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European ecosystems on a changing planet

Integrating climate change and land-use intensity data

Blanke, Jan Hendrik

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European ecosystems on a changing planet

Integrating climate change and land-use intensity data

JAN HENDRIK BLANKE

DEPARTMENT OF PHYSICAL GEOGRAPHY AND ECOSYSTEM SCIENCE | LUND UNIVERSITY

```
100 phen = 1.0;
101
102 if (summergreen) {
103     // Summergreen PFT - phenology based on GDD5 sum
104
105     if (pft.lifeform == TREE) {
106
107         // Calculate GDD base value for this PFT (if not already known) given
108         // current length of chilling period (Sykes et al 1996, Eqn 1)
109
110         if (pft.gdd0[climate.chilldays] < 0.0)
111             pft.gdd0[climate.chilldays] = pft.k_chilla +
112             pft.k_chillb * exp(-pft.k_chillk * (double)climate.chilldays);
113
114         if (climate.gdd5 > pft.gdd0[climate.chilldays] && aphen < APHEN_MAX)
115             phen = min(1.0,
116                 (climate.gdd5 - pft.gdd0[climate.chilldays]) / pft.phengdd5ramp);
117         else
118             phen = 0.0;
119     }
120     else if (pft.lifeform == GRASS) {
121
122         // Summergreen grasses have no maximum number of leaf-on days per
123         // growing season, and no chilling requirement
124
125         phen = min(1.0, climate.gdd5 / pft.phengdd5ramp);
126     }
127 }
128
129 if (raingreen && wscal < pft.wscal_min) {
130     // Raingreen phenology based on water stress threshold
131     phen = 0.0;
132 }
```



European ecosystems on a changing planet

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Integrating climate change and land-use intensity data

by Jan Hendrik Blanke



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DOCTORAL DISSERTATION

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To be defended at Världen auditorium, Sölvegatan 10, Lund.

Friday, February 2nd 2018 at 10:00 am.

Faculty opponent: Professor Dr. Wolfgang Cramer

Organization LUND UNIVERSITY Department of Physical Geography and Ecosystem Science Sölvegatan 12 SE-223 62 LUND, Sweden		Document name DOCTORAL DISSERTATION	
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Abstract Dynamic global vegetation models are mathematical models that provide a bottom-up description of plant communities. They explicitly model physiological and population-level processes such as growth, photosynthesis, carbon allocation, regeneration and mortality. However, there are a number of challenges to meet in the context of mechanistic vegetation models which can be extrapolated to new environmental conditions. This thesis aims to advance our knowledge of the vegetation model LPJ-GUESS by analyzing both sensitivity and uncertainty towards input datasets such as climate and land-use intensity data and their derivation. It further aims to improve the model performance by including former neglected processes like land-use intensity and daily management for grasslands. Beyond these rather technical aims, this thesis also investigates possible trade-offs between society relevant ecosystem functions like crop yield and carbon storage via integrating climate data and up-to-date land-use intensity information. The results show that simulations with LPJ-GUESS for Europe were most sensitive to the spatial resolution of the input climate data followed by the choice of the climate model. When driven with projections of climate and land-use intensity in form of nitrogen fertilizer, simulations of maize yield and nitrogen leaching were most sensitive to nitrogen applications followed by climate while wheat yield was most sensitive to changes in carbon dioxide followed by nitrogen applications. While future yields of wheat and maize increased in Europe under representative concentration pathways 4.5 and 8.5, these increases were accompanied with increases of nitrogen leaching in many regions. However, leaching decreased in about 53% of the regions under pathway 4.5 while it increased in 76% of the regions under pathway 8.5. It is also shown in this thesis that grassland productivity cannot be adequately captured without including land-use intensity data in form of nitrogen fertilizer. Incorporating daily grassland management and fertilizer applications into LPJ-GUESS improved the model significantly. Finally, afforestation had overall positive effects both on plant species richness and carbon storage in Saxony, Germany. However, a number of locations were identified for which afforestation would lead to a decrease in plant species richness.			
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Date 2017-12-8

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Integrating climate change and land-use
intensity data

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A doctoral thesis at a university in Sweden takes either the form of a single, cohesive research study (monograph) or a summary of research papers (compilation thesis), which the doctoral student has written alone or together with one or several other author(s).

In the latter case the thesis consists of two parts. An introductory text puts the research work into context and summarizes the main points of the papers. Then, the research publications themselves are reproduced, together with a description of the individual contributions of the authors. The research papers may either have been already published or are manuscripts at various stages (in press, submitted, or in draft).

Cover illustration front: Forest in Dalarna, Sweden and LPJ-GUESS source code.

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*Dedicated to my beloved parents,
Carmen & Rainer*

Contents

List of publications	iii
Contributions	iv
Abstract	v
Samanfattning	vii
Zusammenfassung	viii
European ecosystems on a changing planet: Integrating climate change and land- use intensity data	I
1 Introduction	1
1.1 Carbon turnover and the nitrogen cycle	3
1.2 Future environmental change in Europe	5
1.3 Ecosystem models as research tools	6
1.4 Problem statement	7
1.5 Aims and objectives	8
2 Model Description and Driving Data	9
2.1 LPJ-GUESS	9
2.2 Recent development strands	10
2.3 Climate projection data	14
2.4 Land-use intensity	17
3 Results and Discussion	19
4 Conclusion and Outlook	24
5 Acknowledgments	26
6 References	28
Scientific publications	35
Paper I: Effect of climate data on simulated carbon and nitrogen balances for Europe	37
Paper II: Assessing the impact of changes in land-use intensity and climate on simulated trade-offs between crop yield and nitrogen leaching	71
Paper III: Implications of accounting for management intensity on carbon and nitrogen balances of European grasslands	97

Paper IV: Trade-offs between plant species richness and carbon storage in the context of afforestation – Examples from afforestation scenarios in the Mulde Basin, Germany	II9
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List of publications

This thesis is based on the following publications, referred to by their Roman numerals:

- I **Effect of climate data on simulated carbon and nitrogen balances for Europe**
J. Blanke, M. Lindeskog, J. Lindström, V. Lehsten
Journal of Geophysical Research: Biogeosciences 121, 1352-1371

- II **Assessing the impact of changes in land-use intensity and climate on simulated trade-offs between crop yield and nitrogen leaching**
J. Blanke, S. Olin, J. Stürck, U. Sahlin, M. Lindeskog, J. Helming, V. Lehsten
Agriculture, Ecosystems & Environment 239, 385-398

- III **Implications of accounting for management intensity on carbon and nitrogen balances of European grasslands**
J. Blanke, N. Boke-Olén, S. Olin, J. Chang, U. Sahlin, M. Lindeskog, V. Lehsten
Submitted to *PLOS ONE*

- IV **Trade-offs between plant species richness and carbon storage in the context of afforestation – Examples from afforestation scenarios in the Mulde Basin, Germany**
S. Lautenbach, A. Jungandreas, J. Blanke, V. Lehsten, S. Mühlner, I. Kühn, M. Volk
Ecological Indicators 73, 139–155

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Contributions

The author and co-authors mentioned below are abbreviated as follows: Jan Hendrik Blanke (JB), Niklas Boke-Olén (NBO), Veiko Lehsten (VL), Johan Lindström (VL), Ullrika Sahlin (US).

- I Effect of climate data on simulated carbon and nitrogen balances for Europe**
JB adapted the model code and performed simulations. JB conducted the analysis, assisted by VL and JL. All authors contributed to the manuscript while JB led the writing.
- II Assessing the impact of changes in land-use intensity and climate on simulated trade-offs between crop yield and nitrogen leaching**
JB performed simulations and conducted the analysis, assisted by US. All authors contributed to the manuscript while JB led the writing.
- III Implications of accounting for management intensity on carbon and nitrogen balances of European grasslands**
NBO and JB elaborated the model code, JB performed the simulations and conducted the analysis. All authors contributed to the manuscript while JB led the writing.
- IV Trade-offs between plant species richness and carbon storage in the context of afforestation – Examples from afforestation scenarios in the Mulde Basin, Germany**
JB adapted the model code and performed simulations with LPJ-GUESS. JB participated in the writing of the paper and commented on the draft.

Abstract

The world's ecosystems are altered by natural forces which are superimposed by human activities. To understand and project the impact of climate change and human management on ecosystems, the need for tools to monitor and make predictions of the Earth system has increased. Dynamic global vegetation models are mathematical models that provide a bottom-up description of plant communities by explicitly modeling physiological and population-level processes such as growth, photosynthesis, carbon allocation and mortality.

However, these models are still associated with considerable predictive uncertainty. Small differences in model input, parameterization and model design can propagate into the output and create this large uncertainty. Some processes such as land-use intensity are not taken into account in many models, partially due to a lack of harmonized input datasets at larger scales. For future climate input data instead, there is a multitude of climate datasets derived from different general circulation models and carbon dioxide concentration trajectories via different downscaling techniques in order to arrive at different spatial resolutions. This thesis aims to advance our knowledge of the vegetation model LPJ-GUESS by analyzing both sensitivity and uncertainty towards input datasets such as climate and land-use intensity data and their derivation. It further aims to improve the model performance by including formerly neglected processes like land-use intensity and daily management for grasslands. Beyond these somewhat technical aims, this thesis also investigates possible trade-offs between society relevant ecosystem functions like crop yield and carbon storage via integrating climate data and land-use intensity information. These trade-offs are studied for Europe under two representative concentration pathways while a regional study analyzes six afforestation scenarios in the German Federal State of Saxony.

The results show that simulations with LPJ-GUESS for Europe were most sensitive to the spatial resolution of the input climate data followed by the choice of the climate model. There was no notable gain from using regionally downscaled climate in preference to bias-corrected, bilinearly interpolated projections. When driven with projections of climate and land-use intensity in the form of nitrogen fertilizer, simulations of maize yield and nitrogen leaching were most sensitive to nitrogen applications followed by climate while wheat yield was most sensitive to changes in carbon dioxide followed by nitrogen applications. While future yields of wheat and maize increased in Europe under representative concentration pathway 4.5 and 8.5, these increases were accompanied by increases of nitrogen leaching in many regions. However, leaching decreased in about 53% of the regions under pathway 4.5 while it increased in 76% of the regions under pathway 8.5. It is also shown in this thesis that grassland productivity cannot be adequately captured without including land-use intensity data in the form of nitrogen fertilizer. Incorporating daily grassland management and fertilizer applications into LPJ-GUESS improved the model significantly. Finally, afforestation had overall positive effects both on plant species richness and carbon storage in

Saxony. However, a number of locations were identified for which afforestation may lead to a decrease in plant species richness.

Sammanfattning

Ekosystemen i vår värld förändras av naturliga krafter, som i sin tur påverkas av mänskliga aktiviteter. För att förstå och beräkna effekterna av klimatförändringar och mänsklig förvaltning på våra ekosystem har behovet av instrument för att övervaka och förutsäga jordsystemet ökat. Dynamiska globala vegetations modeller är matematiska modeller som tillåter en processbaserad beskrivning av växtsamhällen genom modellering av fysiologiska och populationsprocesser såsom tillväxt, fotosyntes, kolallokering, regenerering och dödlighet.

Men dessa modeller har fortfarande stor osäkerhet i sina uppskattningar. Mindre skillnader i parameterisering och modelldesign kan sprida sig i simuleringsresultaten och orsaka stor osäkerhet. Vissa processer, såsom markanvändningsintensitet, har i många modeller ännu inte beaktats, delvis på grund av brist på harmoniserade ingångsdata i större skala. Istället finns det en rad olika framtida klimatdata som skapats av olika klimatmodeller för olika koldioxid scenarier som kan behöver översättas till högre rumsliga upplösningar med olika metoder. Denna studie syftar till att fördjupa vår kunskap om vegetationsmodellen LPJ-GUESS och liknande modeller genom att bedöma både känsligheten och osäkerheten i ingångsdata som till exempel klimat och markanvändningsintensitet. Utöver dessa mer tekniska mål är syftet med detta arbete att undersöka eventuella kompromisser mellan socialt relevanta ekosystemfunktioner såsom skörd och kolbindning genom integrering av klimatdata och den senaste informationen om markanvändningsintensitet. Dessa kompromisser undersöktes för Europa med hjälp av två representativa koncentrationsvägar, medan en regional studie analyserar sex besöksningsscenarier för Sachsen, Tyskland.

Resultaten visar att simuleringar med LPJ-GUESS för Europa är mest känslig för rumslig upplösning, följt av valet av klimatmodell. Det fanns ingen anmärkningsvärd nytta av att använda regionalt nerskalad klimatdata i motsats till att använda bilinjärt interpolerade och korrigerade data. Om modellen är driven med projektioner av klimat och markanvändningsintensitet (kväve gödsling) är den simulerade majsskörden och kväveläckaget mest känslig för kvävegödsling, följt av klimatet medan veteskoroden är mest känslig för förändringar i koldioxid koncentration, följt av kvävegödsling. Trots att framtida vete- och majsskördar i Europa ökar för scenarierna 4.5 och 8.5, följs dessa av ökande kväveläckage i många regioner. Däremot så minskar dock kväveläckaget för scenario 4.5 i ungefär 53% av regionerna, medan det ökar i 76% av regionerna för scenario 8.5. Denna studie visar också att gräsmarksproduktiviteten i Europa inte kan modelleras på ett tillfredställande sätt utan att använda markanvändningsintensitet i form av kvävegödsling. Inkluderingen av daglig simulerad gräsmarkhantering och kvävegödsling i LPJ-GUESS förbättrar dock modellen avsevärt. Slutligen kan det påvisas att skogsplantering i Sachsen, Tyskland, har övergripande positiva effekter på både växternas mångfald och kollagring. Flera platser har dock identifierats där besöksning leder till en minskning av växtarternas mångfald.

Zusammenfassung

Die Ökosysteme unserer Welt werden durch natürliche Kräfte verändert, welche wiederum von menschlichen Aktivitäten überlagert werden. Um die Auswirkungen des Klimawandels und menschlicher Bewirtschaftung auf unsere Ökosysteme zu verstehen und zu berechnen, ist der Bedarf an Instrumenten zur Überwachung und Prognose des Erdsystems gestiegen. Dynamische globale Vegetationsmodelle sind mathematische Modelle, die eine detaillierte Beschreibung von Pflanzengemeinschaften durch eine Modellierung von Prozessen auf physiologischer- und Populationsebene (z.B. Photosynthese, Pflanzenwachstum und Mortalität) ermöglichen.

Diese Modelle sind jedoch immer noch mit einer beträchtlichen Unsicherheit in ihren Berechnungen versehen. Geringe Unterschiede in der Parametrisierung und Modellgestaltung können sich bis in die Simulationsergebnisse fortpflanzen und so diese große Unsicherheit verursachen. Einige Prozesse wie Landnutzungsintensität werden in vielen Modellen noch nicht berücksichtigt, was teilweise durch einen Mangel an harmonisierten Eingabedatensätzen auf größeren Skalen verursacht wird. Stattdessen gibt es eine Vielzahl an Klimadatensätzen, die von verschiedenen Klimamodellen für verschiedene Klimaszenarien erstellt wurden und die mit unterschiedlichen Methoden auf eine höhere räumliche Auflösung umgerechnet werden können. Diese Studie zielt darauf ab, unser Wissen über das Vegetationsmodell LPJ-GUESS und ähnliche Modelle voranzutreiben, indem sie sowohl die Empfindlichkeit als auch die Unsicherheit hinsichtlich der Eingabedatensätze wie z.B. Klima und Landnutzungsintensität analysiert. Jenseits dieser eher technischen Ziele soll diese Arbeit auch mögliche Kompromisse zwischen gesellschaftsrelevanten Ökosystemfunktionen wie Ernteertrag und Kohlenstoffspeicherung durch die Integration von Klimadaten und neusten Informationen zur Landnutzungsintensität untersuchen. Diese Kompromisse werden für Europa anhand von zwei repräsentativen Konzentrationspfaden untersucht, während eine regionale Studie sechs verschiedene Aufforstungsszenarien im Bundesland Sachsen in Deutschland analysiert.

Die Ergebnisse zeigen, dass Simulationen mit LPJ-GUESS für Europa am empfindlichsten auf die räumliche Auflösung reagierten, gefolgt von der Wahl der Klimamodelle. Es gab keinen bemerkenswerten Gewinn bei der Verwendung von regional herunterskalierten Klimadaten im Gegensatz zu bilinear interpolierten und korrigierten Projektionen. Wurde das Modell mit Klima- und Landnutzungsintensitätsprognosen in der Form von Stickstoffdünger verwendet, reagierten die Simulationen von Maisertrag und Stickstoffversickerung am empfindlichsten auf die Stickstoffanwendungen (gefolgt von Klima), während Weizenertrag am empfindlichsten gegenüber Veränderungen in der Kohlenstoffdioxidkonzentration war (gefolgt von den Stickstoffanwendungen). Auch wenn zukünftige Erträge von Weizen und Mais in Europa unter Szenario 4.5 und 8.5 anstiegen, so wurden diese Erhöhungen doch durch zunehmende Stickstoffversickerung in vielen Regionen begleitet. Allerdings sank die

Versickerung in ungefähr 53% der Regionen unter Szenario 4.5, während sie in 76% der Regionen unter Szenario 8.5 anstieg. Diese Studie zeigt zudem, dass die Produktivität von Grasländern in Europa nicht ohne die Verwendung von Daten zur Landnutzungsintensität in Form von Stickstoffdüngung ausreichend erfasst werden kann. Die Einbeziehung von täglich simulierter Graslandbewirtschaftung und Düngieranwendung in LPJ-GUESS verbesserte das Modell deutlich. Zum Schluss konnte gezeigt werden, dass eine Aufforstung in Sachsen, Deutschland, insgesamt hauptsächlich positive Effekte sowohl auf Pflanzenartenvielfalt als auch Kohlenstoffspeicherung erzielte. Es wurden jedoch auch mehrere Standorte identifiziert an denen eine Aufforstung zu einer Verringerung des Pflanzenartenreichtums führen kann.

European ecosystems on a changing planet: Integrating climate change and land-use intensity data

I Introduction

The Earth system has always undergone a continuous change. In the past, the primary drivers of global environmental change have been essentially solar variation, plate tectonics, volcanism, meteorite impact and changes in the Earth's orbit and tilt on its axis. Today, it has an additional pressure which forces change: human activities. The magnitude of the human footprint has become so large that humanity is now a pressure equivalent to some of these important forces of nature. This has led scientists to suggest that Earth has left its previous geological epoch, the Holocene, and has now entered a new one called the Anthropocene (Steffen et al., 2011; Vince, 2011). There is overwhelming scientific evidence that the main driver of global environmental change at present is the growing human population and its demand for food, energy, goods and services as well as its disposal of waste products. It is not surprising that since 1700, the land area devoted for crop production has increased by 466% and now accounts for 10-20% of the ice-free terrestrial surface (Ellis and Ramankutty, 2008) (see Fig. 1). In the last 250 years, global environmental change has caused society-relevant problems such as climate change, extinction of animal species, the collapse of fisheries, desertification, ocean acidification and pollution.

In a nutshell, the world's ecosystems are altered by natural forces which are superimposed by human activities. The distribution of species and the structure and functioning of whole ecosystems is primarily driven by climate, environmental factors such as photosynthetically active radiation, temperature, carbon dioxide concentration ($[CO_2]$) and human management. The responses of organisms to their specific environment are fundamental owing to their significant economic, ecological and cultural services. Understanding the provisioning of these services as well as projecting their changes for the next decades is crucial

for a concerted response to environmental change. To understand and project the impact of climate and atmospheric changes as well as human management on ecosystems, the need for tools to monitor and make predictions of the Earth system has increased. In addition to ground- and satellite-based observations, numerous modeling techniques have been developed to link different types of observation data. While statistical models base on empirical relationships, dynamic global vegetation models (DGVMs) provide a bottom-up description of plant communities. They explicitly model physiological and population-level processes such as photosynthesis, growth and regeneration. This makes it possible to simulate the effects of future climate change on vegetation and the biogeochemical cycles including carbon turnover and the nitrogen cycle.

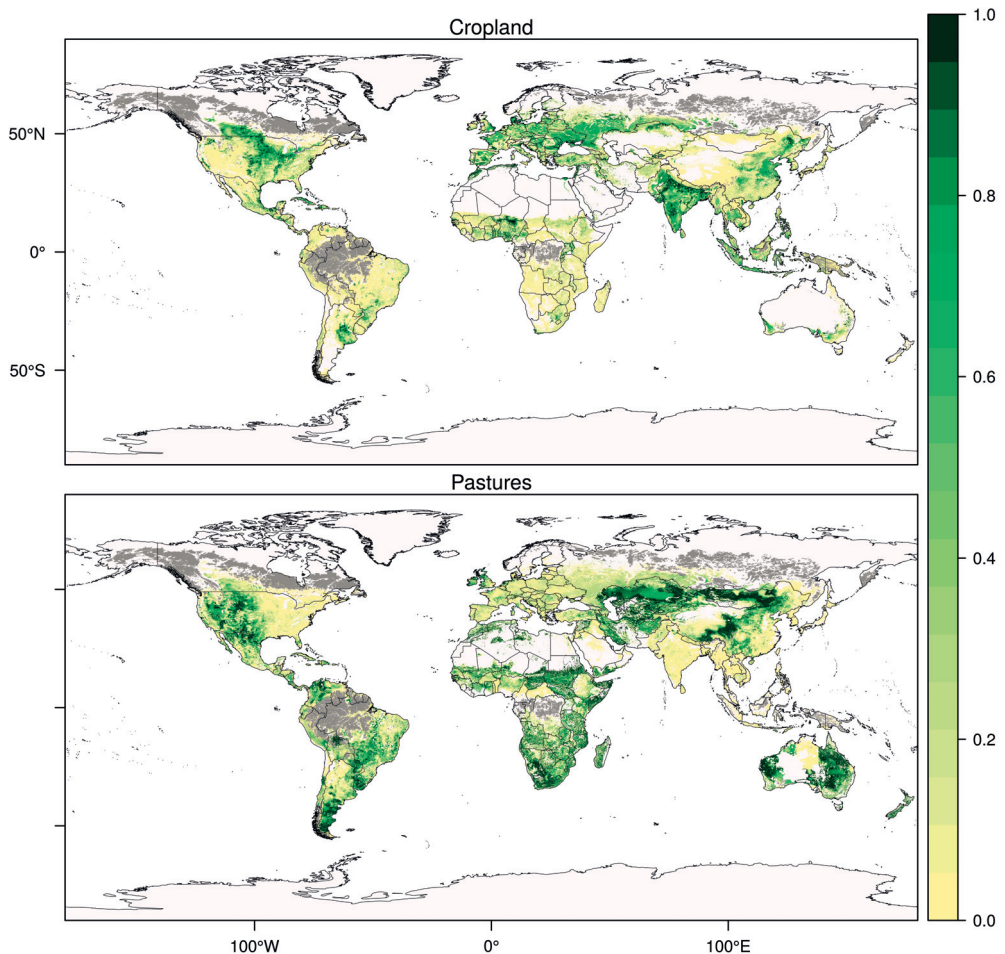


Figure 1: Cropland and pasture fractions within each 5 arc minute grid cell (data from: Ramankutty et al., 2008). Intact forest landscapes are indicated in gray (data from: Potapov et al., 2008).

1.1 Carbon turnover and the nitrogen cycle

Carbon turnover

Carbon (C) is the most important element for life and a very central one in all organic compounds. While the amount of C on Earth today is the same as 4.5 billion years ago when the Earth was formed, its distribution has changed over time. Today, C is distributed among four major pools: the atmosphere, ocean, terrestrial ecosystems (vegetation and soil) and sediments and rocks (geological reservoir). Thereby, most C is stored in the geological reservoir in sedimentary rocks deep within the planet's crust. Together all sedimentary rocks on Earth store about 60,000,000 petagrams (Pg) C (Chapin et al., 2011). The second largest pool is the ocean with 38,000 Pg C, which is mostly stored in deep water where it resides for long time periods. The terrestrial ecosystems of the world contain C in the form of plants, animals, soils and microorganisms and most C is stored in the world's soils, with an estimated amount of 2,500 Pg C (Stockmann et al., 2013). The amount of C in vegetation (650 Pg C) is similar to that in the atmosphere (Chapin et al., 2011). However, the ratio between soil and vegetation C is different according to the biomes of the world. In tropical forests, C stored in soils is equal to the amount stored in standing biomass, whereas in boreal forests, there is five times more C in soils than in vegetation and in wetlands, there is up to 15 times more soil C than vegetation C (Ciais et al., 2013). Even though atmospheric C, which primarily consists of CO₂, is the smallest pool, it is the most dynamic one. There is a constant cycling of C between the atmosphere and the biosphere. It turns over every five years, and every year, approximately 15% of the atmospheric CO₂ is taken up by terrestrial ecosystems via photosynthesis (Ciais et al., 2013). The total amount of C fixed in the process of photosynthesis by plants in an ecosystem is termed gross primary production (GPP) and amounts to 120 gigatonnes (Gt) C yr⁻¹. Around 50% (60 Gt C yr⁻¹) is immediately returned to the atmosphere as a result of plant autotrophic respiration (R_a) due to the costs of biomass accumulation and maintenance of vital functions such as the rebuilding of proteins. The net amount of C left after autotrophic respiration, net primary production (NPP), is then the biomass accumulated in leaves, stems, roots, flowers or seeds. Via litter production, a large fraction of NPP is turned into soil organic matter (SOM). Microbes and other soil biota decompose SOM and return most of the NPP to the atmosphere (50 Gt C yr⁻¹) through heterotrophic respiration (R_h). Whenever NPP is larger than R_h , an accumulation of C takes place. This is especially the case in cold areas since SOM turnover is mainly driven by soil temperature (besides water availability). Not surprisingly, a large portion (1700 Pg C) of the total soil C (2500 pg C) is estimated to be locked in the permafrost regions of the northern hemisphere (Tarnocai et al., 2009).

Human activities are now a significant component of the global C cycle. They have resulted in the removal of C from C deposits (such as oil and coal deposits) and added it directly to the atmosphere. This has been most notable since the 18th and 19th century when the

industrial revolution took place. In addition to the burning of fossil fuels, land-use and land cover change is another anthropogenic activity that influences the C cycle. Through forestry and agriculture, humans have transformed natural and often C-rich ecosystems to managed lands such as agricultural fields and plantations. In recent years, emissions from the combustion of fossil fuels amount to 8.7 Pg year^{-1} while land-use conversion releases another 1.5 Pg year^{-1} via biomass burning and enhanced decomposition (Canadell et al., 2007). Together, these anthropogenic C fluxes are about 15% of the C cycled by terrestrial or marine production, making human C emissions the third largest biologically controlled flux of C to the atmosphere. Because of the cyclical nature of the C cycle, the impacts humans have can lead to numerous amplifications and feedbacks. Increasing atmospheric concentrations of CO_2 and methane (along with other greenhouse gases) cause higher global air temperatures which in turn increases decomposition and R_h in soils, thereby releasing more CO_2 to the atmosphere. However, high $[\text{CO}_2]$ can also have positive effects on plant productivity since CO_2 is the primary substrate in the process of photosynthesis. Additionally, plants can operate at higher stomatal conductance which makes water usage more efficient. Simulations with an ensemble of several DGVMs suggest that increasing atmospheric $[\text{CO}_2]$ led to an increase in global annual GPP of $18 \pm 2 \text{ Pg C}$ since 1900 (Keenan et al., 2016). While the terrestrial C sink seems to be increasing, the mechanisms responsible for its enhancement, and implications for the growth rate of atmospheric CO_2 , remain unclear.

Nitrogen cycle

The productivity of many ecosystems on land is limited in part by the supply of available nitrogen (N). N is one of the main chemical elements required for plant growth and reproduction. In addition to light and water availability, it is the most important limiting factor in many terrestrial ecosystem (e.g. Townsend et al., 1996). N is a component of chlorophyll and hence essential for photosynthesis. It is also the basic element of plant and animal proteins, including the genetic material DNA and RNA, and is important in periods of rapid plant growth. N limitations reduce the production of Rubisco (an enzyme involved in C fixation) and chlorophyll, resulting in a lower maximum carboxylation rate and reduced photosynthesis. Almost all N relevant to biogeochemistry is contained in one single pool (the atmosphere), while organic N pools are very small relative to the atmospheric pool and occur mainly in soils and terrestrial vegetation. N makes up 78% of the atmosphere as N_2 and is unavailable to most organisms owing to the very strong triple bond between the atoms. However, N_2 can be transformed into biologically available forms via N fixation by a limited number of species of bacteria and archaea in soils or living in symbiosis with plants. Annually, approximately 120 teragrams (Tg) N are fixed by the biological fixation on a global scale (Galloway et al., 2004). Before human alteration, N fixation was roughly balanced by returns to the unavailable pools via denitrification and burial in sediments. In

general, N is cycled quite tightly within terrestrial ecosystems, with the annual throughput often being at least fourfold greater than inputs and losses (Chapin et al., 2011). N can be taken up by plants and soil organisms as a chemically available form such as ammonium (NH_4^+), nitrate (NO_3^-), or organic N (e.g. urea) to be incorporated into proteins and other organic N compounds. After N is incorporated into organic matter, it is often turned back into inorganic N by N mineralization via decomposers (such as bacteria and fungi). During this process, a significant amount of N contained within the dead organism is converted to ammonium. Once in the form of ammonium, N is available for use by plants or further transformation into nitrate through the process called nitrification. Through denitrification, oxidized forms of N such as nitrate and nitrite (NO_2^-) are converted to nitrous oxide (N_2O) and finally dinitrogen (N_2). Nitrous oxide is an important greenhouse gas contributing substantially to global climate change.

In the past century, human activities have roughly doubled the amount of N fixed from the atmosphere using the Haber-Bosch process. The Haber-Bosch process uses energy from fossil fuels to convert N_2 to NH_3 to produce fertilizers. This way, humans have been able to overcome the N-limitations in agriculture. These processes, together with the additional NO_x , which are by-products of combustion, have dramatically altered the N cycle of our planet. The massive N additions to terrestrial ecosystems in the form of N deposition, fertilization, food imports and growth of N-fixing plants have led to a dramatic increase in N concentrations in surface and ground waters over the past century. The augmented addition of N in the environment has various effects; it can change the composition of species and may cause different health effects in humans and animals.

1.2 Future environmental change in Europe

Future changes in climate and land-use and consequentially biodiversity depend strongly on the future trajectory of human development and politics. However, as for climate, many studies summarized by the International Panel on Climate Change (IPCC) agree on specific general trends. In northern Europe, agricultural productivity may increase due to a longer growing season and an extension of the frost-free period. Warmer temperatures and longer growing seasons may also allow for cultivating new crops. In southern Europe instead, both extreme heat events and reductions in precipitation can be expected to hamper crop productivity. Large variations in crop yields from year to year are also more likely due to extreme weather events and other factors such as pests and diseases. Soil moisture is projected to decrease in continental areas due to higher temperatures and insufficient increases of rainfall. This is especially meaningful in important areas for agriculture, such as the Ukraine, as they may be particularly prone to future drought. In addition to heat waves and droughts, human-induced climate change has the potential to alter the prevalence and severity of other extreme events such as storms and floods. Extreme weather changes may

increase the severity of diseases for animals and humans while heat waves may also increase forest fires. Finally, climate change may increase the number of global climate refugees from 150 million in 2008 to 800 million in the future.

While a tremendous amount of work has been done on how climate might change for Europe (as reviewed and assessed by the IPCC), there are only a few ideas and projections on how land-use and land-use intensity may change in Europe and land management change remains understudied (Erb et al., 2013). Stürck et al. (2015) combined the results of multimodel simulations in the agriculture and forest sectors for four scenarios from 2000 to 2040. In general, future changes are quite diverse across scenarios which differ in their degree of regionalization versus globalization, as well as in the extent of policy intervention. However, based on their study, there are also common patterns in the land change trajectories among the scenarios considered. An intensification of forest management can be expected in southern Sweden, parts of the Czech Republic and Slovenia. An intensification of cropland and pastures may take place in eastern Europe, including eastern Germany, and regions in Poland, Czech Republic and Romania. A de-intensification of cropland and pastures instead can be expected mostly in parts of France, Portugal and the United Kingdom. An expansion of wild areas and forests can be allocated to more southern Europe, including northern parts of Spain, the Alps, Italy and Greece. The future fate of biodiversity and ecosystem services in turn will depend on the combination of the aforementioned future changes in climate and land-use and land-use intensity.

1.3 Ecosystem models as research tools

Dynamic global vegetation models – DGVMs – are mathematical models of terrestrial ecosystems that provide process-based explanations of the responses of plants to environmental conditions and competition as well as important ecosystem functions (such as NPP and heterotrophic respiration). Ecosystem models are constructed from ecological relationships, such as the relationship between sunlight and photosynthetic rate, which are in turn derived using data gathered from the field or laboratory experiments. The ecological relationships, expressed via mathematical equations, are combined in a computer program which can be run given specific parameter values and input data (see Fig. 2). These model systems may then be studied in order to make predictions about the dynamics of the real system.

DGVMs were initially developed to investigate the role of the terrestrial biosphere within the global C cycle, including climate feedbacks and understanding and reproducing the exchange of matter and energy in ecosystems. They are also an important tool for assessing the regional impact of climate variability and change on vegetation dynamics and allow predictions of ecosystem states in the future. Vegetation models such as IBIS (Foley and Prentice, 1996), BIOME4 (Kaplan, 2003), LPJ (Sitch et al., 2003) and CENTURY (Parton

```

82  }
83  } // END DAILY allocation niklas
84
85  phen = 1.0;
86
87  if (summergreen) {
88
89      // Summergreen PFT - phenology based on GDD5 sum
90
91      if (pft.lifeform == TREE) {
92
93          // Calculate GDD base value for this PFT (if not already known) given
94          // current length of chilling period (Sykes et al 1996, Eqn 1)
95
96          if (pft.gdd0[climate.chilldays] < 0.0)
97              pft.gdd0[climate.chilldays] = pft.k_chilla +
98              pft.k_chillb * exp(-(pft.k_chillk * (double)climate.chilldays);
99
100         if (climate.gdd5 > pft.gdd0[climate.chilldays] && aphen < APHEN_MAX)
101             phen = min(1.0,
102             (climate.gdd5 - pft.gdd0[climate.chilldays]) / pft.phengdd5ramp);
103         else
104             phen = 0.0;
105     }
106 } else if (pft.lifeform == GRASS) {
107
108     // Summergreen grasses have no maximum number of leaf-on days per
109     // growing season, and no chilling requirement
110
111     phen = min(1.0, climate.gdd5 / pft.phengdd5ramp);
112 }
113 }
114 }
115
116 if (raingreen && wscal < pft.wscal_min) {
117
118     // Raingreen phenology based on water stress threshold
119     phen = 0.0;
120 }
121 }

```

Figure 2: Example of computer code inside LPJ-GUESS.

et al., 1993) have greatly improved our ability to understand the response of terrestrial vegetation to past and future environmental variation at global-to-regional scales. Up to date DGVMs which include human management and N processes are designed for the consistent quantification of multiple drivers (climate, CO₂, land management, land-use change) on the future provision of ecosystem services such as food, fiber and energy crops, climate regulation and water purification.

1.4 Problem statement

While terrestrial ecosystem models are constantly improving, there are limitations of constraining all necessary parameters and processes. Even though many processes in DGVMs are relatively well understood, small differences in parameterization and model design can create large uncertainty. This uncertainty has been reported early on (Cramer et al., 2001) and is unlikely to have been reduced by the newer generation of DGVMs. Recent progress in land-use intensity projections for croplands makes it now possible to force LPJ-GUESS with climate data as well as N application projections conjointly. However, the quantitative contributions of the drivers climate, CO₂ and N applications for projections of crop processes are not known yet. While land-use intensity in the form of N application has been included recently for croplands, pasture productivity is still driven mainly by climate and soil properties. Nonetheless, recent developments in LPJ-GUESS now provide the capacity

of simulating changes in C and N pools and fluxes considering hindcasts and projections of land-use, climate and land-use intensity. This makes it feasible to combine LPJ-GUESS with for example biodiversity models in order to investigate the effect of different scenarios on ecosystem functions and services such as C storage and plant biodiversity.

1.5 Aims and objectives

The aims and objectives of this thesis are to:

- (i) Analyze the sensitivity of LPJ-GUESS towards different climate and land-use intensity drivers
- (ii) Assess the incorporation of land-use intensity and daily management for pastures
- (iii) Investigate possible trade-offs between society-relevant ecosystem functions under different climate and management scenarios

2 Model Description and Driving Data

2.1 LPJ-GUESS

The LPJ-GUESS DGVM (Smith et al., 2001; Sitch et al., 2003) is a flexible framework for modeling the structure and dynamics of terrestrial ecosystems at landscape or global scale. It contains numerous ecosystem process formulations which are organized in modules according to relatedness and characteristic spatial and temporal scale. Fast processes such as photosynthesis and regulation of stomata are simulated on a time step of one day while slow processes like C allocation and tree growth are implemented once each simulation year (see Fig. 3). The input data to the core framework consists of monthly or daily climatic variables like incoming radiation/sunlight, temperature and precipitation, atmospheric CO_2 , N deposition and soil properties. The considered ecosystem processes change state variables such as NPP, leaf area index (LAI) or soil water availability which often translate to the output data. Simulations are usually performed across a grid made up of adjacent grid cells which are modeled independently without interactions of neighboring cells. For each grid cell, the simulation flow may follow up to three phases: spinup, historical phase and scenario phase. During the spinup phase, the modeled vegetation, litter and C pools are supposed to accumulate and reach an equilibrium with the climate by starting from “bare ground” and using detrended climate data from the first few years of the historical climate dataset. The spinup phase normally takes 1000 years after which it gives way to the historical phase. Here, the model reads in observed climate and CO_2 data derived by interpolations from climate station data. If model projections into the future are intended, the simulation for each grid cell ends with a scenario phase in which future climate change is considered. Climate input data originates thereby from one of various available coupled atmosphere-ocean general circulation models (GCMs) which quantitatively simulate the climate system.

LPJ-GUESS simulates the development of land vegetation with an individual- and patch-based approach (cohort vegetation mode) which sets it apart from the LPJ DGVM. In cohort mode, vegetation populations and their dynamics are described in more detail with formulations of plant competition for resources and light as well as demography inherited from dynamic forest models (“gap models”). The growth of individuals is thereby simulated within a number of replicate patches which correspond in size approximately to the maximum area of influence of one large adult individual on its neighbors. As one grid cell is normally represented by up to 100 patches (each 0.1 ha in size), stochastic processes such as establishment, mortality and disturbances lead to different dynamics in the specific patches. Over many patches, however, the modeled variables converge on a single average value. For global simulations, species are typically grouped into eleven plant functional types (PFTs) that represent a number of species with similar ecological properties, bioclimatic limits, growth form, phenology and life history strategy. For Europe, the 20 most dominant tree species have been parameterized by Hickler et al. (2012). Recently, C-N

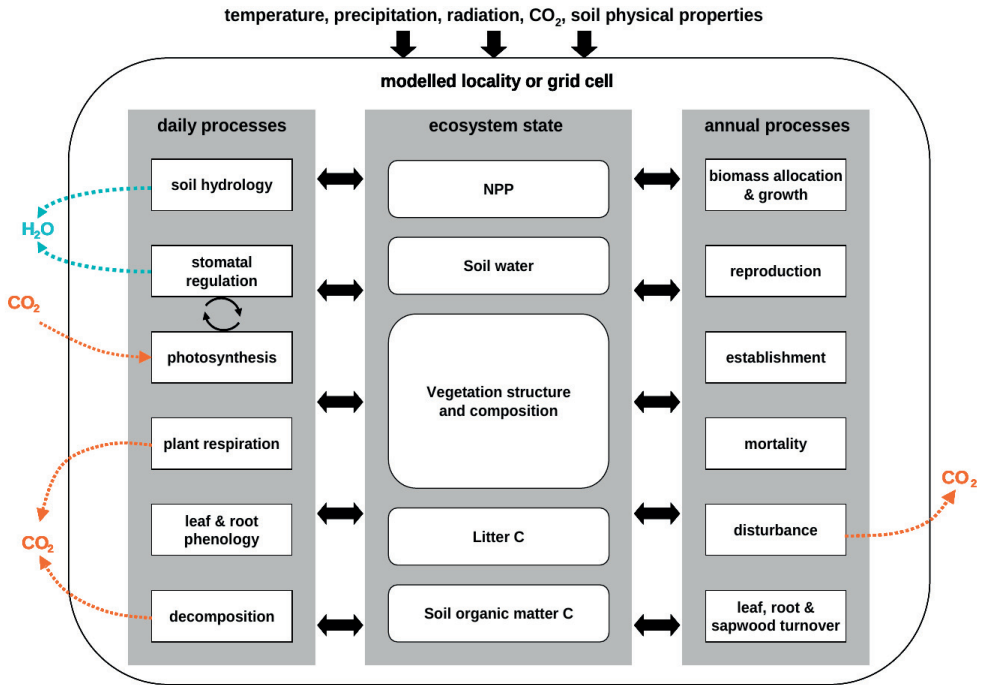


Figure 3: Schematic overview of LPJ-GUESS (C-only).

coupling was incorporated into LPJ-GUESS for potential natural vegetation (Smith et al., 2014; Wärlind et al., 2014). LPJ-GUESS incorporates a detailed representation of land-use and cropland (Lindeskog et al., 2013), simulating generic crop functional types (CFTs) that represent the most widely-grown crop species globally and their fractions explicitly given by land-use input. The LPJ-GUESS model has been evaluated extensively and has demonstrated skill comparable to other approaches in capturing dynamics of the terrestrial C cycle (Morales et al., 2005; Sitch et al., 2015).

2.2 Recent development strands

DGVMs were initially developed to investigate the role of the terrestrial biosphere within the global C cycle, considering potential rather than actual vegetation. They incorporated neither human land management, agricultural areas and land-use and land cover (LULC) changes nor the N cycle. However, recent development strands are now addressing more advanced large-area representations of managed ecosystems including explicit simulations of agricultural and forest management under consideration of the N cycle. The N cycle is of great importance in this context since the N cycle constraints on NPP produce lower and more realistic estimates of future C storage while improving the predictions of the influence

of soil nutrients status control on PFT distribution. Finally, the N cycle is also important for assessing the impacts of anthropogenic N additions on the C cycle and ecosystems.

Nitrogen cycle

Despite being a significant factor influencing vegetation growth and C cycling in the ecosystem, only a few of the current DGVMs include a full and interactive N cycle which takes into account the below-ground controls on N mineralization and N limitations on NPP. The lack of the N cycle in many DGVMs poses an important source of uncertainty as they don't account for the constraint imposed on the production of new biomass by the plant-available pool of N. To account for this uncertainty, the N cycle has been implemented very recently in LPJ-GUESS by Smith et al. (2014) and Wårlind et al. (2014). In these studies, three model components have been elaborated to allow incorporating the N cycle: (i) a new structure for soil organic matter (SOM) which enables representing N dynamics in both inorganic and organic soil systems, (ii) a scheme for plant N allocation, demand, uptake, stress etc., (iii) ecosystem N fluxes. In the following, the implementation of the N cycle in LPJ-GUESS is described (see Fig. 4).

N enters the ecosystem via N deposition (combination of wet and dry deposition) as well as biological N fixation. Thereby, N deposition is prescribed as monthly mean values from an external database (Lamarque et al., 2010, 2011) while biological fixation is estimated as a dynamic function of ecosystem evapotranspiration (Cleveland et al., 1999). Both N sources are distributed to a pool of mineral N, N_{avail} , which is available to both plants (via root uptake) and soil microbes. N leaves the ecosystem via leaching (computed daily as the sum of leached soluble organic N and leached mineral N) as well as via volatilization by wildfires. Additionally, 1% of daily N mineralization is lost into the atmosphere from soils. Soluble organic N leaching is computed from percolation and soil sand fraction while mineral N leaching depends on percolation (calculated daily) as a fraction of available soil water content. C and N dynamics of soils are simulated conjointly by a SOM module that has been adopted from the CENTURY model, a general model of plant-soil nutrient cycling (Parton et al., 1993, 2010). Soil C and N is transferred between eleven different pools of this SOM module, each having its own specific C:N stoichiometry and base decay rate. Daily decomposition for each pool results in heterotrophic respiration as well as a transfer of C and N between pools (this way satisfying mass balance). Plants acquire N each simulation day through root uptake from the soil mineral pool N_{avail} to allocate it to leaves, fine roots and sapwood for woody PFTs. The demand of N is thereby driven by the optimal leaf N content which is computed as a linear function of the carboxylation capacity of Rubisco (V_{max}) that maximizes canopy-level net photosynthesis (given current temperature, light interception, and intercellular CO_2 concentration (following Haxeltine and Prentice, 1996)). N demand for allocation to plant growth in other tissues follows leaf N; it conserves

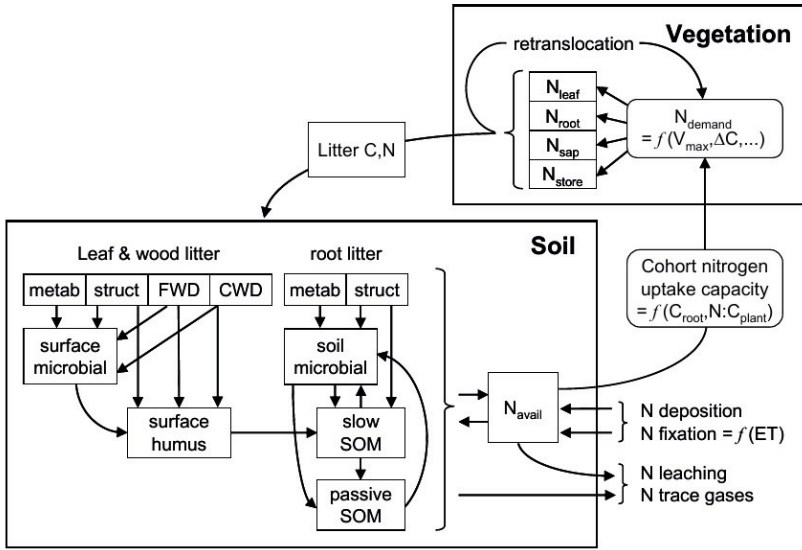


Figure 4: Implementation of the nitrogen cycle in LPJ-GUESS (from: Smith et al., 2014). Abbreviations: FWD = finewoody debris; CWD = coarsewoody debris; N_{avail} = soil mineral N pool; N_{leaf} = leaf N mass; N_{root} = fine root N mass; N_{sap} = sapwood N mass; N_{store} = plant labile N store; N_{demand} = daily plant N demand; V_{max} = canopy rubisco capacity; ΔC = daily biomass increment; $N:C_{plant}$ = aggregate N:C mass ratio for leaves and fine roots; ET = actual evapotranspiration.

the relative differences between leaves, fine roots and sapwood in N concentration of the new growth. Half of the N content of shed roots, leaves and sapwood is retained by plants on conversion to heartwood for retranslocation to tissues remaining. Instead, excess N is retained in the N store that buffers the effects of seasonal and interannual variations in the N demand and supply balance. If plant N demand in a patch cannot be met by the supply of mineral N in the soil, N limitation results. Under these circumstances, plants take up the amount of soil N according to their fine root surface area and reduce their photosynthesis and allocation for the current year. N limitation may lead to an increased relative allocation to fine roots. This promotes a more efficient uptake of N in the next year.

Managed land processes

Efforts are underway to include agricultural management and simulate crop productivity and yields generically using DGVMs (e.g. Kucharik and Brye, 2003; Bondeau et al., 2007; Lindeskog et al., 2013). An important step has been made by Bondeau et al. (2007) who developed LPJml, a model of the managed planetary land surface which bases on the LPJ DGVM. The authors implemented a dynamic and flexible, parameter-scarce representation of global agriculture and grazing land which relies on generic crop functional types (CFTs) capturing the most widespread types of agricultural plant traits. In order to cover the major plant types existing in agricultural ecosystems worldwide, 13 CFTs are now included, all

sharing the fundamental biophysical and physiological functions of natural PFTs, but with additional specific agro-ecosystem-oriented functions and parameters. All CFTs considered in LPJmL have annual life cycles or are harvested within one year (controlled by climate and human actions). Since the seasonal canopy development and the allocation of C to various organs in crops are crucial for yield, additional processes including daily allocation are taken into account for the CFTs. In LPJmL, sowing dates are calculated deterministically as a function of local climatology. Sowing dates determined by temperature are modeled on the basis of the 20 previous years' average date on which mean daily temperatures cross a specific threshold. Sowing dates determined by water availability instead are modeled from the precipitation accumulated during the last ten days. Phenological development towards maturity is modeled by accumulating daily mean temperatures above a specific base temperature up to a maturity threshold. Instead of distinct phenological phases, a phenological scalar is derived increasing from 0 at sowing to 1 at maturity. CFTs in LPJmL use a daily C allocation scheme, compared to the yearly scheme used for PFTs (Sitch et al., 2003). As soon as maturity is reached, harvest is triggered. At harvest, all storage organs are removed while their C content is assumed to be respired within the same year. Root C is added to the belowground litter pool. Different options can be considered for the management of crop residues, which depends on the regional agricultural system. Final benchmarking exercises performed by the authors have demonstrated the validity of the concept.

Lindeskog et al. (2013) then further developed the approach of Bondeau et al. (2007) and integrated managed land and LULC change functionalities into LPJ-GUESS. The main modifications in the model compared to LPJmL are: (i) a new phenology scheme for crops (coupling LAI and leaf C mass on a daily time step), (ii) a dynamic potential heat unit (PHU) calculation based on local climate conditions, (iii) the simulation of regeneration and recovery of vegetation by creating a new natural vegetation stand following cropland abandonment and (iv) a revised calculation of crop sowing dates which follows the approach by Waha et al. (2012). In LPJ-GUESS, supported land cover types in addition to potential natural vegetation (PNV) are cropland, pasture and managed forest. Land cover change is based on net area fraction input data for the land cover types and stand types within a land cover type (e.g. different crops). Croplands are harvested each year and a PFT-specific fraction of the harvestable organs (the harvest efficiency) then constitutes the yield which is assumed to be oxidized within a year. Of the leaf C, a further fraction (the residue removal fraction) is removed and oxidized within one year. Managed grassland is simulated by removing 50% of the above-ground C to represent grazing. At the conversion of forest to cropland, 70% of tree stems are harvested while the rest is oxidized the same year. 67% of harvested wood is oxidized the same year to represent firewood while the rest is moved to a pool with a 25 year turnover period, representing paper and timber. In the initial cropland representation of LPJ-GUESS as elaborated by Lindeskog et al. (2013), the PHU sum which is needed for full development of the specific crop (determining the time at which the crop

is harvested) is calculated dynamically, using a ten year running mean of heat unit sums as reported by Bondeau et al. (2007). The dynamic PHU calculation can be done either for an initial time period only (to calibrate for the local climate) or also for an extended period (to simulate adaptation to a changing climate by selecting suitable crop varieties/genotypes).

Olin et al. (2015b) recently updated the cropland representation of Lindeskog et al. (2013) in LPJ-GUESS by adding N limitations to crops. The new model allocates daily NPP based on the crop's development stage (DS) and allows for an adjustment of the allocation scheme based on the current nutrient and water status of the crop. Compared to the PHU implementation described above, Olin et al. (2015b) define DS as a number between 0 and 2 (where: $0 < DS < 1$ is the main vegetative phase, at $DS = 1$ anthesis occurs and $DS > 1$ represents the grain filling phase). DS at a given time is a cumulative function of the maximal development rate which differs between the vegetative phase and the reproductive phase. According to Wang and Engel (1998), DS is also modified using dimensionless scaling factors dependent on temperature, vernalization days and photo-period. For the allocation of assimilates (and their partitioning to the plant organs during the growing season), the authors use the established allocation scheme from Penning de Vries et al. (1989). This scheme differs from the one described by Lindeskog et al. (2013) in that the allocation of C to the different organs is related to daily NPP and DS. N requirements for the plant vary during the growing period. During the first part of the vegetative phase, most of the assimilates are used for root and leaf growth in order to maximize the uptake of water and nutrients and the absorption of radiation for photosynthesis. This phase is followed by a period when more of the assimilated C is allocated to the stem. After anthesis, the grain-filling period starts. During this period, most assimilates are allocated to the storage organs and cereal crops reallocate some of their nutrients from the vegetative organs to the grains.

These recent development strands now provide the capacity to predict changes in global C and N pools and fluxes in historic or future land-use change scenarios. They also allow to quantify and explore the effect of different managements on the global C and N budgets, considering hindcasts and projections of land-use change, climate change and historic or future N fertilizer application rates.

2.3 Climate projection data

Climate projection data for DGVMs is provided by general circulation models –GCMs– which describe global climate variation in time and space. GCMs are numerical models and represent physical processes in the atmosphere, ocean, cryosphere and land surface. At present, they are the most advanced tools available for simulating the effect of increasing greenhouse gas concentrations on the global climate system. GCMs (possibly in conjunction with nested regional models) have the potential to provide both geographically and

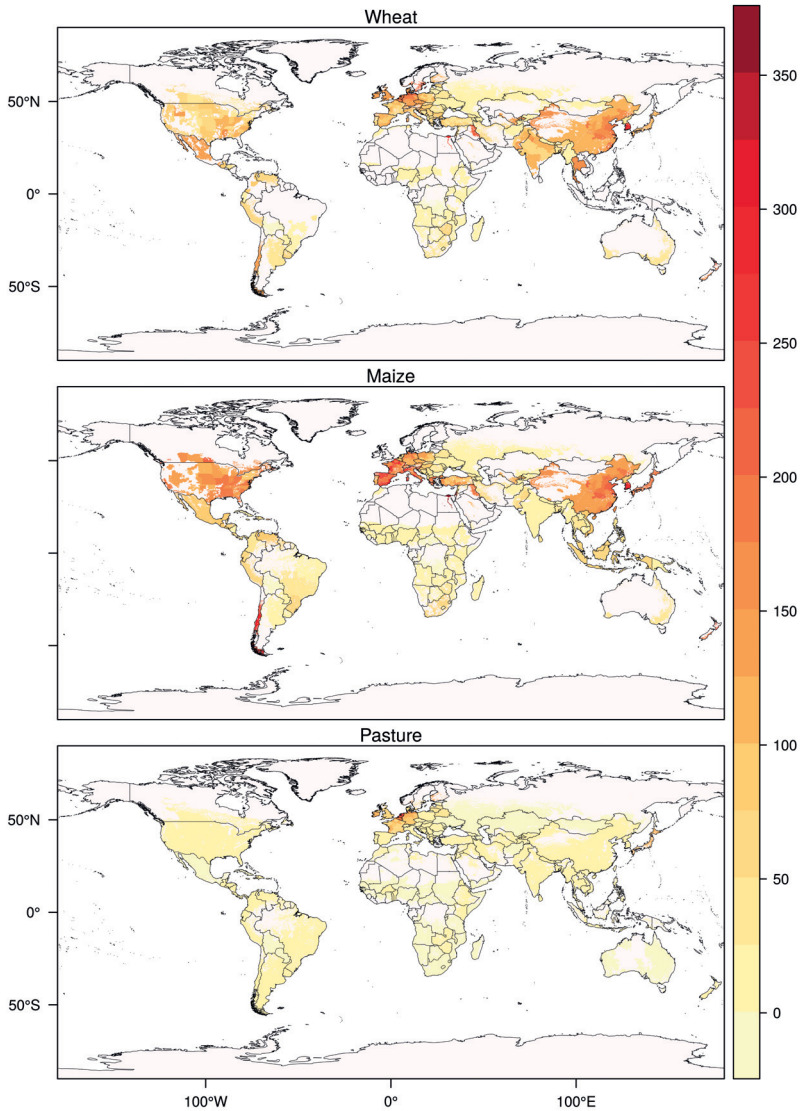


Figure 5: Amount of nitrogen fertilizer applied yearly (in kg/ha, centered on the year 2000) for wheat, maize and pastures (data from: Mueller et al., 2012).

physically consistent calculations of regional climate change which are required in impact analysis (for society-relevant evaluations of climate change adaptation using impact assessment models).

GCMs represent the climate by using a 3D grid over the globe. One grid cell typically

has a horizontal resolution of 250-600 km, ten to 20 vertical layers in the atmosphere and up to 30 layers in the oceans. Hence, their spatial resolution is relatively coarse compared to the scale of exposure units in most impact assessments. Furthermore, many physical processes (such as those related to clouds) occur at smaller scales and thus cannot be properly modeled. One solution for this problem is to average over the known properties of the process (parameterization). However, this is one of the primary sources of uncertainty in simulations of future climate. Uncertainty is increased by the different representations of feedback mechanisms in GCMs concerning e.g. water vapor and warming or clouds and radiation. This leads to GCMs simulating different responses to the same forcing, simply because of the way the contained processes and feedbacks are modeled.

A large number of GCMs have been developed by different climate modeling groups, of which around 28 have been involved in the Coupled Model Intercomparison Project (CMIP5, Taylor et al. (2012)) coordinated by the World Climate Research Programme (WCRP). Each GCM predicts the climate response to different representative concentration pathways (RCPs) (van Vuuren et al., 2011) and is thereby increasing the number of potential input datasets for impact assessment models. Due to the coarse spatial resolution, different downscaling methods have been developed which produce climatic information at scales finer than the initial large-scale projections. These methods can be classified into two approaches (Maraun et al., 2010). The first approach is called dynamical downscaling and uses output from GCMs to drive a numerical regional climate model (RCM) (Caya and Laprise, 1999; Mearns et al., 2003) which represents the atmospheric physics with a higher spatial resolution. Due to the higher spatial resolution and improved representation of surface elevations, RCMs resolve important atmospheric processes (such as orographic rainfall) better than the host GCM. Since dynamical downscaling is computationally demanding (Wilby et al., 2009), the individual simulations are conducted within a limited area of interest and cover a subglobal domain (e.g. Europe). The Coordinated Regional Climate Downscaling Experiment (CORDEX) (Giorgi et al., 2009) is the major project coordinating international efforts of such regional climate downscaling to provide ensembles of transient (1951-2100) regional climate simulations generated from CMIP5 projections. The second approach is called statistical downscaling and establishes statistical links between large-scale and observed local-scale weather. Several methods have been developed within this approach, varying in accuracy, spatial domain (local to global), computational and time requirements, and climatic science robustness (i.e. theoretical background). For flood risk assessments for example, extreme precipitation events are highly important which needs to be taken into account when downscaling. One common method which relates to model output statistics is the delta-change method, which is based on the sum of interpolated anomalies to high-resolution monthly climate surfaces from historical observations (e.g. Ahlström et al., 2013; Olin et al., 2015a).

2.4 Land-use intensity

LPJ-GUESS has been considerably improved by including human management processes in combination with the N cycle. The recent efforts to integrate historical and scenario-based land cover data into LPJ-GUESS incorporate fractional land cover data (crop, pasture, forest, natural, urban) at a resolution of 0.5×0.5 degree. These LULC maps assume that land management is uniform for all areas sharing a common land-use class. Subtle changes in the land systems that may have important environmental impacts are instead neglected. Land-use intensity is certainly a critical characteristic of both agricultural and forest land systems (see Fig. 5) and land-use management intensity and livestock keeping should not be neglected (van Asselen and Verburg, 2012).

Extensively managed croplands, for instance, have often less impact on the natural environment compared to intensively managed croplands. This is in particular the case in forestry, where management effects on forest ecosystem functioning vary substantially depending on forest management intensity. The intensity by which forest are managed affects for example forest structure (Vilén et al., 2012), soils (Jandl et al., 2007), biogeochemical cycles (Nabuurs et al., 2013), biodiversity (Paillet et al., 2010) and ecosystem service provisioning (Gamfeldt et al., 2013). Understanding these spatial patterns of agricultural and forest management intensity and its driver is therefore important for assessing the environmental trade-offs of agriculture and forestry and for identifying opportunities for sustainable intensification. Levers et al. (2014) showed in their study that forest harvesting intensity in Europe is distributed unevenly; harvested timber volumes were mostly well below the net growth of wood which indicates the potential for sustainable intensification in timber yields. Forest harvesting intensity was well explained by forest resource related variables (i.e., share of plantation species, growing stock), topography (i.e., terrain ruggedness), and country-specific characteristics. Levers et al. (2016) analyzed agricultural intensity changes in Europe focusing on yields and fertilizer application for the period 1990-2007. They found that both yields and N applications across crop types were particularly high in Western and Central Europe, while Eastern Europe was characterized by lower yields and N applications. They also found strong sub-national variation in intensity levels with respect to crop types. Higher yields were typically related to higher fertilization, high soil quality and high labor productivity.

In general, land-use intensification is an understudied land-use change process (van Vliet et al., 2016) and the knowledge on the patterns and drivers of agricultural and forestry intensification remains incomplete, especially at global scales (Erb, 2012). However, substantial progress has recently been made in mapping spatial patterns of agricultural intensity in terms of crop land-use intensity and field size, global yield gaps and global distribution and density of livestock (e.g. Monfreda et al., 2008; Neumann et al., 2010; Siebert et al., 2010; Temme and Verburg, 2011; Robinson et al., 2014; Fritz et al., 2015; Estel et al., 2016).

It is essential to include this current knowledge in terrestrial ecosystem models when conducting simulations with regard to environmental impact assessment.

3 Results and Discussion

Climate data sensitivity

First, in paper I, we systematically assessed the spatial variability in C and N balance simulations concerning the choice of GCMs, RCPs, spatial resolutions, and the downscaling methods used. Our results showed that the variability in simulated output caused by the different climate datasets was moderate with 35.6%–93.5% of the total variability being attributed to common structures independent of the four factors.

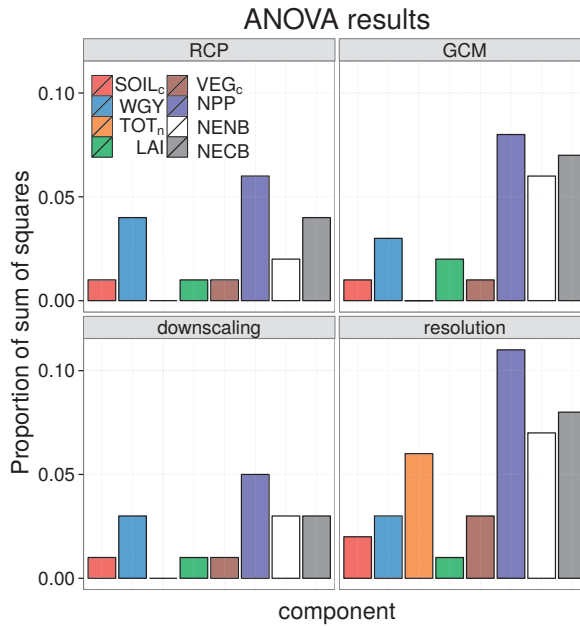


Figure 6: Global sensitivity indices, calculated as the proportion of the sum of squares, for the four factors RCP, GCM, spatial downscaling and spatial resolution which have been altered within the complete factorial design. The different colors indicate the eight investigated model outputs (from left to right): soil carbon pool, wheat dry grain yield, total nitrogen pool, leaf area index, vegetation carbon pool, net primary productivity, net ecosystem nitrogen balance, net ecosystem carbon balance.

The areas of low variability included large, low-lying regions in central Europe such as Germany, France and Poland. The spatial resolution was the most important factor among the examined ones and explained 1.5%–10.7% of the total variability (see Fig. 6). GCMs ranked second with 0.3%–7.6%, followed by RCPs (0%–6.3%) and downscaling methods (0.1%–4.6%). The most distinct hot spots of variability included the mountain ranges in northern Scandinavia and the Alps, and the Iberian Peninsula. While total C stocks, total N stocks and LAI simulations were least sensitive to the input data, NPP, and especially NECB and net ecosystem nitrogen balance (NENB) simulations showed the most pronounced variability. Based on our findings, it can be advised to conduct the application of ecosystem

models such as LPJ-GUESS at a reasonably high spatial resolution which is supported by the model structure. There appears to be no notable gain in simulations of ecosystem C and N stocks and fluxes from using regionally downscaled climate in preference to bias-corrected, bilinearly interpolated CMIP₅ projections.

Land-use intensity and crop processes

Recently, land-use intensity data for croplands has become more and more available. In paper II, we forced LPJ-GUESS with N application data on Nomenclature of Units for Territorial Statistics (NUTS) 2 level which was derived from a model chain informing the Common Agricultural Policy Regionalized Impact (CAPRI) model. We analyzed the com-

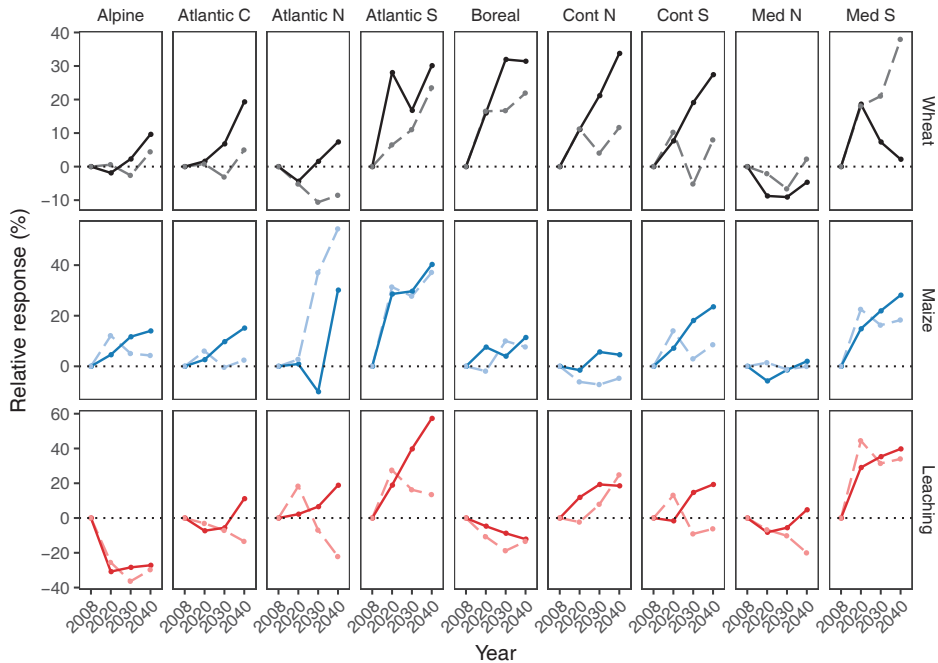


Figure 7: The simulated response of wheat yield, maize yield and nitrogen leaching under two future scenarios (RCP 4.5, dashed line; RCP 8.5, solid line) relative to the year 2008. The dotted line indicates no change. Simulations are summarized for nine agro-climatic regions: Alpine area, Atlantic Central, Atlantic North, Atlantic South, Boreal area, Continental North, Continental South, Mediterranean North, Mediterranean South. Results for maize yield and the Atlantic North are reduced by a factor of two for clarity.

combined role of climate change and land-use intensity change for trade-offs between agricultural yield and N leaching in the European Union (EU) under two plausible scenarios up to 2040. Furthermore, we assessed both driver importance and uncertainty in future trends based on an alternative land-use intensity dataset derived from an integrated assessment model. LPJ-GUESS simulated an increase in wheat and maize yield but also N leaching

for most regions when driven by changes in land-use intensity and climate under RCP 8.5 (see Fig. 7). Under RCP 4.5, N leaching was reduced in 53% of the regions while there was a trade-off in crop productivity. The most important factors influencing yield were CO₂ (wheat) and climate (maize), but N application almost equaled these in importance. For N leaching, N application was the most important factor, followed by climate. Therefore, using a constant N application dataset in the absence of future projections has a substantial effect on simulated ecosystem responses, especially for maize yield and N leaching. This study is a first assessment of future N leaching and yield responses based on projections of climate and land-use intensity. It further highlights the importance of accounting for changes in future N applications and land-use intensity in general when evaluating environmental impacts over long time periods.

Land-use intensity and pastures

For many years, climate data (as investigated in paper I) has been the major driver for LPJ-GUESS and other DGVMs. In recent development strands, land-use and partially land-use intensity data has been added as a driver to LPJ-GUESS (see paper II). Pastures, however are still mainly driven by climate. In paper III, we aimed to improve the representation of pastures in LPJ-GUESS by incorporating daily allocation for grasses and daily land management routines and land-use intensity data into the model to distinguish between intensively and extensively used regions.

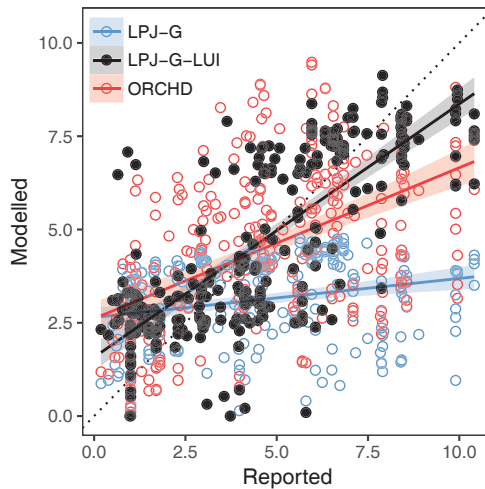


Figure 8: Scatterplot of productivity reported from Smit et al. (2008) versus simulated data from the default version of LPJ-GUESS (blue), the updated version LPJ-GUESS-LUI (black) and simulated data with ORCHIDEE-GM (red) from Chang et al. (2015). The dotted line indicates the 1:1 line.

Our results demonstrated that grassland productivity could not be adequately captured

without including land-use intensity data in the form of N application. When the model was mainly driven by climate, pasture productivity was comparatively low and homogeneous over most parts of Europe. Our updated version (from this point called LPJ-GUESS-LUI) instead reproduced the hotspots of high productivity in central Europe, mostly the Netherlands, Germany and France and pasture productivity was in general closer to reported data (see Fig. 8). When compared to observed LAI values for a site in Switzerland, the updated model followed the observations quite well, especially in the middle of the growing season. However, LPJ-GUESS-LUI tended to underestimate the first harvest and could not reproduce the steep LAI increase observed in early spring. When compared to simulations with standard LPJ-GUESS, ecosystem simulations for NPP, NECB and N leaching were significantly increased in the extended version. Finally, LPJ-GUESS-LUI simulated an increase in potential grassland productivity until 2050 mostly in the Mediterranean North and Mediterranean South due to increases in N applications. Even though the current status of N application data availability is intermediate, it is important to advance with incorporating grassland management intensity in the form of N fertilization into DGVMs. Incorporating land-use intensity will improve predictions of terrestrial C sinks and sources as well as N leaching.

Trade-offs between ecosystem processes

Papers I-III stressed the importance of both climate and land-use intensity drivers on ecosystem simulations. In paper IV, we use both types of data at a river basin in Germany. Since the German Federal State of Saxony aims to increase forest cover, we analyzed consequences of an increase in forest cover by investigating possible trade-offs between C storage and plant biodiversity caused by afforestation. Six afforestation scenarios with total forest cover ranging from 27.7% to 46% were generated in the Mulde river basin in Saxony with regard to different forest types. C storage was calculated by LPJ-GUESS while random forest models were used to predict changes in plant species richness.

We used eight different plant groups as responses: total number of plant species, endangered species, as well as species grouped by native status (three groups) and pollination traits (three groups). Afforestation led to an increase in C storage that was slightly stronger in coniferous forests as compared to deciduous forests. The relationship between plant species richness and afforestation was context dependent. Species richness showed a non-linear relationship with forest cover share. The relationship was influenced by shares of land-use types, climatic conditions and land-use configuration expressed by the number of land-use patches. The effect of forest type on plant species richness was marginal. On average, the relationship between C storage and plant species richness was synergistic for most plant groups. However, the relationship between change in species richness and change in C storage varied across space. This changing relationship was then used to identify prior-



Figure 9: Increase in species number per increase in ton carbon for the all plant species group for all afforestation scenarios. The maps show the number of species gained compared to the reference situation per ton carbon storage gained compared to the reference situation.

ity areas for afforestation. The different plant groups responded differently to an increase in forest cover. The change in species richness for Red List species was relatively distinct from the other species groups. Neophytes and archaeophytes showed a similar response to the afforestation scenarios. While afforestation had overall positive effects both on plant species richness and C storage, a number of locations could be identified for which afforestation may lead to a decrease in plant species richness (see Fig. 9). Spatial planning should, therefore, avoid afforestation at these locations.

4 Conclusion and Outlook

Recent development strands now provide the capacity of predicting changes in global C and N pools and fluxes considering hindcasts and projections of land-use, climate and historical or future N fertilizer application rates. However, despite the fact that many processes in DGVMs are represented now, small differences in parameterization, input data and model design can propagate to create large uncertainty. Since it can be assumed that this uncertainty is unlikely to have been reduced by the latest generation of DGVMs, one needs to be cautious when conducting for example risk assessments or trade-off analyses with DGVMs.

Our study has contributed in this respect by analyzing the sensitivity of C and N balances simulated over Europe to various datasets of climate and N applications. Our results reveal a clear hierarchy of effects with respect to the choice of climate data: a negligible effect of using different downscaling methods and RCPs, a somewhat higher but still relatively small effect of the GCMs chosen, and the largest effect caused by the spatial climate data resolution. While total C stocks, total N stocks and LAI simulations are least sensitive to the input data, NPP, and especially NECB and NENB simulations show the most pronounced variability. Based on our findings, we advise to conduct the application of models such as LPJ-GUESS and subsequent decisions at the highest reasonable spatial resolution of meteorological input data which is supported by the model structure. Future N application rates result in substantial uncertainty for crop yield and N leaching in Mediterranean and Atlantic regions; uncertainty is smallest in the Continental North and South. This is due to each dataset differing in underlying assumptions and uncertainty inherited from its specific model chain. Given the high importance of N applications as driving data compared to climate and CO₂, there is a strong need for harmonized, crop-specific N-application scenarios with high temporal and spatial resolution.

The desire to include additional processes in DGVMs (and increase versatility) is bound to add to the problem of constraining uncertainty about parameters and processes. However, our results have shown that even though the current status of data availability is intermediate, it is important to advance with incorporating grassland management intensity in the form of N fertilization in DGVMs. Otherwise, reported spatial patterns of potential grassland productivity in Europe cannot be reproduced.

Even though models and data are not perfect, it is important to conduct studies such as trade-off analyses already now to allow for a concerted response from policy and society tomorrow. This study has shown that future yields of wheat and maize are expected to increase in Europe, while they will be accompanied by increases of N-leaching in many regions of Europe. From an environmental viewpoint, our results illustrate the need to achieve modest population growth and arrange environmental policies (such as the ecosystem service concept) and treaties for climate mitigation and adaptation. Nevertheless,

N management needs to be improved even further to reduce the costs to environmental services such as water quality also under RCP 4.5. The case study in Saxony, Germany, has shown that trade-offs of afforestation for plant biodiversity were influenced by the context of where forest is grown. This adds complexity to spatial planning decisions compared to decisions that only take an increase in C storage into account. Afforestation should be planned taking the different objectives into account.

While there are benefits of single model studies, an important attempt of reducing predictive uncertainty is using ensembles of DGVMs just as DGVMs use ensembles of for example GCMs and climate data. Moreover, our world is now unprecedentedly data-rich. This is true for many types of data such as plant traits, fluxes between ecosystems and atmosphere and remotely-sensed land properties. Models could be far better constrained, if observations were used at all stages of model development, and if the different types of observation were combined (for example by inverse modeling in a Bayesian framework).

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6 References

- Ahlström, A., Smith, B., Lindström, J., Rummukainen, M., and Uvo, C. B.: GCM characteristics explain the majority of uncertainty in projected 21st century terrestrial ecosystem carbon balance, *Biogeosciences*, 10, 1517–1528, 2013.
- Bondeau, A., Smith, P. C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D., Lotze-Campen, H., Müller, C., Reichstein, M., and Smith, B.: Modelling the role of agriculture for the 20th century global terrestrial carbon balance, *Global Change Biology*, 13, 679–706, 2007.
- Canadell, J. G., Le Quéré, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T. J., Gillett, N. P., Houghton, R. A., and Marland, G.: Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks., *Proceedings of the National Academy of Sciences of the United States of America*, 104, 18 866–18 870, 2007.
- Caya, D. and Laprise, R.: A semi-implicit semi-Lagrangian regional climate model: The Canadian RCM, *Monthly Weather Review*, pp. 341–362, 1999.
- Chang, J., Viovy, N., Vuichard, N., Ciais, P., Campioli, M., Klumpp, K., Martin, R., Leip, A., and Soussana, J.-F.: Modeled Changes in Potential Grassland Productivity and in Grass-Fed Ruminant Livestock Density in Europe over 1961–2010, *Plos One*, 10, e0127 554, 2015.
- Chapin, F. S., Matson, P. A., and Vitousek, P. M.: *Principles of Terrestrial Ecosystem Ecology*, pp. 259–296, Springer New York, New York, NY, 2011.
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R., Piao, S., and Thornton, P.: Carbon and Other Biogeochemical Cycles, book section 6, pp. 465–570, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2013.
- Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., Perakis, S. S., Latty, E. F., Von Fischer, J. C., Elseroad, A., and Wasson, M. F.: Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems, *Global Biogeochemical Cycles*, 13, 623–645, 1999.
- Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., Cox, P. M., Fisher, V., Foley, J. A., Friend, A. D., Kucharik, C., Lomas, M. R., Ramankutty, N., Sitch, S., Smith, B., White, A., and Young-Molling, C.: Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models, *Global Change Biology*, 7, 357–373, 2001.

- Ellis, E. C. and Ramankutty, N.: Putting people in the map: anthropogenic biomes of the world, *Frontiers in Ecology and the Environment*, 6, 439–447, 2008.
- Erb, K.-H.: How a socio-ecological metabolism approach can help to advance our understanding of changes in land-use intensity, *Ecological Economics*, 76, 8 – 14, 2012.
- Erb, K.-H., Haberl, H., Jepsen, M. R., Kuemmerle, T., Lindner, M., Müller, D., Verburg, P. H., and Reenberg, A.: A conceptual framework for analysing and measuring land-use intensity, *Current opinion in environmental sustainability*, 5, 464–470, 2013.
- Estel, S., Kuemmerle, T., Levers, C., Baumann, M., and Hostert, P.: Mapping cropland-use intensity across Europe using MODIS NDVI time series, *Environmental Research Letters*, 11, 024 015, 2016.
- Foley, J. and Prentice, I.: An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochemical Cycles*, 10, 603–628, 1996.
- Fritz, S., See, L., McCallum, I., You, L., Bun, A., Moltchanova, E., Duerauer, M., Albrecht, F., Schill, C., Perger, C., Havlik, P., Mosnier, A., Thornton, P., Wood-Sichra, U., Herrero, M., Becker-Reshef, I., Justice, C., Hansen, M., Gong, P., Abdel Aziz, S., Cipriani, A., Cumani, R., Cecchi, G., Conchedda, G., Ferreira, S., Gomez, A., Haffani, M., Kayitakire, F., Malanding, J., Mueller, R., Newby, T., Nonguierma, A., Olusegun, A., Ortnier, S., Rajak, D. R., Rocha, J., Schepaschenko, D., Schepaschenko, M., Terekhov, A., Tiangwa, A., Vancutsem, C., Vintrou, E., Wenbin, W., van der Velde, M., Dunwoody, A., Kraxner, F., and Obersteiner, M.: Mapping global cropland and field size, *Global Change Biology*, 21, 1980–1992, 2015.
- Galloway, J., Dentener, F., Capone, D., Boyer, E., Howarth, R., Seitzinger, S., Asner, G., Cleveland, C., Green, P., Holland, E., Karl, D., Michaels, A., Porter, J., Townsend, A., and Vörösmarty, C.: Nitrogen cycles: Past, present, and future, vol. 70, 2004.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusinski, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., and Bengtsson, J.: Higher levels of multiple ecosystem services are found in forests with more tree species., *Nature communications*, 4, 1340, 2013.
- Giorgi, F., Jones, C., and Asrar, G. R.: Addressing climate information needs at the regional level: the CORDEX framework, *Bulletin - World Meteorological Organization*, 58, 175–183, 2009.
- Haxeltine, A. and Prentice, I. C.: A General Model for the Light-Use Efficiency of Primary Production, *Functional Ecology*, 10, 551–561, 1996.

- Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T. R., Cramer, W., Kuehn, I., and Sykes, M. T.: Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model, *Global Ecology and Biogeography*, 21, 50–63, 2012.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkinen, K., and Byrne, K. A.: How strongly can forest management influence soil carbon sequestration?, *Geoderma*, 137, 253 – 268, 2007.
- Kaplan, J. O.: Climate change and Arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections, *Journal of Geophysical Research*, 108, 8171, 2003.
- Keenan, T., Prentice, I. C., Canadell, J. G., Williams, C., Wang, H., Raupach, M. R., and Collatz, G. J.: Recent pause in the growth rate of atmospheric CO₂ due to enhanced terrestrial carbon uptake, *Nature Communications*, 7, 1–9, 2016.
- Kucharik, C. and Brye, K.: Plant and Environment Interactions, *Journal of Environmental Quality*, pp. 247–268, 2003.
- Lamarque, J.-F., Bond, T. C., Eyring, V., Granier, C., Heil, A., Klimont, Z., Lee, D., Liousse, C., Mieville, A., Owen, B., Schultz, M. G., Shindell, D., Smith, S. J., Stehfest, E., Van Aardenne, J., Cooper, O. R., Kainuma, M., Mahowald, N., McConnell, J. R., Naik, V., Riahi, K., and van Vuuren, D. P.: Historical (1850–2000) gridded anthropogenic and biomass burning emissions of reactive gases and aerosols: methodology and application, *Atmospheric Chemistry and Physics*, 10, 7017–7039, 2010.
- Lamarque, J.-F., Kyle, G. P., Meinshausen, M., Riahi, K., Smith, S. J., Vuuren, D. P., Conley, A. J., and Vitt, F.: Global and regional evolution of short-lived radiatively-active gases and aerosols in the Representative Concentration Pathways, *Climatic Change*, 109, 191–212, 2011.
- Levers, C., Verkerk, P. J., Müller, D., Verburg, P. H., Butsic, V., Leitão, P. J., Lindner, M., and Kuemmerle, T.: Drivers of forest harvesting intensity patterns in Europe, *Forest Ecology and Management*, 315, 160–172, 2014.
- Levers, C., Butsic, V., Verburg, P. H., Müller, D., and Kuemmerle, T.: Drivers of changes in agricultural intensity in Europe, *Land Use Policy*, 58, 380–393, 2016.
- Lindeskog, M., Arneth, A., Bondeau, A., Waha, K., Seaquist, J., Olin, S., and Smith, B.: Implications of accounting for land use in simulations of ecosystem carbon cycling in Africa, *Earth System Dynamics*, 4, 385–407, 2013.
- Maraun, D., Wetterhall, F., Chandler, R. E., Kendon, E. J., Widmann, M., Brien, S., Rust, H. W., Sauter, T., Themeßl, M., Venema, V. K. C., Chun, K. P., Goodess, C. M.,

- Jones, R. G., Onof, C., Vrac, M., and Thiele-Eich, I.: Precipitation downscaling under climate change: Recent developments to bridge the gap between dynamical models and the end user, *Reviews of Geophysics*, 48, 1–38, 2010.
- Mearns, L. O., Giorgi, F., McDaniel, L., and Shields, C.: Climate scenarios for the southeastern US based on GCM and regional model simulations, *Climatic Change*, 60, 7–35, 2003.
- Monfreda, C., Ramankutty, N., and Foley, J. A.: Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000, *Global Biogeochemical Cycles*, 22, 2008.
- Morales, P., Sykes, M. T., Prentice, I. C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viovy, N., Sabate, S., Sanchez, A., Pla, E., Gracia, C. A., Sitch, S., Arneth, A., and Ogee, J.: Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes, *Global Change Biology*, 11, 2211–2233, 2005.
- Mueller, N. D., Gerber, J. S., Johnston, M., Ray, D. K., Ramankutty, N., and Foley, J. A.: Closing yield gaps through nutrient and water management, *Nature*, 490, 254–257, 2012.
- Nabuurs, G.-J., Lindner, M., Verkerk, P. J., Gunia, K., Deda, P., Michalak, R., and Grassi, G.: First signs of carbon sink saturation in European forest biomass, *Nature Climate Change*, 3, 792–796, 2013.
- Neumann, K., Verburg, P. H., Stehfest, E., and Müller, C.: The yield gap of global grain production: A spatial analysis, *Agricultural Systems*, 103, 316 – 326, 2010.
- Olin, S., Lindeskog, M., Pugh, T. A. M., Schurgers, G., Wårlind, D., Mishurov, M., Zaehle, S., Stocker, B. D., Smith, B., and Arneth, A.: Soil carbon management in large-scale Earth system modelling: implications for crop yields and nitrogen leaching, *Earth System Dynamics*, 6, 745–768, 2015a.
- Olin, S., Schurgers, G., Lindeskog, M., Wårlind, D., Smith, B., Bodin, P., Holmér, J., and Arneth, A.: Modelling the response of yields and tissue C : N to changes in atmospheric CO₂ and N management in the main wheat regions of western Europe, *Biogeosciences*, 12, 2489–2515, 2015b.
- Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., and Virtanen, R.: Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe., *Conservation biology : the journal of the Society for Conservation Biology*, 24, 101–12, 2010.

- Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Gilmanov, T. G., Scholes, R. J., Schimel, D. S., Kirchner, T., Menaut, J.-C., Seastedt, T., Garcia Moya, E., Kamnalrut, A., and Kinyamario, J. I.: Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide, *Global Biogeochemical Cycles*, 7, 785–809, 1993.
- Parton, W. J., Hanson, P. J., Swanston, C., Torn, M., Trumbore, S. E., Riley, W., and Kelly, R.: ForCent model development and testing using the Enriched Background Isotope Study experiment, *Journal of Geophysical Research: Biogeosciences*, 115, 2010.
- Penning de Vries, F. W. T., Jansen, D. M., ten Berge, H. F. M., and Bakema, A.: Simulation of ecophysiological processes of growth in several annual crops, Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, Netherlands, 1989.
- Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Ak-senov, D., Egorov, A., Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manisha, A., Tsybikova, E., and Zhuravleva, I.: Mapping the world's intact forest landscapes by remote sensing, *Ecology and Society*, 13, 2008.
- Ramankutty, N., Evan, A. T., Monfreda, C., and Foley, J. A.: Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000, *Global Biogeochemical Cycles*, 22, 2008.
- Robinson, T. P., Wint, G. R. W., Conchedda, G., Van Boeckel, T. P., Ercoli, V., Palamara, E., Cinardi, G., D'Aiatti, L., Hay, S. I., and Gilbert, M.: Mapping the Global Distribution of Livestock, *PLOS ONE*, 9, 1–13, 2014.
- Siebert, S., Portmann, F. T., and Döll, P.: Global Patterns of Cropland Use Intensity, *Remote Sensing*, 2, 1625, 2010.
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9, 161–185, 2003.
- Sitch, S., Friedlingstein, P., Gruber, N., Jones, S. D., Murray-Tortarolo, G., Ahlström, A., Doney, S. C., Graven, H., Heinze, C., Huntingford, C., Levis, S., Levy, P. E., Lomas, M., Poulter, B., Viovy, N., Zaehle, S., Zeng, N., Arneth, A., Bonan, G., Bopp, L., Canadell, J. G., Chevallier, F., Ciais, P., Ellis, R., Gloor, M., Peylin, P., Piao, S. L., Le Quéré, C., Smith, B., Zhu, Z., and Myneni, R.: Recent trends and drivers of regional sources and sinks of carbon dioxide, *Biogeosciences*, 12, 653–679, 2015.
- Smit, H., Metzger, M., and Ewert, F.: Spatial distribution of grassland productivity and land use in Europe, *Agricultural Systems*, 98, 208–219, 2008.

- Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space, *Global Ecology and Biogeography*, 10, 621–637, 2001.
- Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S.: Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model, *Biogeosciences*, 11, 2027–2054, 2014.
- Steffen, W., Persson, Å., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., Crumley, C., Crutzen, P., Folke, C., Gordon, L., Molina, M., Ramanathan, V., Rockström, J., Scheffer, M., Schellnhuber, H. J., and Svedin, U.: The anthropocene: From global change to planetary stewardship, *Ambio*, 40, 739–761, 2011.
- Stockmann, U., Adams, M. A., Crawford, J. W., Field, D. J., Henakaarchchi, N., Jenkins, M., Minasny, B., McBratney, A. B., de Courcelles, V. d. R., Singh, K., Wheeler, I., Abbott, L., Angers, D. A., Baldock, J., Bird, M., Brookes, P. C., Chenu, C., Jastrow, J. D., Lal, R., Lehmann, J., O'Donnell, A. G., Parton, W. J., Whitehead, D., and Zimmermann, M.: The knowns, known unknowns and unknowns of sequestration of soil organic carbon, *Agriculture, Ecosystems and Environment*, 164, 80–99, 2013.
- Stürck, J., Levers, C., van der Zanden, E. H., Schulp, C. J. E., Verkerk, P. J., Kuemmerle, T., Helming, J., Lotze-Campen, H., Tabeau, A., Popp, A., Schrammeijer, E., and Verburg, P.: Simulating and delineating future land change trajectories across Europe, *Regional Environmental Change*, pp. 1–17, 2015.
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., and Zimov, S.: Soil organic carbon pools in the northern circumpolar permafrost region, *Global Biogeochemical Cycles*, 23, 2009.
- Taylor, K. E., Stouffer, R. J., and Meehl, G. A.: An overview of CMIP5 and the experiment design, *Bulletin of the American Meteorological Society*, 93, 485–498, 2012.
- Temme, A. and Verburg, P.: Mapping and modelling of changes in agricultural intensity in Europe, *Agriculture, Ecosystems & Environment*, 140, 46 – 56, 2011.
- Townsend, A. R., Braswell, B. H., Holland, E. A., and Penner, J. E.: Spatial and Temporal Patterns in Terrestrial Carbon Storage Due to Deposition of Fossil Fuel Nitrogen, *Ecological Applications*, 6, 806–814, 1996.
- van Asselen, S. and Verburg, P. H.: A Land System representation for global assessments and land-use modeling, *Global Change Biology*, 18, 3125–3148, 2012.
- van Vliet, J., Magliocca, N. R., Büchner, B., Cook, E., Rey Benayas, J. M., Ellis, E. C., Heinemann, A., Keys, E., Lee, T. M., Liu, J., Mertz, O., Meyfroidt, P., Moritz, M.,

- Poeplau, C., Robinson, B. E., Seppelt, R., Seto, K. C., and Verburg, P. H.: Meta-studies in land use science: Current coverage and prospects, *Ambio*, 45, 15–28, 2016.
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J. F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. J., and Rose, S. K.: The representative concentration pathways: An overview, *Climatic Change*, 109, 5–31, 2011.
- Vilén, T., Gunia, K., Verkerk, P., Seidl, R., Schelhaas, M.-J., Lindner, M., and Bellassen, V.: Reconstructed forest age structure in Europe 1950 - 2010, *Forest Ecology and Management*, 286, 203 – 218, 2012.
- Vince, G.: An Epoch Debate, *Science*, 334, 32–37, 2011.
- Waha, K., van Bussel, L. G. J., Müller, C., and Bondeau, A.: Climate-driven simulation of global crop sowing dates, *Global Ecology and Biogeography*, 21, 247–259, 2012.
- Wang, E. and Engel, T.: Simulation of phenological development of wheat crops, *Agricultural Systems*, 58, 1 – 24, 1998.
- Wärlind, D., Smith, B., Hickler, T., and Arneth, A.: Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model, *Biogeosciences*, 11, 6131–6146, 2014.
- Wilby, R. L., Troni, J., Biot, Y., Tedd, L., Hewitson, B. C., Smith, D. M., and Sutton, R. T.: A review of climate risk information for adaptation and development planning, *International Journal of Climatology*, 29, 1193–1215, 2009.