonly used ecological terms describing the terrestrial carbon balance: (i) Gross Primary Production (GPP), (ii) Net Primary Production (NPP), (iii) Net Ecosystem Exchange (NEE) and (vi) Net Biome Production (NBP). GPP is defined as the rate of the total amount of carbon fixed by plants in the process of photosynthesis in a given length of time. NPP is defined as the difference between GPP and autotrophic respiration, and measures the net production or accumulation of dry matter in plants over a period (Roxburgh et al., 2005). NEE, also known as net ecosystem production (NEP), refers to the balance in ecosystems among carbon uptake during photosynthesis (i.e. GPP), carbon loss during plant respiration, and carbon loss by organisms other than the plants. NEE measures net storage of carbon in the ecosystem in the absence of disturbance (e.g. fire and human activities). NBP, also known as Net Biome Exchange (NBE), refers to the change in carbon stocks and takes into account carbon losses due to natural or anthropogenic disturbances. NBP and NEE are used interchangeably when the ecosystem is not typically affected

by disturbances. NBP is usually applied as much to the biome level as to the regional level. When it is applied at global level, it can also refer to the terrestrial net carbon sink.

GPP is the main ecological term used for model uncertainty analysis, model evaluation and model-data fusion in this thesis. In DGVMs, GPP represents the origin of carbon within the simulated ecosystem, controlling many other downstream processes. If GPP is simulated incorrectly, errors propagate to other processes and affect all carbon pools and fluxes of the simulated ecosystem (Luo et al., 2003). As mentioned in section 1.3, there are three widely applied research approaches to estimate GPP from local to global scale: (i) CO<sub>2</sub> flux measurement by the eddy covariance technique (Baldocchi et al., 2001, Baldocchi, 2003, Goulden et al., 2011), in which continuous measurement of NEE, between terrestrial ecosystems and the atmosphere from eddy flux towers, can be partitioned into ecosystem respiration and GPP at local scale (e.g. Reichstein et al., 2005, Papale et al., 2006), and can be further upscaled to the regional and global scale (e.g. Jung et al., 2011, Jung et al., 2017). (ii) Production efficiency models, which are based on the radiation conversion efficiency concept of light-use efficiency (LUE) with the inputs of satellite images and climate data (Potter et al., 1993, Running et al., 1999, Peng and Gitelson, 2012). Finally, (iii) process-based biogeochemical models (e.g. Cox, 2001, Smith et al., 2001, Sitch et al., 2003, Krinner et al., 2005), which incorporate a number of physiological processes and use climate data as inputs. Most of these models use the Farquhar et al. (1980) model or its derivatives (Collatz et al., 1991, Collatz et al., 1992, Haxeltine and Prentice, 1996) to estimate GPP.

## 1.5. Disagreement between model simulations and observations

Many different types of contemporary observations (derived from ground-based and satellite-based measurements) are used to test model performance in estimating terrestrial carbon exchange. Currently there is a considerable mismatch between observations and model simulations; here the model-data mismatch is illustrated in terms of the CO<sub>2</sub> sink and GPP. The temporal correlation of the global terrestrial CO<sub>2</sub> sink between data on the global carbon budget (GCB) and the outputs from 14 DGVMs ranged from 0.51 to 0.77 for the period 1959 to 2015 (Le Quéré et al., 2016). The global annual CO<sub>2</sub> sink across the DGVMs ( $2.2 \pm 0.7$  PgC yr<sup>-1</sup>), averaged over the last decade (2006-2015), was approximately 30% higher than the estimation of the GCB ( $1.7 \pm 0.7$  PgC yr<sup>-1</sup>). Anav et al. (2015) reported that the global terrestrial GPP averaged across 3 DGVMs ( $149.7 \pm 3.5$  PgC yr<sup>-1</sup>) and across 5 ESMs ( $143.6 \pm 2.8$  PgC yr<sup>-1</sup>) was overestimated by 20-33% in comparison to a data-driven GPP product derived from eddy covariance measurements ( $119 \pm 1.3$  PgC yr<sup>-1</sup>) and

satellite measurements ( $112 \pm 0.8 \text{ PgC yr}^{-1}$ ) during 1990-2009. Furthermore, the average linear GPP trends over 1990-2009 derived from models ( $0.41 \pm 0.18 \text{ PgC yr}^{-1}$ ) are much stronger than those derived from the data-driven products ( $0.01 \pm 0.01 \text{ PgC yr}^{-1}$ ). For longer periods (1982-2008), Piao et al. (2013) showed global terrestrial GPP averaged across 10 DGVMs was approximately 13% higher than a data-driven GPP product (Jung et al., 2011), with the temporal correlation typically lower than 0.4. In order to avoid over-interpretation of model-data mismatches in evaluation or assimilation schemes, it is mandatory to also consider the limitations of the observational data.

### **1.5.1. Observational uncertainty**

The terrestrial  $\text{CO}_2$  sink derived from the GCB accounting method represents the residual of anthropogenic fossil fuel emissions, atmospheric growth and oceanic uptake of carbon (Le Qué é et al., 2018). This data is widely used to constrain carbon cycle models. However, any errors in either the emissions or in the atmospheric or oceanic sinks are therefore debited to the net land flux, where errors accumulate.

The eddy covariance technique provides measurements of surface-atmosphere  $\text{CO}_2$  exchange from towers with a very high temporal resolution (Baldocchi et al., 2001, Baldocchi, 2003), and the derived flux products are widely used for model evaluation (Williams et al., 2009). Recent developments in statistical modelling have enabled such flux tower-derived measurements to be scaled up, using satellite observations to interpolate across space, to create globally gridded products (e.g. FLUXCOM GPP; Jung et al., 2011, Jung et al., 2017). However, flux tower-derived measurements inevitably include systematic and random errors (e.g. instrument failure, gaps when conditions are unsuitable for making measurements) and uncertainties. For instance, uncertainties in flux measurements can originate from discriminating between low and well mixed fluxes (Papale et al., 2006), estimation of missing values (Moffat et al., 2007), and flux partitioning (i.e. partitioning the observed NEE into GPP and ecosystem respiration) (Reichstein et al., 2005, Lasslop et al., 2010). These uncertainties, furthermore, propagate when extrapolating to the globe, e.g. by the Model Tree Ensembles (MTE) approach (Jung et al., 2011).

Satellite-based products (e.g. GPP, NPP) are widely used to evaluate DGVMs (e.g. Maignan et al., 2011), notably the Moderate Resolution Imaging Spectroradiometer (MODIS) products. MODIS provides various gridded data products of vegetation state, by interpreting the spectral reflectance data (e.g. its intensity, spectral properties and angular properties)

acquired from a spectroradiometer, which helps infer the structure, composition, and functioning of plant canopies (Running et al., 1999, Zhao et al., 2005). However, it is important to bear in mind that these products (often used as observations) derived from the raw satellite data are also based on a range of assumptions and algorithms. The potential sources for uncertainties in biophysical products derived from optical satellite systems are: (i) noise in satellite data, e.g. caused by clouds, atmospheric constituents, sensor view and sun angles, canopy background, sensor problems, and weather conditions like snowfall, rain and haze (Eklundh et al., 2011); (ii) uncertainty in climate inputs, e.g. air temperature and relative humidity, in the LUE algorithm (Monteith, 1972, Monteith and Moss, 1977, Running et al., 1999) and (iii) the lack of representation of certain processes within the algorithm, e.g. soil moisture (Coops et al., 2007).

Another satellite products which are based on vegetation optical depth (VOD) have been used to monitor changes in vegetation carbon (Liu et al., 2015, Tian et al., 2016, Brandt et al., 2018), which is also used for evaluation in this thesis. The VOD signal derived from passive microwave observations, quantifying brightness temperature based on the NASA-VU Land Parameter Retrieval Model (LPRM) (Owe et al., 2008). VOD is sensitive to the water content in the aboveground vegetation, including both photosynthetic (e.g. leaf) and non-photosynthetic (e.g. wood) compartments (Shi et al., 2008). Therefore, VOD has been applied for measuring water content of aboveground vegetation and further has been used as a proxy for vegetation biomass (Liu et al., 2015, Tian et al., 2016, Brandt et al., 2018). Furthermore, due to the longer wavelength and stronger penetration capacity of microwave, VOD is insensitive to the effects of atmosphere and cloud contamination, providing reliable information of aboveground vegetation in cloudy region such as tropics where has shortage of observation data. However, large data gap and noise as well as background soil moisture conditions can influence the quality of VOD products.

### **1.5.2. Model uncertainty**

Ecosystem models help explore possibilities and aid understanding of the complex interactions among biomes as well as the flows of carbon, nutrients and water through ecosystems under rapidly changing environmental conditions (Sykes, 2009). However, it is not possible to incorporate all ecological factors and processes into one model. The art of modeling is to determine what should be explicitly represented in models and what can be ignored. Therefore, all models have a range

of assumptions and uncertainties that users must be aware of before attempting to interpret model outputs. A sub-optimal performance of current models can result from biases in any of the three following components across time and space: model structure, model parameters and external drivers (Luo et al., 2011, Luo et al., 2016).

### *Model structure*

Model structure is the set of equations used to describe the dynamic patterns of ecological processes. The components of terrestrial ecosystems and the interactions among them are complicated or not well understood, so simplifying assumptions must be made to describe them. Different modeling strategies adopt different simplifying assumptions, leading to different model complexity and behavior and thus structural uncertainty between models. For instance, model structural uncertainty can arise from differences in the representation of ecological processes, the scaling of these processes, their interactions and linkages to drivers and descriptors of ecosystem state, as well as the inclusion of certain processes, e.g. wildfires or nutrient interactions, in some models but not others (Cramer et al., 2001, Tebaldi and Knutti, 2007, Sitch et al., 2008, Zaehle et al., 2014). In addition, even when models apply the same theory for an ecological process (e.g. photosynthesis), Rogers et al. (2017) have shown that their varying numerical implementation of that theory leads to divergent simulation results.

Structural uncertainty has been addressed by numerical experiments with multi-model ensembles (MMEs), whereby a group of models is run with the same drivers (Cramer et al., 2001, Adams et al., 2004, Tebaldi and Knutti, 2007, Sitch et al., 2008, Carvalhais et al., 2014, Zaehle et al., 2014, Sitch et al., 2015). Recent studies have pointed out that the large spread of the predicted terrestrial C sinks among models can result from differences in NPP (Cramer et al., 2001), soil decomposition (Jones et al., 2003), biome shifts (Friedlingstein et al., 2006) and vegetation turnover (Todd-Brown et al., 2013, Friend et al., 2014). Besides, different models are sensitive to different climate variables (Sitch et al., 2008, Galbraith et al., 2010).

### *Model parameters*

Once the model structure is defined, differences in parameter values (i.e. parameterization) for mathematical formulations of ecological processes can generate divergent modeling results. Previous studies have demonstrated a large spread in model output within a single model structure arising from parameter uncertainty, e.g. (Booth et al., 2012). The parameterization-induced uncertainty is mainly due to different model calibration strategies (Knorr and Heimann, 2001, Zaehle et al., 2005, Wramneby et al., 2008). In practice, it is difficult to identify parameters in a complicated model that can be effectively calibrated to fit data well across diverse landscapes, i.e. a model with well-calibrated parameters at one site may not reliably work at other sites (Xiao et al., 2014). Differences among DGVMs in structure and parameterization mean that they have different response functions

relating rates of carbon and water fluxes to environmental change (e.g., CO<sub>2</sub> concentration, temperature, and precipitation or soil moisture content). Subtle changes to response functions and parameterizations can yield large divergences in the modelled responses of ecosystems and has been demonstrated by parameter sensitivity studies (e.g. White et al., 2000, Zaehle et al., 2005) and model intercomparison studies (e.g. Friedlingstein et al., 2006, Todd-Brown et al., 2013).

### *External drivers*

Models also require reliable external drivers, representing the physical and biological environment the ecosystem experiences or will experience. External drivers usually include CO<sub>2</sub> concentration, N deposition, land use and climatic drivers (typically air temperature, precipitation and shortwave radiation). As ecological processes are highly sensitive to environmental change, small biases in external drivers can lead to large divergences in model results. The following discussion focuses on historical and projected climatic drivers and land use data.

Historical climate data can, at least in part, originate from historical instrumental records that are either site-specific or have been interpolated into a standard spatial grid. Interpolation of climate values across areas of unmeasured territory inevitably introduces uncertainty and propagates through the ecosystem model (Zhao et al., 2006). Much of the climate data used by models come from General Circulation Models (GCMs), which model gridded climate data for the past, present and future at large scales. The projected climate datasets stem from GCMs, simulating the response of the global and regional climate system to greenhouse gas emission scenarios (Stocker, 2014). These scenarios represent possible emission levels derived from the results of different socioeconomic storylines, which describe possible future conditions (e.g. economic development, technological development, population growth, etc.), although none of these scenarios is likely to be the future. GCMs may produce quite different results even using the same drivers, because of the way certain processes and feedbacks are modeled (Flato et al., 2013).

At the global scale, land use data is often specified as gridded products, recording the fractional area of each grid cell is occupied by land type (e.g. forest, pasture and cropland, etc.). For instance, the History Database of the Global Environment (HYDE) data (Goldewijk, 2001, Goldewijk et al., 2011) and its derivatives (Hurtt et al., 2006, Hurtt et al., 2011), which are currently widely used in many DGVMs attempting to estimate the effects of spatially and temporally variable patterns of human land-use activities on terrestrial ecosystem dynamics (e.g. Arneeth et al., 2017, Piao et al., 2018). The HYDE data is model-derived products and inevitably



contains uncertainties. The uncertainties can be originated from input sources (e.g. population, cropland and pasture statistics, and satellite-derived land cover) and specific allocation algorithms (Goldewijk et al., 2011, Hurtt et al., 2011). Besides, the land use data presented as the fractional area of grid cell may not capture the actual land use transitions. For instance, the same fractional coverage of cropland for two consecutive years, which can be read as no land use transition, or the abandonment of any area of cropland offset by the establishment of an equal area of new cropland during the period.

In previous studies, climatic drivers were found to be a large source of uncertainty in DGVMs (McGuire et al., 2001, Jung et al., 2007, Poulter et al., 2011, Ahlström et al., 2012, Ahlström et al., 2013). The choice of historical climate dataset input can result in 9% - 20% uncertainty of estimated global GPP (Jung et al., 2007, Barman et al., 2014, Wu et al., 2017), and also influences the spatial patterns of simulated GPP (Jung et al., 2007, Poulter et al., 2011). Similarly for projected climate data, Ahlström et al. (2012) found large differences in total carbon uptake, ranging from  $-0.97$  to  $2.27$  PgC yr<sup>-1</sup> over the coming century by using 18 climate datasets from the Coupled Model Intercomparison Project Phase 5 (CMIP5) climate change projections. Besides, the choice of land use data can induce  $1.10$  PgC yr<sup>-1</sup> uncertainty of estimated global NEE (Poulter et al., 2011).

### **1.5.3. Model-data fusion**

By learning about the origins of model uncertainty mentioned above, and together with the rapid increase of biomass and flux observations at different space and time scales, it is becoming increasingly important to identify strategies that are capable of making the best use of existing information and optimally integrate various data sources for improving model. Data assimilation, a model-data fusion method, was recognized as the highest priority to improve predictions of carbon dynamics in ESMs (Luo et al., 2015). This technique integrates multiple sources of information from observational data (e.g. ecosystem flux tower data, remote sensing data, biomass and soil inventories) to constrain parameters of carbon cycle models at different spatial and temporal scales (Xu et al., 2006, Scholze et al., 2007, Weng and Luo, 2011, Zhou et al., 2012, Haverd et al., 2013, Niu et al., 2014). The key model parameters are optimized by using statistically rigorous methods, e.g. the Bayesian approach and Markov Chain Monte Carlo (MCMC) technique, to reduce a cost function until the reduction is smaller than a prescribed tolerance. Here the cost function quantifies the deviation between the model outputs (depending on the specified parameters) and the various observational data. A more detailed description of the data assimilation technique can be found in the Carbon Cycle Data Assimilation System (CCDAS) (Kaminski et al., 2003, Rayner et al., 2005).

#### **1.5.4. When can we say the model is acceptable?**

There is no such thing as a model that perfectly represents terrestrial carbon dynamics or the observational data. Models are developed in order to interpret observations and identify the underlying mechanisms in the functioning of ecosystems, and allow to make predictions for the future based on knowledge derived from past observations. All models are idealized to some degree and consensus is drawn on whether a model is suitable for a specific purpose by weighing up the different lines of evidence (e.g. state estimation, process definitions). Successful application of the model is contingent on the modelers' understanding of ecosystem changes in terms of space, time, and prognostic variables. Due to ecological complexity, a single model cannot comprehensively capture the dynamics of an ecosystem. However, if a model community (an ensemble of multiple models) can capture the range of possible ecosystem dynamics, then modeling approaches worth more attention and acceptance.

## 2. Aims and objectives

The objective of this PhD thesis is to analyze the causes of uncertainties in modeling the terrestrial carbon pool and carbon flux dynamics and improve model performance. This study investigates and quantifies model uncertainty focusing on climate inputs and model structure. In an attempt to improve model performance, a model-data fusion method is used to reduce the model-data mismatch in ecosystem state by combining model and data from site measurements and remote sensing. The thesis can be divided into the following main aims:

- I. Quantifying the influence of climate data uncertainties on simulations of carbon uptake by vegetation, and how much each climate variable contributes to total climate induced uncertainties.
- II. Assessing the suitability of contemporary climate datasets for simulations of GPP with respect to a given research purpose and study area, acknowledging the large uncertainties in climate data.
- III. Quantifying the effect of land use and land cover changes on the terrestrial carbon sink.
- IV. Determining which carbon cycle processes are associated with the greatest model-data mismatch (e.g. in terms of terrestrial carbon storage and flux)

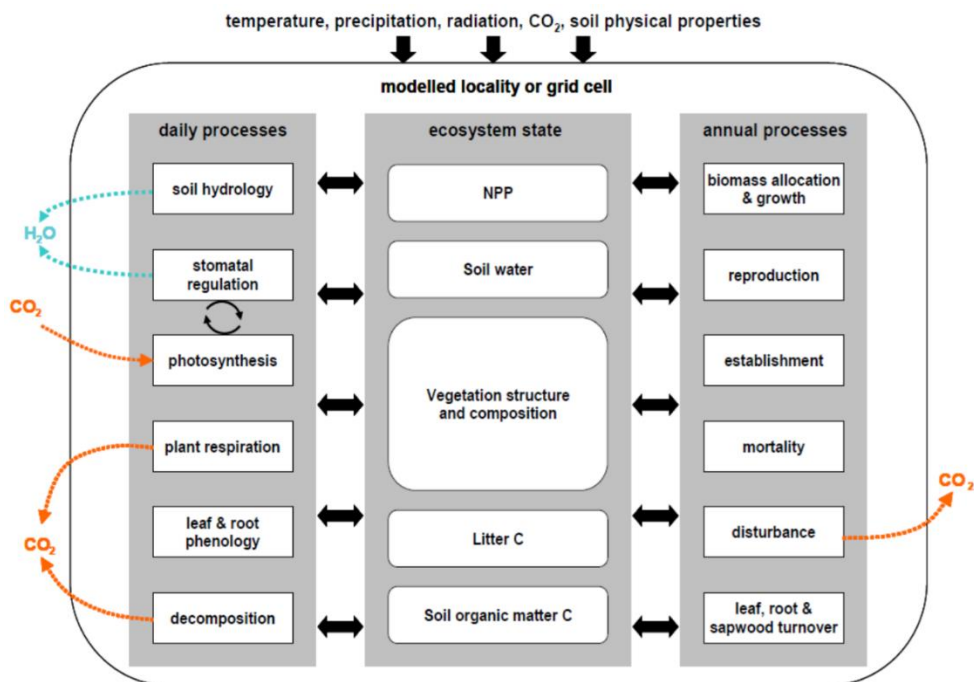
# 3. Methods

## 3.1. LPJ-GUESS

As one out of many DGVMs, the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS; Smith et al., 2001, Smith et al., 2014) was applied in a wide range of studies and showed relatively similar predictive skills and response to climate variations compared to other global ecosystem models (McGuire et al., 2012, Murray-Tortarolo et al., 2013, Piao et al., 2013, Sitch et al., 2015), thus LPJ-GUESS is employed as the model platform for this thesis. LPJ-GUESS is a process-based dynamic global vegetation model, which uniquely combines an individual-based representation of plant growth, demography and interspecific competition with process-based physiology and biogeochemistry (Figure 2). LPJ-GUESS implements two categories of processes corresponding to the characteristic time scale of the processes: daily processes and annual processes. Daily processes simulate the diurnal cycle including energy and gas exchange at the canopy-atmosphere interface, and plant-soil water exchange. Annual processes include biomass allocation, growth, reproduction, establishment, mortality and disturbance.

LPJ-GUESS employs gridded time series of climate data (air temperature, precipitation and incoming shortwave radiation), atmospheric CO<sub>2</sub> concentrations, land use, N deposition and soil properties as drivers, and simulates the effects of environmental change (e.g. climate and land use change) on vegetation structure and composition in terms of plant functional types (PFTs), soil hydrology and biogeochemistry. PFTs are characterized by properties such as growth form, leaf phenology, life history strategy and bioclimatic limits which govern their performance and competitive interactions under the driving conditions and realized ecosystem state (Sitch et al., 2003). Simulations are initialized with spin-up (e.g. 1000 years) by recycling de-trended the first few years (e.g. 30 years) of historical drivers, which enable the vegetation as well as soil and litter carbon pools accumulate and approach an equilibrium, then start subsequent simulations under historical and future driving conditions. Each simulated grid cell is represented by a number of replicate patches (e.g. 20). These patches share the common climate and soil type, while plants on different patches do not affect one another (e.g. in the capture of light, water uptake, and disturbances), which results in different vegetation dynamics (section 3.1.4) in different patches. The independence among the replicate patches enables to simulate succession following patch-destroying

disturbances in realistic way. The simulated properties for a grid cell tend to converge on a single value, which is averaged over the all inner patches.



**Figure 2.** Conceptual representation of LPJ-GUESS showing the main processes, time steps, state variables and environmental input data. The potential output of the model includes current values of the ecosystem state variables (e.g. biomass for different plant functional types, PFTs) as well as biogeochemical fluxes of CO<sub>2</sub> and H<sub>2</sub>O from ecosystems to the atmosphere or hydrosphere.

### 3.1.1. Physiology and biogeochemistry

Plants absorb carbon from the atmosphere via photosynthesis, by which light energy is used to produce carbohydrates from CO<sub>2</sub> and water. LPJ-GEUSS simulates photosynthesis coupled with stomatal conductance, water uptake and evapotranspiration, using a derivative of the Farquhar et al. (1980) model adapted from the BIOME3 model (Haxeltine and Prentice, 1996). Photosynthesis is a function of absorbed photosynthetically active radiation (APAR), temperature, CO<sub>2</sub> concentration and canopy conductance.

Carbon is released back to the atmosphere by autotrophic respiration (plant) and heterotrophic respiration (organic matter in soil). Autotrophic respiration is separated into maintenance and growth components. Maintenance respiration differs among tissues (e.g. according to C:N ratio of the tissue) and follows a

modified Arrhenius response to temperature (Ryan, 1991, Lloyd and Taylor, 1994). Growth respiration is accounted for by a 25% reduction in the carbon remaining following deduction of maintenance respiration from gross photosynthesis. Heterotrophic respiration refers to the carbon released when organic matter in litter and soil is consumed by heterotrophic organisms, and is regulated by soil moisture and temperature (Lloyd and Taylor, 1994).

### **3.1.2. Carbon allocation and turnover**

The remaining assimilated carbon, after accounting for maintenance and growth respiration and a fixed fractional allocation to reproduction, is allocated to the living tissue compartments (leaf, wood and root) as new biomass following allometric relationships (Shinozaki et al., 1964a, Shinozaki et al., 1964b, Waring et al., 1982, Huang et al., 1992). Allocation is performed at the end of a simulation year.

Carbon enters the soil as litter associated with tissue turnover (e.g. leaf and root shedding) and vegetation mortality. Mortality of individuals is caused by the age of an individual going beyond its mean non-stressed longevity (PFT-specific), growth efficiency (the ratio of individual net annual production to leaf area) dropping lower than a threshold (PFT-specific), climatic conditions becoming unsuitable for survival, allometric failure (assimilated carbon can not satisfy the growth of various compartments of a vegetation individual), anthropogenic disturbance (e.g. harvest and land use change), or natural disturbance (see next section). Part of the litter and soil carbon are decomposed, with the carbon subsequently either respired as CO<sub>2</sub> or transferred to receiving pools with longer residence times. In this thesis, LPJ-GUESS incorporates the CENTURY model (Parton et al., 1993) and inherits its coupled soil C and N scheme (Smith et al., 2014). The structure of the soil pools is illustrated in Figure 3.

### **3.1.3. Disturbance**

LPJ-GUESS incorporates a dynamic representation of disturbances rather than applying turnover constants for vegetation carbon as used in other DGVMs, e.g. IBIS (Foley et al., 1996). Modelled wildfires burn live and dead plants, litter, and carbon in the top soil layers, resulting in the removal of carbon from these pools. The amount, moisture content and flammability of biomass fuels (e.g. litter) control the probability of fires (Thonicke et al., 2001). PFTs differ in their resistance to fire, so that the degree of damage caused to standing biomass depends on the vegetation composition. Additional disturbances (representing ensembles of the other disturbances, e.g. insect outbreaks, windstorms and extreme events) occur at random with a prescribed probability (e.g. 0.01, i.e. interval of disturbance is 100

years), and kill all individuals on an affected patch in a particular year, converting their biomass to litter.

### **3.1.4. Vegetation dynamics**

Vegetation dynamics are associated with the establishment, growth and mortality of individuals which results from disturbance and competition for light, space and soil resources among PFTs. This changes the composition of PFTs in each of the replicate patches over time. In LPJ-GUESS, multiple PFTs are allowed to co-occur in a patch if they can survive under the climate condition of the patch and effectively compete for resources. The carbon storage within each PFT is updated at the end of each year in response to resource competition, allocation, biomass turnover, mortality, establishment and fire. Smith et al. (2001) showed that when LPJ-GUESS incorporated the ‘forest gap’ model FORSKA (Prentice et al., 1993) and implemented individual-based population dynamics, it resulted in more accurate and realistic estimates of PFT dynamics, when compared to the more generalized, area-based approach of the LPJ-DGVM model (Sitch et al., 2003).

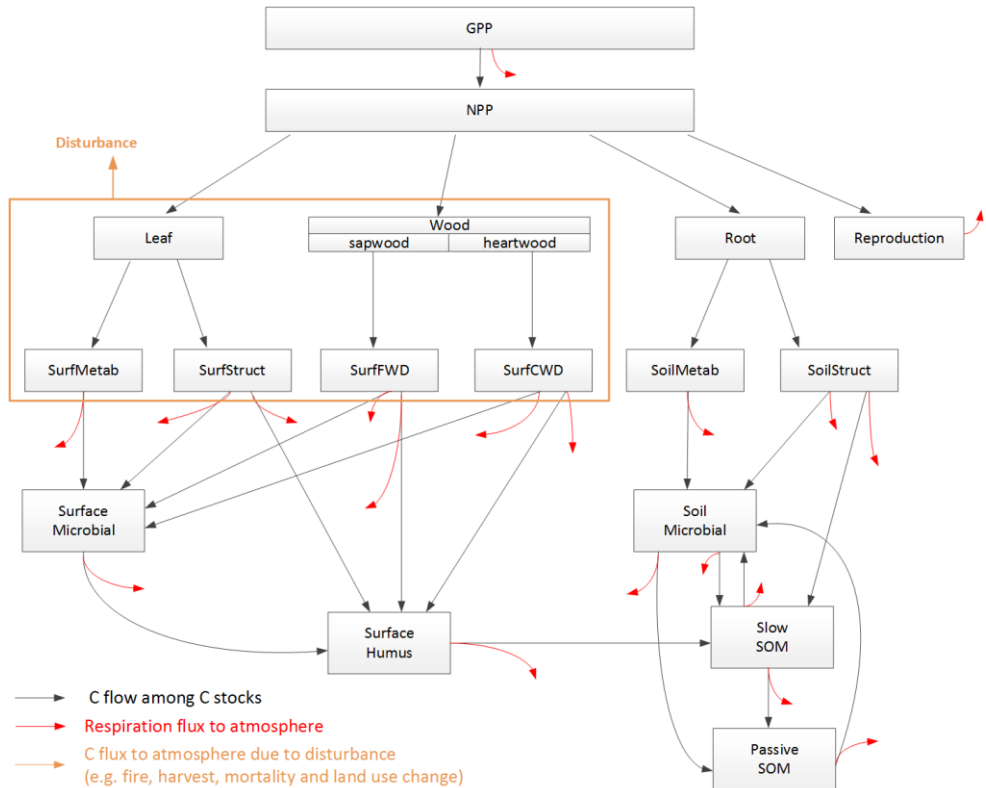
## **3.2. Traceability Framework (TF)**

For most of the process-based global dynamic vegetation models like LPJ-GUESS, their complex carbon cycle among vegetation, litter and soil can be illustrated as in Figure 3. Carbon enters the ecosystem via photosynthesis. Part of the photosynthate is consumed by plant respiration. The rest is partitioned into the growth of leaf, wood and root biomass. Dead plant material is transferred to litter pools. Part of the litter carbon is respired (e.g. decomposed by microbes) and part of it is converted to soil organic matter (SOM) and transferred among soil carbon pools.

The carbon cycle in most DGVMs can be characterized by four fundamental properties (Luo and Weng, 2011):

- the carbon cycle in a terrestrial ecosystem is usually initiated with plant photosynthesis.
- the photosynthetic carbon is first partitioned into various plant pools (i.e., leaf, root, and woody biomass) and then allocated to litter and soil pools after the plant parts die.
- the carbon transfers are dictated by the donor pools.

- the decomposition of litter and soil carbon can be described by first-order decay functions.



**Figure 3.** Schematic representation of the C transfers among multiple pools in the vegetation and soil (including litter) in the LPJ-GUESS model.

These shared properties of carbon cycling among the DGVMs make systematical analysis possible (Luo et al., 2015, Luo et al., 2016), and carbon movements from one pool to another in most DGVMs can be represented by ordinary differential equation in a matrix form (Luo et al., 2003, Xia et al., 2013, Sierra and Muller, 2015, Luo et al., 2017), namely the traceability framework:

$$X'(t) = B(t)U(t) - A(t)\xi(t)KX(t) \quad (1)$$

where  $B(t)$  is a vector of allocation coefficients of the photosynthesized carbon into different plant pools (e.g. leaf, wood and root) at time  $t$ .  $U(t)$  is the photosynthetic input (i.e. NPP or GPP).  $A(t)$  is a matrix of transfer coefficients of carbon exiting from one pool into another pool.  $\xi(t)$  is a diagonal matrix of environmental scalars (e.g. temperature, moisture and nutrient scalars), reflecting the control of physical and chemical properties (e.g., temperature, moisture, nutrients, litter quality and soil texture) on C decomposition.  $K$  is a diagonal matrix of the first-order baseline



turnover rate for plant pools and decomposition rate for litter and soil pools.  $X(t)$  is a vector of carbon pool sizes.  $X'(t)$  is the net change of an individual C pool at time  $t$ .

The traceability framework keeps the structure of C cycling of the DGVMs, and preserves all relative flows between C pools, so that it exactly reproduces the C dynamics of the original models. This framework can help to accelerate model spin-up, quantify the relevant processes' responses to global changes and enable model-data fusion.

### 3.2.1. Steady state

By letting  $X'(t)$  equal zero and transforming the equation (1), i.e.

$$X_{ss}(t) = (A(t)\xi(t)K)^{-1} * B(t)U(t) \quad (2)$$

Xia et al. (2013) decomposed steady state ecosystem C storage ( $X_{ss}$ , the maximum C amount that an ecosystem can potentially store) into two fundamental components: (i) net primary productivity, i.e.  $U(t)$ , and (ii) ecosystem residence time ( $\tau_e$ ), i.e.  $(A(t)\xi(t)K)^{-1} * B(t)$ .  $\tau_e$  is codetermined by the transfer coefficients ( $A$ ), the environmental scalar ( $\xi$ ), the baseline turnover rate ( $K$ ) and allocation coefficients ( $B$ ). This matrix,  $(A(t)\xi(t)K)^{-1}$ , is called redistribution matrix ( $\tau_{ch}$ ), as it measures the time needed for the net C pool change to be redistributed in the network containing all C pools (Luo et al., 2017).

### 3.2.2. Transient dynamics

Luo et al. (2017) further analyzed the determinants and the characteristics of transient dynamics of terrestrial C storage and extended the steady state traceability framework by Xia et al. (2013) to the transient traceability framework. By multiplying both sides of the equation (1) with  $(A(t)\xi(t)K)^{-1}$ , the equation can be transformed to:

$$X(t) = (A(t)\xi(t)K)^{-1} * B(t)U(t) - (A(t)\xi(t)K)^{-1} * X'(t) \quad (3)$$

$$X_p(t) = (A(t)\xi(t)K)^{-1} * X'(t) \quad (4)$$

Combining equation (2-4), the transient traceability framework can therefore decompose modeled transient C storage dynamics into two components, the C storage capacity ( $X_{ss}$ ) and C storage potential ( $X_p$ ).  $X_p$  represents the internal capacity of an ecosystem to equilibrate C input and output for a network of pools, a product of the redistribution matrix ( $\tau_{ch}$ ) and the net change of individual C ( $X'$ ). In this thesis, the transient traceability framework has been implemented for the



### **3.2.4. Improving model capacity**

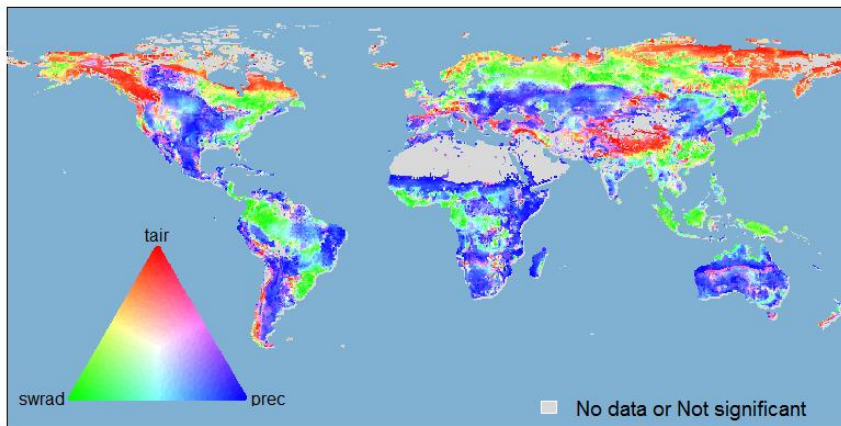
The traceability framework tracks model uncertainty deeply into specific processes or parameters, which can explicitly guide modelers to improve their models. This framework, using matrix representation, enables pool-based data assimilation to be easily applied in ecosystem models. For instance, the capacity of ecosystem models such as the TECO model (Shi et al., 2015, Du et al., 2017) and the CLM-CASA model (Hararuk et al., 2014) in projecting C pool and flux dynamics have been substantially improved via data assimilation using matrix representation of these models. In this thesis, the traceability framework was applied to perform model-data fusion by correcting the model state and/or parameters which by replacing traceable components with observational data (e.g. replacing modeled NPP with observed NPP), can be used for identifying those processes that are poorly represented in the model.

# 4. Results and discussion

## 4.1. Paper I

The choice of published climate dataset has been found to lead to differences in model- based vegetation GPP estimation of about 20% (Jung et al., 2007, Barman et al., 2014). This study illustrated how much each climate variable contributed to the total climate induced uncertainty, and further illustrated the uncertainties associated with the climate data range (uncertainty in the magnitude of the drivers) and the apparent sensitivity of the modeled GPP to the driver (apparent model sensitivity).

The results showed that precipitation dominates climate induced uncertainty in arid regions, and the areas where the uncertainty were dominated by precipitation covers approximately half (~48%) of the terrestrial vegetated land surface (Figure 5). The areas in which the uncertainty were dominated by temperature and shortwave radiation were roughly equal in areal extent and made up the remainder of the terrestrial vegetated surface, with shortwave radiation dominating in moderate to



**Figure 5.** Relative importance of climate factors (red: temperature; blue: precipitation; green: shortwave radiation) to ensemble uncertainty of GPP. Non-vegetated regions and areas with no significant relationship between GPP change and climate change are masked as grey. Among the three drivers, precipitation dominates the climatic uncertainty over the largest area.

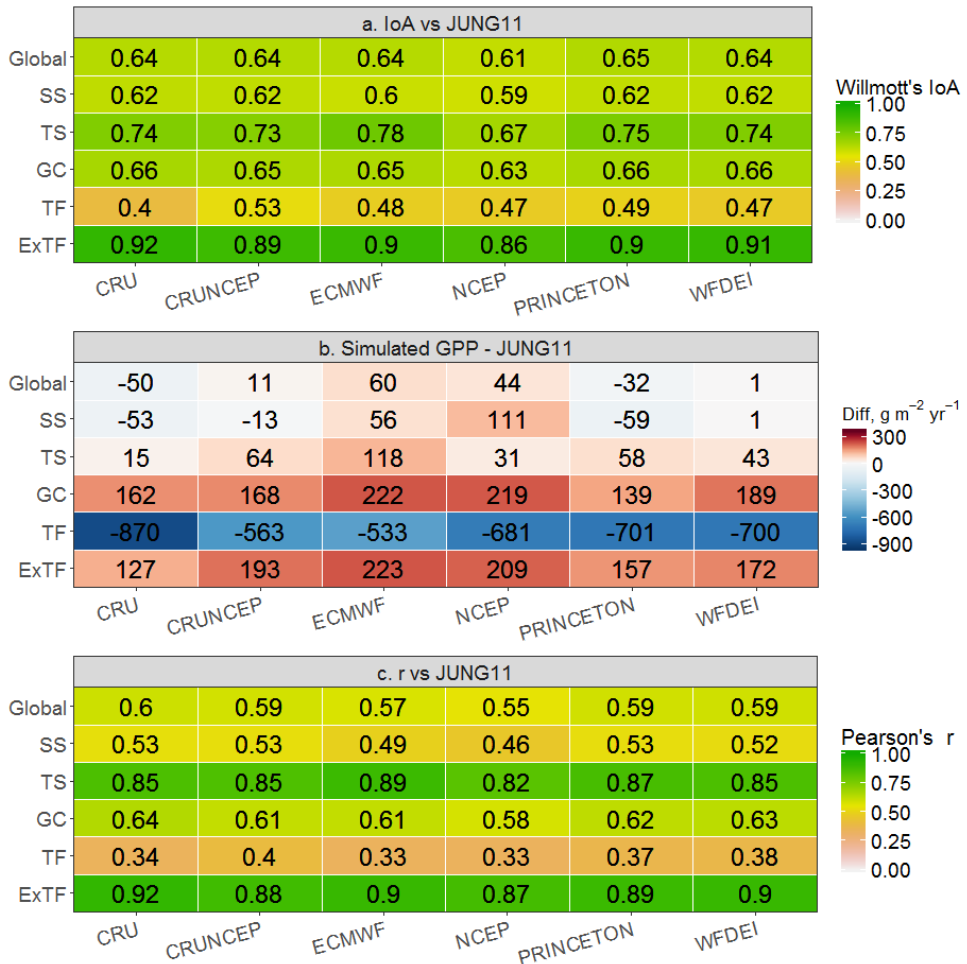
densely wooded ecosystems whereas temperature tended to dominate in high latitude and/or high altitude areas. The tropical regions showed disproportionately large climate induced uncertainty and empirical uncertainty based on observations. Data limitations in the tropics were likely to be an important source of the large spread in estimated GPP. The climate induced uncertainty in tropical forests was most strongly associated with shortwave radiation and precipitation drivers. In addition to data limitations, Jung et al. (2007) suggested that cloud and aerosol physics (which govern precipitation and radiation transfer) are most likely the principal causes of differences in precipitation and radiation estimates between datasets. Overall, the climate data range contributed more uncertainty to simulated global GPP than the sensitivity of the simulated ecosystem processes to climate driver. This implied that uncertainties in the climate datasets played an important role in model-based carbon cycle estimations, and most likely exceeded the importance of shortcomings in ecosystem model structure or parameterization.

This study highlighted the need to better constrain tropical climate (e.g. further develop climate data products) and showed that climatic driver uncertainties must be considered when comparing and evaluating model results and empirical datasets.

## 4.2. Paper II

Uncertainty among different historical climate datasets stems mainly from the source and processing of the raw data. Such gridded climate data are derived either from quasi-point based measurements and subsequent spatial interpolation, model-based reanalysis, or are generated as an observational-reanalysis hybrid. Given the source and manifold methodological differences, it is a challenge to determine whether all datasets are equally reliable or if any of them is better suited for a certain study region or purpose than others, when applying ecosystem models to explore and quantify an ecosystem's response to climate change. This study assessed the impact of six widely used climate datasets on simulated GPP and evaluated the suitability of them for reproducing the global and regional carbon cycle as mapped from independent GPP data.

The results (Figure 6) showed that all datasets tested produced relatively similar GPP simulations at a global scale, corresponding fairly well to the observation-based data with a difference between simulations and observations ranging from -50 to 60 g C m<sup>-2</sup> yr<sup>-1</sup>. However, all simulations also showed a strong underestimation of GPP (ranging from -533 to -870 g C m<sup>-2</sup> yr<sup>-1</sup>) and low temporal agreement ( $r < 0.4$ ) compared with observations over tropical areas and a large overestimation in the non-tropical regions. This indicated that the choice of climate dataset for estimating regional GPP was more critical than when estimating GPP at the global



**Figure 6.** Comparison of monthly index of agreement (IoA), annual mean GPP and monthly temporal correlation during 1982-2010 as estimated by LPJ-GUESS forced by six climate datasets versus the observation-based GPP product JUNG11. Panel (a) shows the IoA, panel (b) shows the average difference and the last panel (c) shows the temporal correlation coefficient between simulated GPP and observations for each land cover class: global; semi-arid ecosystems (SS); tundra and arctic shrub land (TS); grasslands and land under agriculture (GC); tropical forest (TF) and extra-tropical forest (ExTF) including boreal and temperate forest.

scale, since there was a compensation for regional discrepancies between the overestimation in the non-tropics and the underestimation in the tropics.

As the shortwave radiation for tropical areas was found to have the highest uncertainty in the analyzed historical climate datasets, I tested whether simulation results could be improved by a correction of the shortwave radiation dataset for tropical areas using a new radiation product from the International Satellite Cloud Climatology Project (ISCCP). A large improvement (up to 48%) in simulated GPP

magnitude was observed with bias-corrected shortwave radiation, as well as an increase in spatio-temporal agreement between the simulated GPP and observation-based GPP. However, the correction of a given climate variable within a climate dataset should be done with caution, as improving a single variable from a climate dataset may introduce an imbalance in relation to other co-varying climate variables of that dataset. Therefore, I consider it preferable to first select a suitable climate dataset for a study area and then, if deemed necessary, a given variable of this dataset can additionally be bias-corrected.

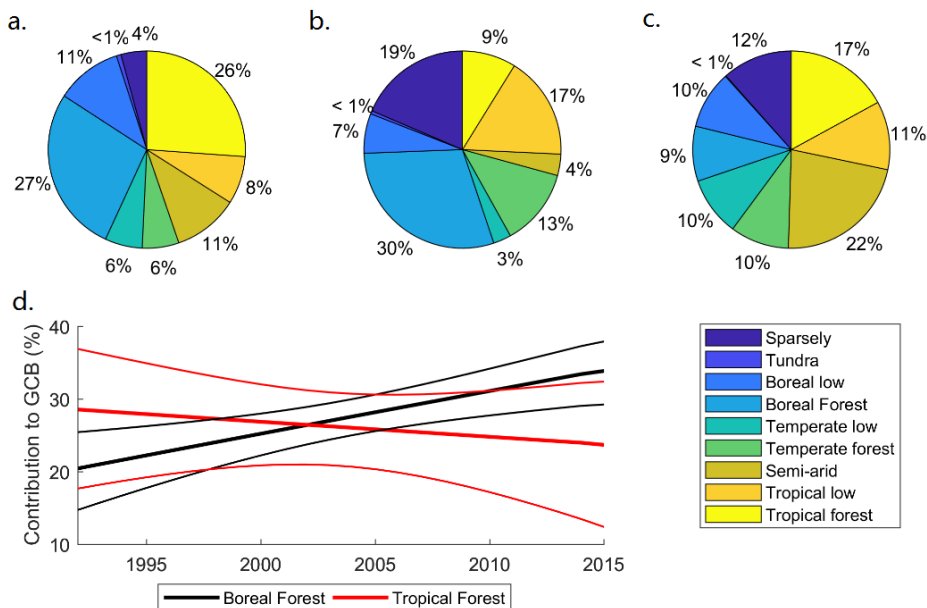
### 4.3. Paper III

The impact of land use and land cover changes (LULCC) on the terrestrial carbon sink during 1992-2015 was analyzed by forcing LPJ-GUESS with a dynamic global land cover product from the European Space Agency (ESA) Climate Change Initiative (CCI). The ESACCI data, derived from state-of-the-art high resolution Earth observation data, showed that the area of tropical forest was reduced by  $4.56 \times 10^5$  km<sup>2</sup> during 1992-2015, which was in line with increasing anthropogenic LULCC in tropical regions, e.g. deforestation, forest degradation and cropland expansion.

The strongest contributors to the mean global terrestrial C sink in 1992-2015 were found to be boreal (27%) and tropical forests (26%) (Figure 7a), and all other biomes had a relatively small contribution (0.8-11%). Boreal forests dominated the contribution to the trend in the terrestrial C sink for 1992-2015 with a 30% contribution (Figure 7b). The evolution of the contribution of different biomes to the terrestrial carbon sink during 1992-2015 (Figure 7d) showed that the contribution of tropical forests declined from 29% to 24%, while the contribution of boreal forests increased from 20% to 33%. The decreasing importance of tropical forests within the terrestrial C sink was due the offset between the sink effect of CO<sub>2</sub> and N fertilization and the release effect of meteorological driver and LULCC causing only a small net change in tropical forest NBP. However, meteorological driver and LULCC played minor roles on the trend in boreal forest NBP compared to CO<sub>2</sub> and N fertilization, resulting in a large sink effect for the boreal forests, which resulted in increased importance of boreal forests within the increasing terrestrial C sink. Semi-arid ecosystems contributed most to the inter-annual variability (22%) (Figure 7c), which is consistent with (Ahlström et al., 2015a) who found the inter-annual variability was strongly associated with circulation-driven variations in both precipitation and temperature.

Although the model output still suggested tropical forests were a net carbon sink, the anthropogenic LULCC decreased the role of tropical forests in contributing to

the terrestrial carbon sink, and boreal forest ecosystems became the most dominant biome contributing to the terrestrial carbon sink.



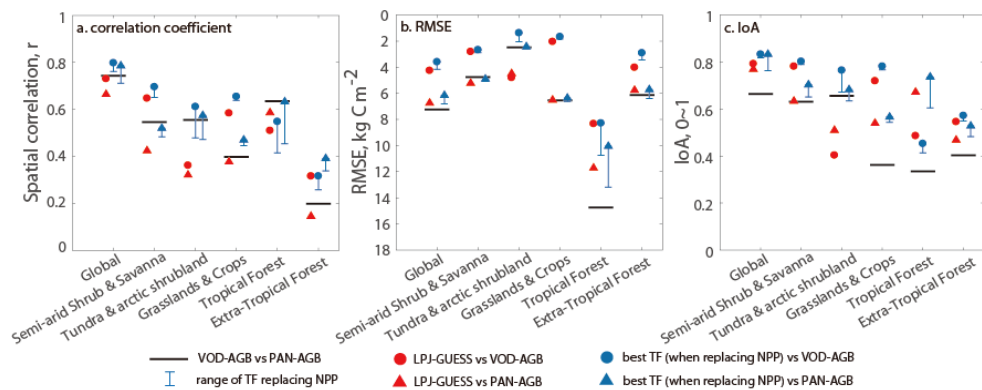
**Figure 7.** Contribution of biomes to the mean, trend and inter-annual variability in the terrestrial C sink. Contributions to: a) the mean; b) trend; and c) inter-annual variability in the terrestrial C sink 1992-2015. d) Average change in contribution to the terrestrial C sink 1992-2015 for the boreal and tropical forests.

#### 4.4. Paper IV

Empirical datasets and models differ in their estimates of carbon influx and turnover, resulting in uncertain and diverging estimates of carbon uptake and storage. Which carbon cycle processes most strongly contribute to model-data disagreement on carbon uptake and storage is currently unknown. Here I used the Traceability Framework (TF; Luo et al., 2003, Xia et al., 2013, Luo et al., 2017) to represent the structure and carbon dynamics of an individual-based dynamic ecosystem model, LPJ-GUESS. The method preserved the model structure and carbon dynamics perfectly in space and time and allowed us to replace model simulated C-influx, vegetation C turnover rate, and soil C turnover rate with empirical datasets and products derived by combining empirical datasets. This study thereby allowed a quantification of the role of C-influx and C turnover on model-data disagreement on C uptake and storage.



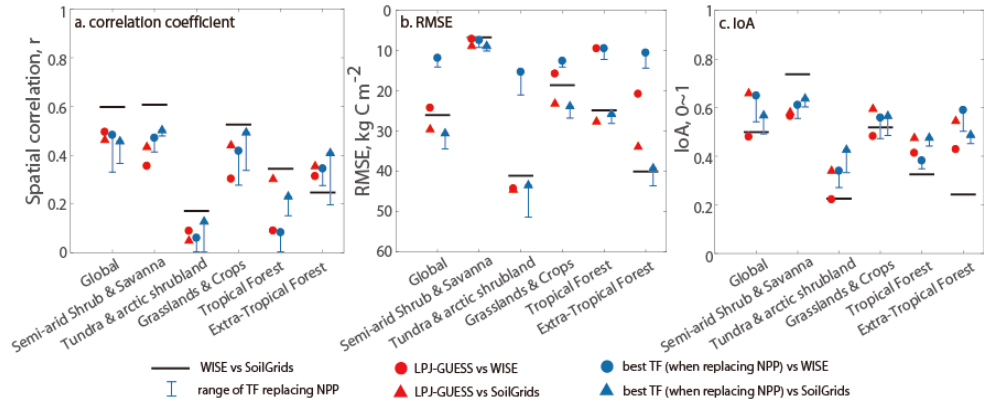
The resulting vegetation and soil C storage and global land C fluxes by TF-realizations (replacing model-simulated C-influx and/or C turnover rates with empirical datasets) were compared to independent empirical datasets. I found small improvements in estimation of aboveground biomass (AGB) (Figure 8) and soil C storage (Figure 9) at the global scale by correcting simulated C influx, with a compensation for regional discrepancies in improvements across global land cover classes. However, fully dynamic simulation and the TF-realizations showed model-data agreements (dots and triangles in Figure 8c and 9c) that exceeded the baseline (the agreement between the two independent empirical datasets, black segments) at the global scale and over most of the land cover classes, suggesting that the increase in agreement should be interpreted with caution due to the limited understanding of the actual conditions (i.e. a rather high uncertainty in one of the independent empirical datasets or both).



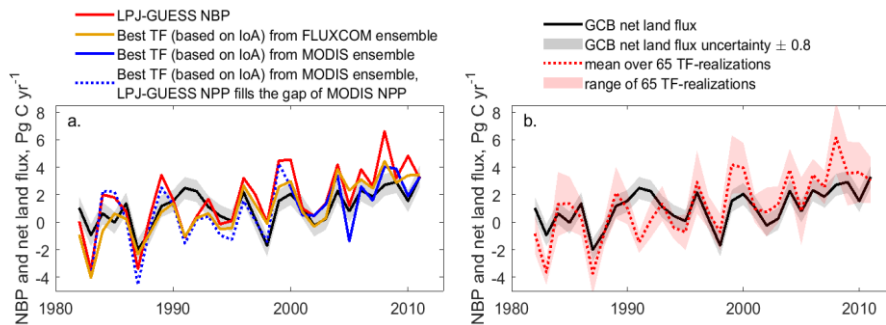
**Figure 8.** Comparison of predicted AGB with two empirical datasets (panel a, b and c) over six land cover classes. Black line segments show the comparison between two independent contemporary empirical datasets of AGB. Output from LPJ-GUESS simulation before replacing NPP is marked in red. TF-realizations by replacing simulated NPP with refined NPP derived from MODIS NPP and FLUXCOM GPP are marked in blue. Error bars show the range of results from replacing simulated NPP with the five refined NPP datasets.

The two empirical datasets of AGB and two datasets of soil C were used to generate apparent turnover rate (here using C-influx instead of C-efflux would have introduced a bias in non-steady state systems, which is referred to as apparent turnover rate), and applied to investigate the role of C turnover rate on model-data disagreement. Correcting simulated vegetation and soil C turnover together with C-influx led to the largest improvement in the agreement between predicted NBP and the GCB net land C flux (Figure 10a). The generally low agreement between contemporary empirical datasets identified here limits our confidence in inferring what processes in the simulated terrestrial C cycle caused the largest share of overall uncertainty. Our results do however indicate that replacing both C-influx and turnover rates with products derived from empirical datasets may lead to large

changes in global NBP (Figure 10b), vegetation (Figure 8) and soil C stocks (Figure 9) in the LPJ-GUESS model.



**Figure 10.** Comparison of spatial soil carbon (representing 2000s) with two independent contemporary empirical datasets (panel a, b and c) over six land cover classes. Black line segments show the comparison between two empirical datasets of soil carbon. Output from LPJ-GUESS simulation before replacing NPP is marked in red. TF-realizations by replacing simulated NPP with the refined NPP derived from MODIS NPP and FLUXCOM GPP are marked in blue. Error bars show the range of results from replacing simulated NPP with the five refined NPP datasets.



**Figure 9.** Global annual net land flux and NBP during 1982-2011. (a) Lines show the temporal pattern of the net land flux derived from LPJ-GUESS (red), the best TF-realization (based on IoA) when using MODIS NPP to correct NPP and C turnover (blue), and the best TF-realization (based on IoA) when using FLUXCOM GPP to correct NPP and C turnover (orange). (b) The red shaded area shows the range of 65 TF-realizations (5 for replacing NPP only, 10 for replacing vegetation turnover, 10 for replacing soil turnover, and 40 for replacing NPP and turnover, including vegetation, soil and both turnovers). The net land flux from GCB in (a-b) is shown in black lines with  $\pm 0.8$  PgC uncertainty range (grey shaded area).

Our analysis suggested that we may be approaching a point where only a marginally improved understanding of land C cycle simulations is gained from comparisons between models and the present generation of global datasets of vegetation and soil C. We concluded that decreased uncertainty in global datasets of vegetation and soil

C would allow valuable global benchmarking of simulated C storage and model-data fusion using global vegetation and soil C datasets.

## 5. Conclusions

In this thesis, a series of model implementations and model evaluations have been conducted, which provides new insights into model uncertainty in term of climate inputs and model structure. The traceability framework (a matrix approach) is introduced to identify the ecological processes contribute most strongly to the model-data mismatch and an attempt to reduce the model-data mismatch by model-data fusion which combines model and data derived from site measurement and remote sensing. The conclusions and responses to the research aims are summarized as follow:

- I. The differences between global climate datasets induce considerable uncertainty (up to 32%) in simulated GPP, and the relative importance of each climate variable to ensemble uncertainty in GPP was demonstrated in a spatially explicit manner. Overall, for a given climate variable, the difference between datasets contributed more to the climate induced uncertainty than the sensitivity of the modeled processes to those differences.
- II. The choice of the climate dataset when estimating GPP at the regional scale was more critical than when estimating GPP at the global scale. Tropical area exhibited large model-data mismatch, which highlighted a need to improve the incoming shortwave radiation estimates of most of the climate datasets tested (except CRUNCEP).
- III. Anthropogenic LULCC decreased the role of tropical forests in contributing to the terrestrial carbon sink, and the boreal forest ecosystem became the biome contributing the most to the terrestrial carbon sink.
- IV. Improving modeling of C-influx (i.e. C assimilation) and C turnover can decrease the model-data disagreement in predicted land carbon storage and dynamics. However, the model-data agreement is at the time of writing comparable or even higher than the agreement between independent empirical datasets, which suggests that improved agreement by model-data fusion should be interpreted with caution due to the limited understanding of the actual conditions driving carbon influx and turnover.

## 6. Future studies

With modelers' increased understanding of ecological processes (e.g. associated with disturbances, land management, vegetation dynamics, and nutrients), more and more processes have been incorporated into ecosystem models resulting in more complex models. The increasing complexity of models raises challenges of identification and quantification of which ecological processes contribute to the divergence between model outputs and observational data. In this thesis I have shown the advantages of the traceability framework in exploring the effects of C-fluxes, vegetation and soil C turnover on terrestrial C storage dynamics. This matrix approach can also trace the deep level of ecological processes, e.g. change of vegetation C turnover can be traced back to tissue turnover, mortality (due to longevity, growth efficiency and bioclimatic limit), fire disturbance and land management. Therefore, this approach can further help diagnose which processes should be explicitly represented in order to improve the model and allow fast feedback between performance evaluation and model development.

With the advent of new techniques in ground-based and satellite-based measurements and observatory networks, we are entering the data abundant era. There is a challenge of how to use these diverse and abundant data for improving ecological understanding and forecasting. One approach is known as data assimilation, one of the model-data fusion methods, which compares model outputs with a particular dataset in order to find optimal parameters and improve the model. Instead of looking for optimal parameters, in this thesis I have shown an example of model-data fusion by replacing traceable components with observational data via the traceability framework, e.g. replacing simulated NPP with observation-based NPP to estimate terrestrial C storage and its annual changes. Similarly, the traceability framework can translate diverse observational data into ecological terms under the model structure, which turns raw data into interpretable information. However, we need to consider the uncertainties in the observational data itself as well, as these uncertainties greatly limit our ability to accurately diagnose and assess the performance of complex models, therefore there is a need for better quality observational data (e.g. low-frequency passive microwaves (L-VOD) products; Brandt et al., 2018).

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