



Modelling Herbivory Impacts on Vegetation Structure and Productivity

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Abstract. Animal herbivory can have large and diverse impacts on vegetation and hence on the state and function of ecosystems. Despite this, quantitative understanding of vegetation responses to consumption of green leaf tissue by herbivores is currently lacking and presents a critical gap. More and more species are becoming endangered or extinct, whereas ecosystem restoration and rewilding are also increasingly moving into the focus of the scientific community. The large-scale impacts of changes in herbivore abundance on ecosystem function have yet to be investigated. Process-based modelling can help to quantify how animals affect important processes, such as ecosystem carbon cycling. To do so, we linked the dynamic global vegetation model LPJ-GUESS with the Madingley model, a model of multi-trophic functional diversity. This implementation allows us to simulate feedbacks between the availability of green vegetation biomass, herbivory and the whole trophic chain and vice versa. In the coupled model system, we see an overall reduction in ecosystem productivity, leaf area index and carbon mass, compared to the stand-alone version of LPJ-GUESS. The impact of herbivory is most prominently visible in the boreal ecosystems. We evaluated LPJ-GUESS output against remote sensing datasets and flux measurements and find that the coupled LPJ-GUESS/Madingley model preserves LPJ-GUESS's ability to predict realistic biome distributions and carbon pools.

1 Introduction

A number of review papers have highlighted animals' potential to notably affect local ecosystem functioning by altering canopy structure, productivity and biomass (Arneth et al., 2020; Cardinale et al., 2012; Schmitz et al., 2014, 2018; Sobral et al., 2017; Wilmers and Schmitz, 2016), but whether the highlighted interactions affect carbon-, nutrient-, and water cycles globally, and how these interactions may change in time, remains unclear. For example the scientific community still debates whether an increase in abundance of herbivores enhances the ecosystems productivity by accelerating nutrient cycles (Enquist et al., 2020), reduces overall autotroph biomass through damaging plant individuals (Jia et al., 2018) or shifts the distribution of plant species (Schmitz et al., 2014). Given the urgency of climate change, the importance of nature in combatting climate change and providing important contributions to people, and the ongoing changes in global biodiversity including size structured defaunation, and efforts to reverse this loss through ecosystem restoration and rewilding (Schmitz



et al., 2022, 2023), gaining a better understanding the role of animals for terrestrial ecosystem functioning is fundamentally important (Forest et al., 2023; Weiskopf et al., 2022).

Biogeochemical cycle models have largely omitted the influence of animals. Still, a limited number of local and regional-scale modelling experiments exist to investigate animal impacts on vegetation dynamics and nutrient cycling. For instance, 35 Pachzelt et al. (2015) coupled a physiological grazer population model with a dynamic vegetation model. They found for African savannas net primary productivity together with precipitation to be the strongest predictor of modelled grazer densities but that vegetation biomass and burned area in turn were not affected substantially by varying grazer density. Similar results were found by Riggs et al. (2015), who coupled a landscape fire succession model with a multi-species herbivory module to study ungulate herbivory as driver for the emergent fire regime. Even though herbivory was found to 40 play a role within single stands, across larger scales herbivory did not significantly impact respiration, primary production, carbon mass or the area burned. In contrast, Dangal et al. (2017) demonstrated with a combined mammalian herbivore population and land ecosystem model, that herbivores have a significant negative impact on net primary production and respiration. Berzaghi et al. (2019) incorporated elephant disturbance in the Ecosystem Demography model and showed that introducing herbivores increases the long-term equilibrium above-ground biomass in the African rainforests but decreased 45 the forest's net primary production.

So far, model studies on interactions between vegetation productivity and herbivores did not investigate how these reverberate to the entire trophic chain. Consequently, it is also unknown whether the model-based results – or observation-based evidence from experimental plots - can be generalised to larger regions, different environmental contexts, and how herbivore-omnivore-carnivore interactions would feedback on the biomass consumed. To our knowledge, the only globally 50 applicable model of functional animal diversity is the Madingley model (Harfoot et al., 2014). Madingley has been shown to reproduce large scale ecological patterns alongside relationships in food webs (Hoeks et al., 2020), as well as being able to simulate small-scale field experiments (Unravelling the Role of Vegetation Structure in Ecosystem Functioning with LIDAR, Field Studies and Modelling - Environmental Research: Ecology - IOPscience, 2023). In Krause et al. (2022) we presented a version of the Madingley model that is driven by vegetation biomass simulated with the LPJ-GUESS (Smith et 55 al., 2014; Wårlind et al., 2014) dynamic global vegetation model. The previous work explored how the amount and dynamics of green biomass available for consumption to herbivores affects the modelled trophic chain. Here, we investigate how higher trophic level organisms in turn influence canopy leaf area index, light transmission and photosynthesis, as well as vegetation composition. This work is a further step towards a fully coupled modelling system that eventually will enable exploration of the effects of interactive vegetation, soil and animal processes on carbon and nitrogen cycling under present 60 conditions, future climate change and under multiple other scenarios of anthropogenic influence.



2 Methods

We developed a coupled model system that consists of two independent models. Both modified models can run separately from another or are able to exchange data. For LPJ-GUESS, we based the model developments for this study on the LPJ-GUESS trunk version r10042 and implemented defoliation methods similar to (Kautz et al., 2018). The new LPJ-GUESS model code is not integrated into the main LPJ-GUESS repository and therefore does not have a definitive model version. For Madingley, we based our development on the model code from Krause et al. (2022).

2.1 The Madingley Model

The Madingley model simulates plant-animal and animal-animal functional interactions, based on ecological principles and using an agent based approach (Harfoot et al., 2014; Purves et al., 2013). Animals are modelled as agents, referred to as cohorts, which are grouped into animal functional types (AFTs) that share basic ecological traits. Based on their food source, herbivores, omnivores and carnivores are differentiated. These AFTs are further distinguished into exothermic and endothermic cohorts to reflect different thermoregulation strategies. In each model grid location multiple, rivalling cohorts of the same AFT co-exist, which are distinguishable by their body mass, the number of individuals forming the cohort and the cohort's age. The cohorts undergo a set of ecological processes: metabolism, predation, feeding, reproduction (semelparity or iteroparity) and mortality (Harfoot et al., 2014). Cohorts can migrate between grid cells, with a probability based on the grid cell's size and a randomly drawn movement distance. Madingley doesn't consider the amount of available food or environmental conditions to determine cohort migration. Live vegetation biomass in each grid cell is represented by an evergreen and deciduous autotroph stock. Herbivores and omnivores both feed from the vegetation stocks, but omnivores are less efficient at converting vegetation ingested into living biomass than herbivores. Carnivores and omnivores can prey on other heterotrophic cohorts within the same grid cell. The probability of a predation event and the rate of feeding is a function of the body masses of the predator and prey organisms. For more information see (Harfoot et al., 2014; Krause et al., 2022).

2.2 LPJ-GUESS

LPJ-GUESS is a dynamic global vegetation model which combines the advantages of an individual-based growth model with a global process-based representation of carbon, water and nutrient cycling to simulate vegetation-soil-atmosphere dynamics (Smith et al., 2014; Wårlind et al., 2014). LPJ_GUESS is analogous to the Madingley model in that plant species that share key ecological traits are grouped into plant functional groups (PFTs). The PFTs are defined by categorical traits such as bioclimatic preferences, photosynthesis pathways, lifeforms, leaf physiognomy, phenology and shade tolerance. Cohorts within the woody PFTs, which share identical traits are distinguished by properties like carbon and nitrogen masses, age or height. A list of all simulated plant functional types with a selection of their characteristics can be found in Table S1. Processes like soil hydrology, stomata regulation, photosynthesis, plant respiration, decomposition and phenology are



simulated on a daily basis, while leaf, root and sapwood turnover, biomass allocation and growth, and mortality are computed annually. To represent fire in the model, the integrated SIMFIRE module was used. We also implemented the necessary ability to switch the temporal and spatial grid cell handling loop, which allows herbivory related to animal migration between grid cells to be incorporated. These alterations allowed for defoliation as a partial loss of leaf biomass. Our model version deviates from the formulations of (Kautz et al., 2018) in that monthly herbivory-driven defoliation is incorporated, whereas Kautz et al. used a yearly defoliation event at the 180th day of the year.

2.3 The Coupled Model System

Both models need to run through an offline and a coupled spin-up phase. Madingley starts with autotrophs, herbivores, omnivores and carnivores having the exact same biomass density. During the first years of spin-up, the interactions between the groups and the simulated physiological processes in Madingley rapidly shifts the cohort and autotroph biomass density towards more realistic magnitudes. Typically, this phase is completed after five simulation years, using a monthly timestep. LPJ-GUESS establishes its vegetation starting from bare soil and the spin-up includes an upscaled 10.000-year loop which accounts for the fact that soil carbon in some regions need much longer to reach an equilibrium. After the simplified soil spin-up, vegetation establishment and growth result in increasing litter input, which gradually decomposes and builds up carbon and nitrogen pools in the soil (Smith et al., 2014). Thus, a longer offline spin-up phase is needed. 500 years have proven to be a sufficient timespan for LPJ-GUESS.

After both models complete the offline spin-up phase, the data exchange between the models is enabled and a coupled online spin-up phase of 500 years is initiated to equilibrate LPJ-GUESS vegetation with Madingley herbivory, and Madingley's trophic pyramid with LPJ-GUESS vegetation biomass. During the first 50 years of this joint spin-up phase, the percentage of leaf biomass reduction in LPJ-GUESS in response to Madingley herbivory is gradually increased so as to not kill off plant age-cohorts with initially unrealistically high herbivory rates. After 50 years, 100% of the herbivory reduction is passed to LPJ-GUESS and the models are considered fully coupled at this timestep. An illustration of the coupled model system, including the different spin-up phases, can be found in Figure 1.

We assume that the animals will digest all the biomass they have eaten within one timestep. Since Madingley does not yet have a coupled carbon-nitrogen cycle, we here simplify the impacts of herbivory on the nitrogen cycle by adding all eaten leaf nitrogen mass directly towards the litter pool in LPJ-GUESS at the time of the defoliation event, given that animal faeces and carcasses are enriched in nitrogen. Analogously, all leaf carbon mass removed gets accounted towards the carbon litter pool. This latter assumption results in an overestimation of carbon remaining in the system, since animals respire carbon during growth. We therefore concentrate our initial analysis here on impacts of herbivory on photosynthesis and growth and will quantify impacts of plant-animal interactions on total ecosystem carbon and nitrogen cycling in a future analysis with an updated version of Madingley which incorporates the animal stoichiometry and explicit C and N cycling (in prep.).



2.4 The Coupling Loop

125 Data is exchanged between both models through a file exchange approach, which ensures that updates of both models can easily be integrated. It also gives flexibility such that LPJ-GUESS can be coupled to different version of Madingley, while Madingley in turn could be coupled to a number of different vegetation models. Coupling via file exchange also allows tracking of the exchanged data without the need of any further process memory.

In LPJ-GUESS, a PFT age-cohort's monthly leaf carbon mass is determined by an estimate of its annual maximum leaf carbon mass m_c multiplied with a phenology factor f_{ph} , which is set to unity for evergreens, but varies between 0 to 1 for
130 deciduous plants, depending on how environmental and climatic conditions develop over the course of the year. Every month, we sum up the leaf carbon mass of the PFT age-cohorts into an evergreen carbon stock m_e and a deciduous stock mass m_d based on their phenology. Herbaceous PFTs are accounted towards the deciduous leaf carbon stock m_d .

The monthly leaf carbon sums are captured per grid cell and then passed to Madingley. In case of evergreen stock mass, only
135 one third is passed on. This is due to different assumptions in the two models regarding the vegetation stock: The original Madingley model is calibrated with a monthly regrowing vegetation stock for both deciduous and evergreen plants. In contrast, LPJ-GUESS regrows its PFT age-cohorts at the start of each year. Giving herbivores access to the complete evergreen vegetation stock would cause unrealistically high damage to the evergreen PFTs at the start of each year – also due to the seasonality of deciduous trees, which leads to only evergreens being available as nutrition source. Furthermore,
140 evergreen PFTs in LPJ-GUESS have a 3-year leaf lifespan. This means, that damage to evergreen leaves persists 3 times longer than damage to deciduous PFTs. To show impacts of passing different amounts of evergreen biomass to Madingley, we conducted a sensitivity study (see Figure S3, S4 and S5). The formulations for aggregating the individual leaf carbon masses m_i in LPJ-GUESS into an evergreen leaf carbon mass per grid cell m_e (respectively m_d for deciduous and grasses) can be summarized as the following:

$$145 \quad m_e = \sum_i m_i * 1/3 \quad \left| \quad \forall i \text{ in evergreen individuals} \right.$$
$$m_d = \sum_i m_i * f_{ph} \quad \left| \quad \forall i \text{ in deciduous individuals} \right.$$

After receiving the vegetation data from LPJ-GUESS, Madingley runs its ecological processes, which result in a reduction of the leaf biomass by the herbivores and omnivores. This reduction of the stock biomass $m_{r,e}$ and $m_{r,d}$ is recorded and returned to LPJ-GUESS. LPJ-GUESS determines subsequently how much biomass has to be removed according to
150 Madingley. This reduction is calculated as separate evergreen and deciduous herbivory reduction fractions f_e and f_d :

$$f_e = \frac{m_{r,e}}{3 * m_e} , \quad f_d = \frac{m_{r,d}}{m_d}$$

which is then weighted with f_{ph} and applied to every age-cohort's maximum annual leaf carbon mass. This assures that a PFT age-cohort that did not contribute to the original leaf stock that was supplied to herbivores and omnivores is not



155 damaged by herbivory. This would be an issue e.g. early in the season when f_{ph} is still zero for some age-cohorts. The new individual's leaf carbon mass is then therefore calculated for evergreen or deciduous PFTs like the following:

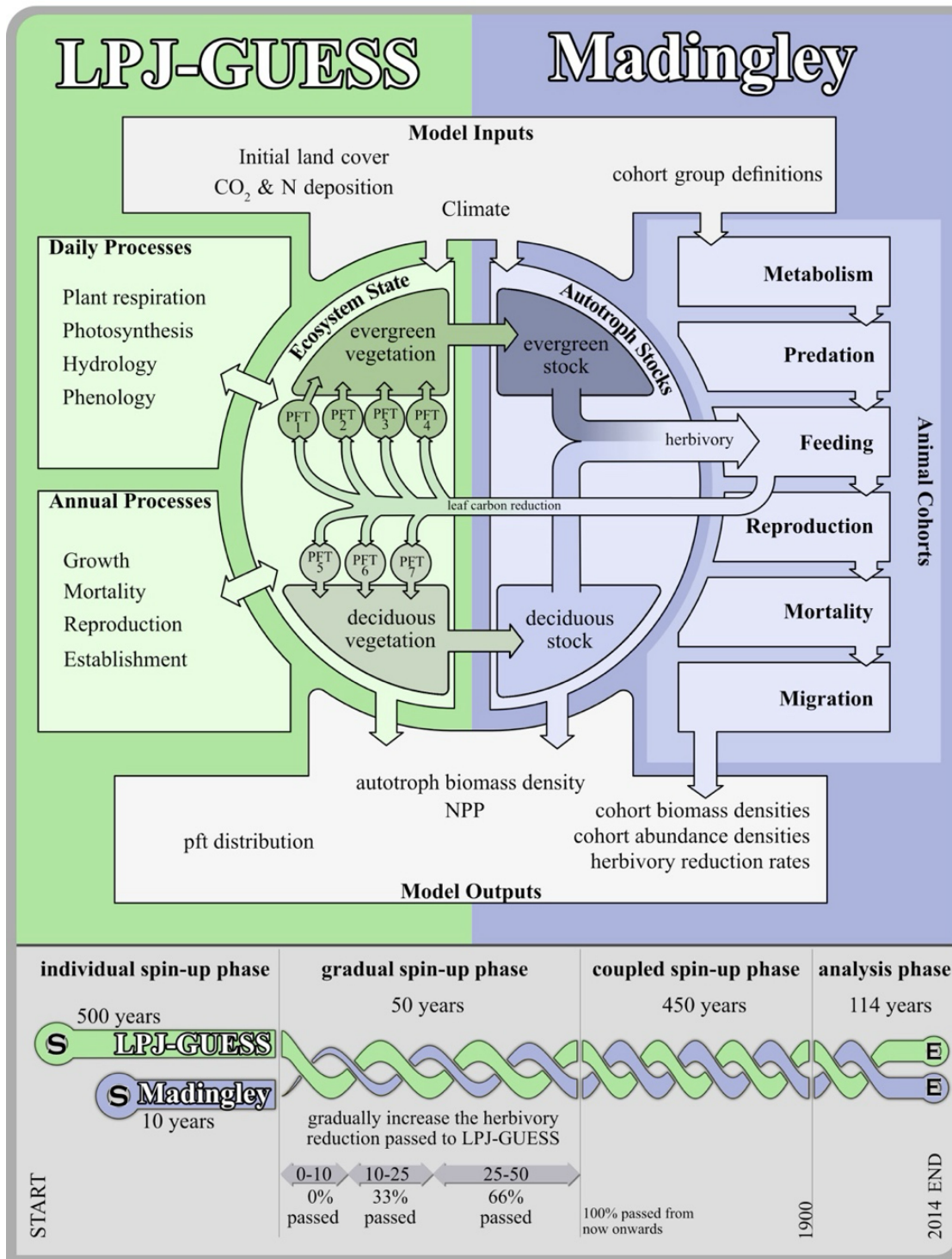
$$\begin{aligned} m_{i,new} &= m_i - m_i * f_e && | \forall i \text{ in evergreen individuals} \\ m_{i,new} &= m_i - m_i * f_d * f_{ph} && | \forall i \text{ in deciduous individuals} \end{aligned}$$

2.5 Study Setup

160 We simulate impacts of animal herbivory for the European-African continents, as a model domain that captures a large variety of biomes and climates (20°E – 50°W, 35°S – 75°N). We used historical climate data input from the CRUJRA v2.1 dataset (Harris, 2020), and historic CO₂ concentrations from 1901 onwards. During the spin-up phases, both models cycle repeatedly the climate data from 1901 to 1930, applying a standard CO₂ concentration of 296 ppm. Since we focus on carbon cycling, we kept the nitrogen deposition constant at 2 kg N ha⁻¹ yr⁻¹ (Smith et al., 2014).

2.6 Analysis

170 The simulation was run over the period 1901 to 2014. Changes in continental-scale NPP, vegetation composition, carbon and autotrophic respiration are presented as percentage increase or decrease of the coupled (“online”) simulation when compared to the stand-alone, uncoupled (“offline”) LPJ-GUESS simulation. Second, we analyse the distributions of the dominant PFTs, as determined by maximal leaf area index (LAI), throughout the model domain. We chose LAI as metric for PFT dominance since the PFT with the highest LAI is also the PFT with the largest surface available for photosynthesis within a grid cell. To examine the impacts of vegetation-animal interactions in more detail, we further identified 10 locations, shown in Figure 2. We arranged them from highest productivity (A1 & E1) to lowest productivity (A5 & E5).



175 **Figure 1: Illustration of the coupling process. The upper panel shows how both models exchange data and how the time loop is synchronized. The lower panel how the coupling is initialised and run.**

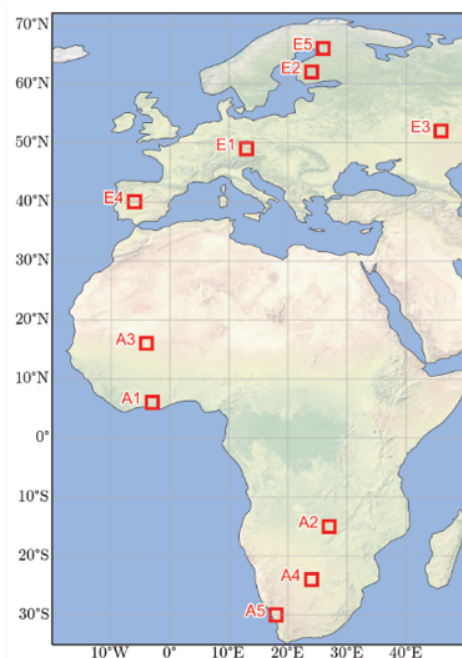


Figure 2: Locations selected for detailed analysis. Background map created with stock_img() by cartopy python package.

We compared the model output of the stand-alone LPJ-GUESS model and the coupled model system against monthly GPP flux measurements from the FLUXNET network and against satellite data, which are available via the International Land Modelling Benchmark Project (Collier et al., 2018) and are designed to be used for benchmarking ecosystem models. Since the FLUXNET measurement sites encompass the local site-climate but the simulation uses gridded 0.5° climate input, we preferentially aimed for regions within the simulation grid which include multiple FLUXNET stations and averaged the measured fluxes within the area. This was only possible in Europe, because there are only five FLUXNET stations in Africa. Thus, we compared FLUXNET station GPP data to the GPP of the corresponding simulated grid cell for three African stations. The FLUXNET dataset covers a time span from 1994 to 2014, but the individual stations only provide data for a fraction of the time span (see Figure S6). We averaged the available monthly GPP fluxes of the FLUXNET stations and compared them to the simulated average monthly GPP flux between 1994 and 2014.

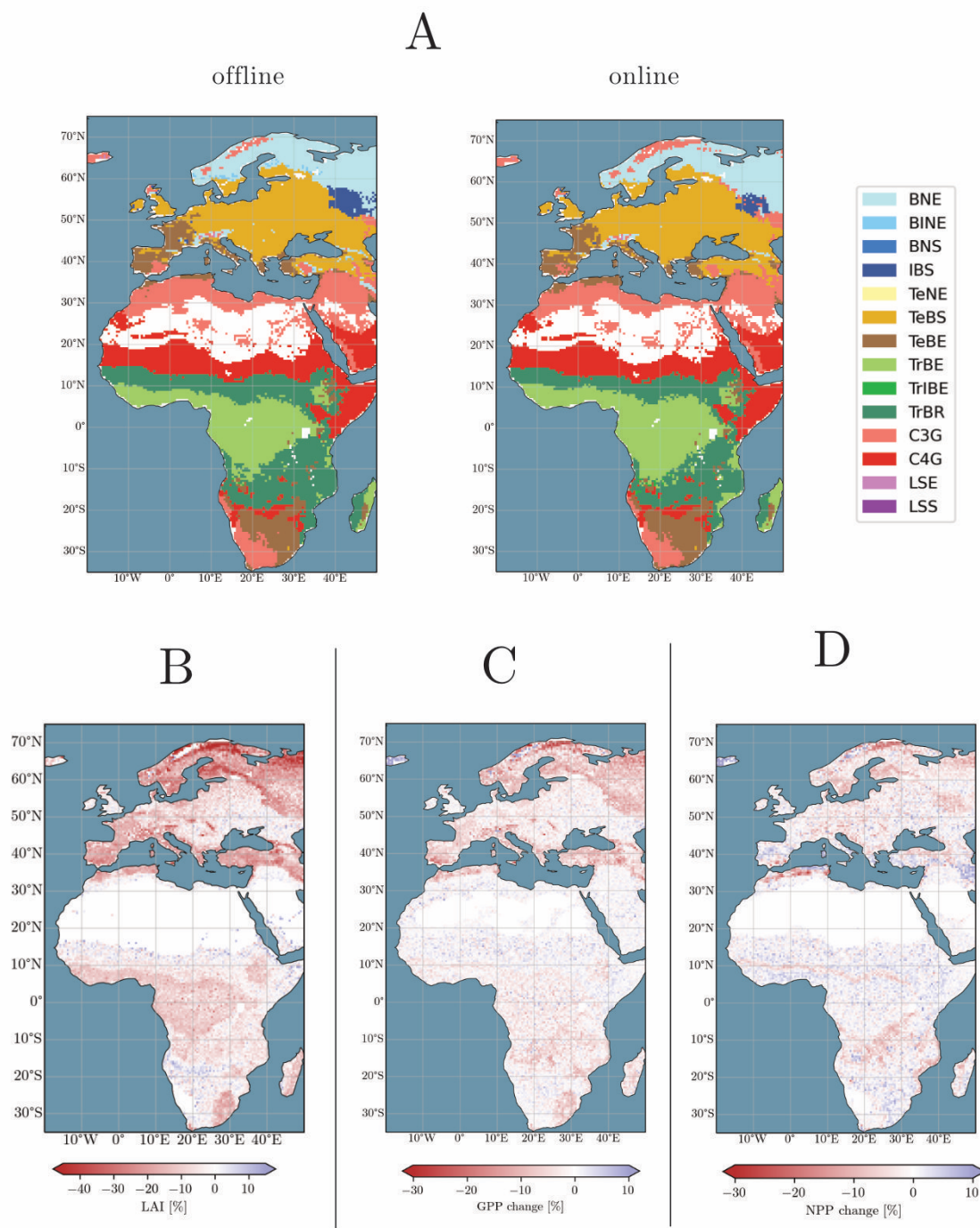
We compared the simulation output to GPP data from the FLUXCOM dataset (Tramontana et al., 2016), LAI from the AVHRR dataset (Fang et al., 2019), evapotranspiration from the GLEAMv33a dataset (Miralles et al., 2011) and woody vegetation carbon from a combination of multiple datasets (Pugh et al., 2023; Saatchi et al., 2011; Thurner et al., 2014). The underlying data is of a much higher resolution than the 0.5° resolution of LPJ-GUESS, but the International Land Model Benchmarking project maintains a collection of downscaled 0.5° datasets. Besides the AVHRR dataset, the datasets contain additional uncertainty estimates based on human impact factors like forest management and land use. The AVHRR data is also a model product and includes human land use. Forest vegetation (above- and below-ground) carbon estimates in



195 Thurner et al. (2014) covers northern boreal and temperate forests, including the European region of our model domain for
which Thurner et al. (2014) indicate low-medium uncertainty in their estimates. The data was compared to the simulated
vegetation carbon from 1980 to 2000. For tropical forest and savanna total biomass estimates, we used the African fraction
of the Saatchi et al. 2011 dataset (35°N - 35°S, 20°W - 50°E) which covers the time period 1995-2005. They estimate a
relatively high (30-45%) uncertainty, especially in the tropical rainforest. The impact from human timber extraction is
200 included in the estimates derived from remote-sensing information, while we simulate potential natural vegetation, including
a simplified estimates of natural disturbances and wildfires. Pugh et al. 2023 provided data that combined remotely sensed
disturbance-intervals with LPJ-GUESS derived vegetation carbon for the years 2001-2014. To minimize human influence in
our comparison, we chose the low disturbance natural vegetation scenario from Pugh et al. 2023, in which they focussed on
protected areas to keep human influence in their estimates to a minimum. Finally, we compared our simulations against a
205 dataset which intends to quantify aboveground biomass on non-cropland and non-pasture vegetation (thus also excluding
grassland) i.e. present land use distributions. It is based on the ESA 100m aboveground biomass dataset (Santoro and Cartus,
2023) and the ESA 300m land cover dataset (ESA Land Cover Climate Change Initiative (Land_Cover_cci): Global Land
Cover Maps, Version 2.0.7, 2024). For the comparison to our simulations, we assumed that aboveground biomass represents
70% of the total vegetation biomass, since LPJ-GUESS does not explicitly model aboveground biomass.

210 **3 Results**

When zooming in from the continental scale, where we only see small effects, introducing herbivory into LPJ-GUESS on a
country-level can affect the modelled vegetation composition substantially.



215 **Figure 3: Coupling related changes in grid cell's A) dominant PFT (based on PFT leaf area index) and B) grid cell's total leaf area index and C) the yearly average GPP flux and D) the annual NPP for the offline and online simulations. A shows only a dominant PFT in a grid cell, if that grid cell's total LAI is larger than 1. B, C and D show percentage-wise difference caused by the coupling. All figures were rendered over the last 30 years of the simulation.**

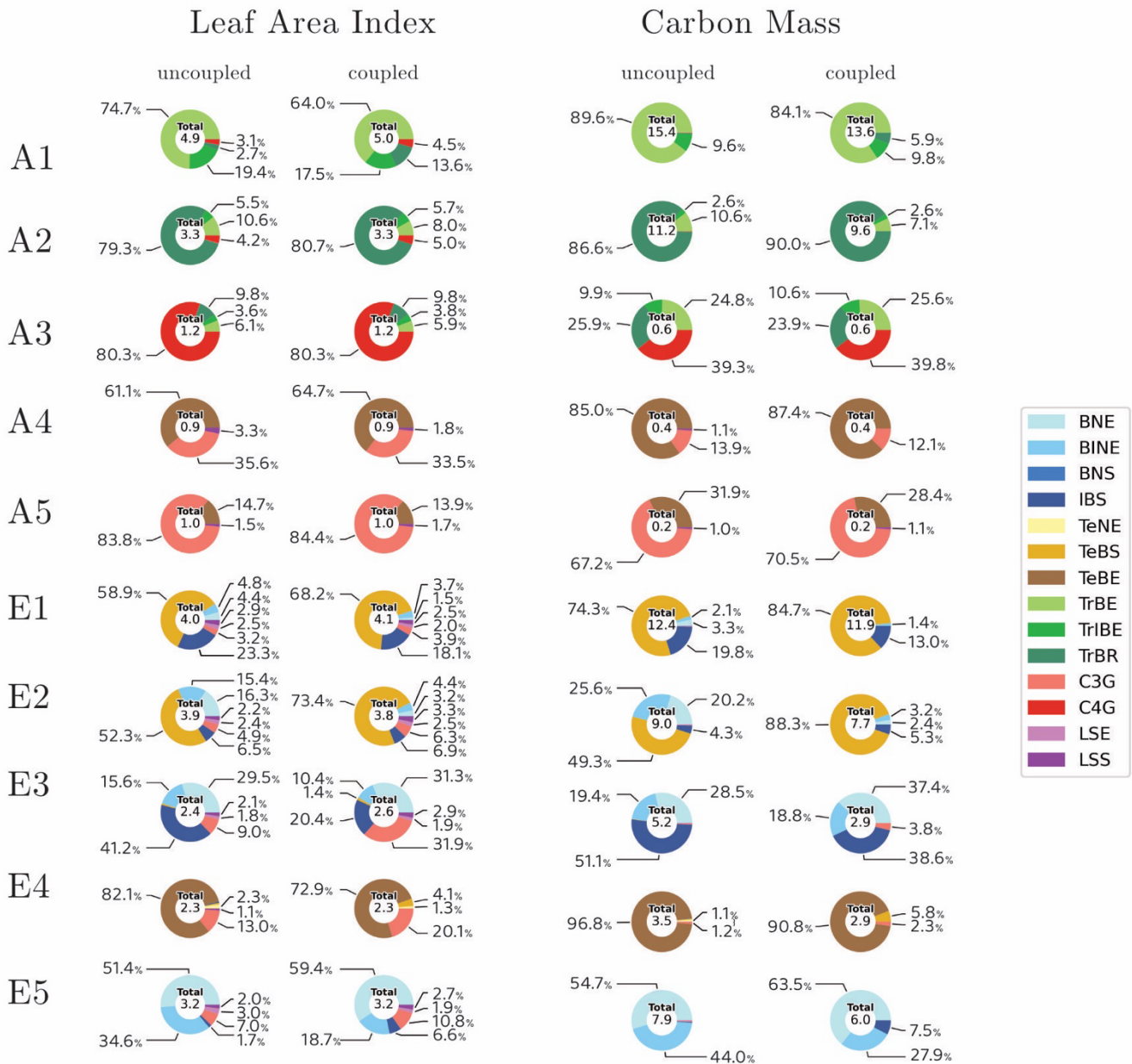


Figure 3A shows each grid cell's dominant plant functional type, i.e. the PFT with the highest leaf area index, averaged over the last 30 years of the simulation. Most notable are the shifts from woody towards C3 herbaceous vegetation in eastern Europe. Changes in overall grid cell LAI are visible in Figure 3B. Across the model domain, the average LAI decreases by -9.0% ($\pm 10.1\%$) in response to herbivory with the largest losses again in the boreal ecosystems. The spatial pattern of the responses in the overall grid cell GPP are broadly similar to those of LAI (Figure 3C), although the % changes are smaller. Across the model domain, GPP is decreased by -2.4% ($\pm 4.4\%$).

When aggregated across the model domain, changes in simulated NPP are also small when comparing LPJ-GUESS with (27.5 \pm 1.4 PgC) vs. without (29.0 \pm 1.4 PgC) the coupling. Herbivory thus leads to an overall reduction of NPP by 1.5 PgC (5.2% \pm 5.1%). A large spatial variability exists across the model domain, however, as NPP increased in response to herbivory throughout most of the African continent, while declining throughout Europe with exception of the Iberian Peninsula (Figure 3D). The impacts on total vegetation carbon mass are overall larger compared to NPP and GPP, with an average decline of -9.7% ($\pm 17.3\%$) in response to herbivory (Figure S1). The strongest effects are observed in the boreal regions of Scandinavia where between 60°N and 70°N, vegetation carbon is decreased by -29.4% with some grid cells showing a response as low as -45%.

In Africa, the vegetation carbon response is the strongest in the warm temperate regions of southern Africa (26°S, 25°E), where vegetation carbon is decreased by -28.6% (Figure S1). Autotrophic respiration is decreased on average by -3.6% ($\pm 6.0\%$), with strongest responses in the boreal ecosystems above 60°N, similar to the patterns found in vegetation carbon. Changes in the upper soil water content are showing no clear response with an average increase of +0.1% ($\pm 0.3\%$). However, we see an increase in soil water content of ~3% in the southeast of Spain and the Mediterranean shore north of the Atlas mountains (See Figure S1).

When exploring the individual locations in more details, for the Africa locations, no shifts in vegetation composition are found, except in *A1*, where the *TrBR* (tropical broadleaf raingreen) has a much higher carbon mass and LAI in the coupled simulation (Figure 4). Reductions in overall carbon masses are most pronounced in the central and northern European temperate locations, where *TeBS* (temperate broadleaf summergreen) is becoming more prominent when compared to the boreal evergreen PFTs (see location *E1*, *E2*). Furthermore, in boreal ecosystems (*E2*, *E3* & *E5*), the C3 herbaceous PFT has a higher LAI in the coupled simulation. This response is strongest at the most eastern location, *E3*. Without herbivory, *E3* is dominated by IBS (boreal shade-intolerant broadleaf summergreen) age-cohorts, both in regards of carbon mass and LAI. The area, which is dominated by IBS around *E3* is reduced significantly in size (Figure 4) in response to the coupling. The evapotranspiration rates of the PFTs responds to the coupling in a way similar to the LAI (Figure S2). Likewise, the NPP of the PFTs responds in a way similar to the carbon mass distribution (Figure S2). In (sub-)tropical and semi-arid regions, herbivory did thus not alter competition for water and nutrients between the PFTs significantly.



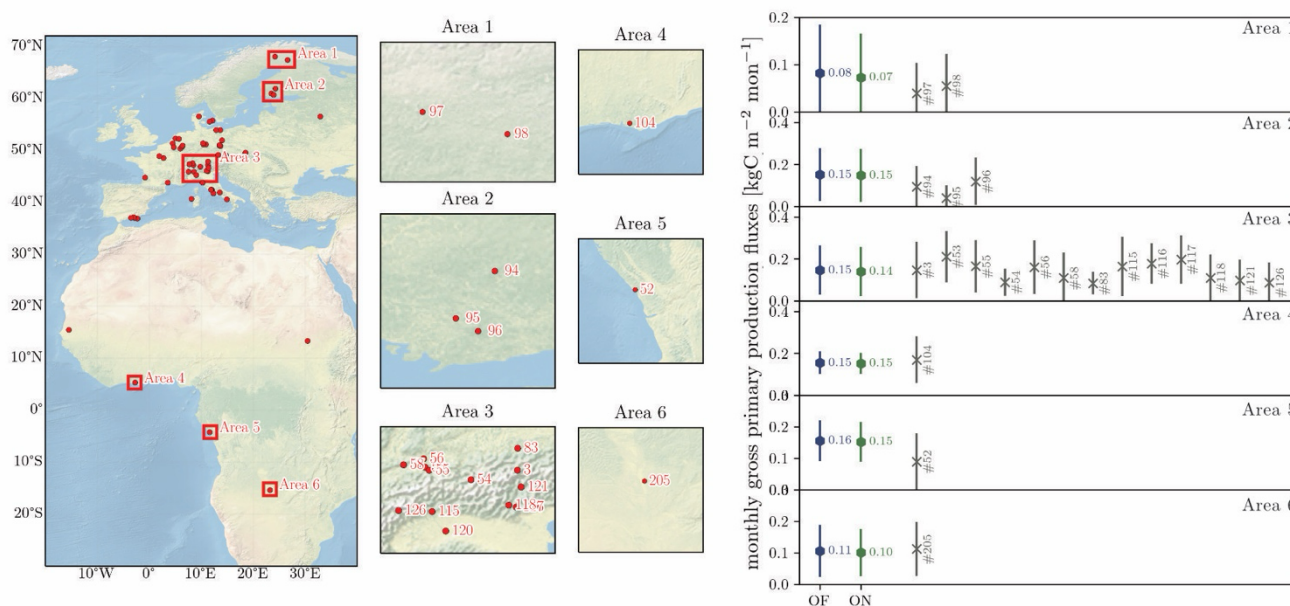
250 **Figure 4: Impacts of herbivory on carbon mass and LAI per PFT.** Colours are similar to Figure 3A. The pie charts show only PFTs which have a share of over 1% of the total carbon mass or LAI. The output was averaged over the last 30 years of the simulation.

3.1 Evaluation

Stand-alone LPJ-GUESS outputs and outputs from the coupled version are compared to GPP derived from FLUXNET sites
 255 (Reichstein et al., 2007). Modelled monthly GPP fluxes are well within the standard deviation range of the measured GPP



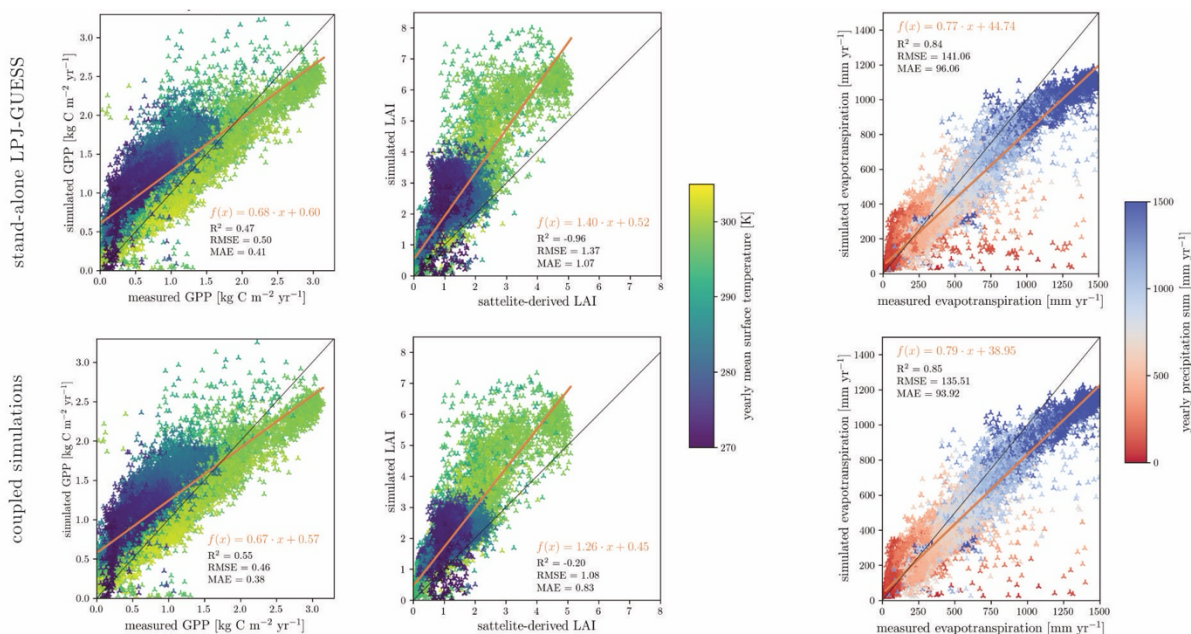
fluxes, both for stand-alone LPJ-GUESS but also the coupled version (Figure 5). Only for the boreal Area 1 and 2 (which correspond to boreal forests in Finland and Sweden) simulated GPP has a tendency to be higher than GPP derived from the flux towers in these regions.



260 **Figure 5: (Left) Distribution of FLUXNET eddy covariance measurement sites over the model domain with selected Areas and**
station numbers. (Right) Comparison between stand-alone LPJ-GUESS (OF), the coupled simulation (ON) and the FLUXNET
measurements with station number. The displayed GPP fluxes are monthly fluxes from the selected area which contains the
FLUXNET sites. Simulated GPP are for the period 1994 to 2014. The time spans of the corresponding eddy flux data (within that
 265 **same period) is provided by the separate FLUXNET stations and can be found in Figure S6. Background map “Shaded Relief and**
Water” by Natural Earth I.

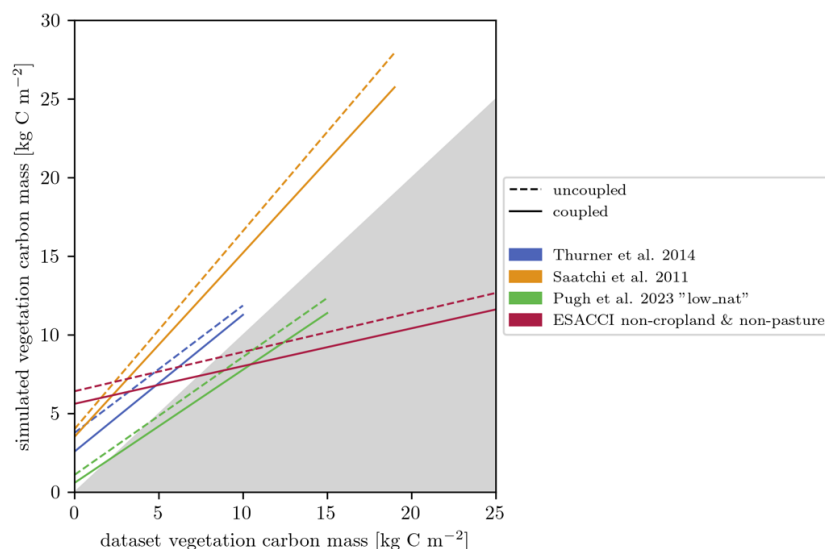
For evapotranspiration and GPP across the larger model domain, the modelled regression lines of stand-alone LPJ-GUESS and the coupled simulations show little deviation (Figure 6). The coupled model system appears to be simulating GPP estimates somewhat closer to the measured GPP, especially for grid cells in boreal ecosystems.

270 Furthermore, the stand-alone version of LPJ-GUESS shows a tendency to overestimate the leaf area index, most prominently in the warm ecosystems in southern Africa, where the satellite-derived LAI between 2 and 3 is doubled by the stand-alone LPJ-GUESS simulation. The coupled model system also overestimates the LAI, compared to the AVHRR-derived values but not as drastically as the stand-alone simulation.



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Figure 6: Left) Linear fit of simulated and measured GPP after FLUXCOM dataset (Tramontana et al., 2016). Middle) Linear fit of simulated and measured LAI after the AVHRR dataset (Fang et al., 2019). Right) Linear fit of simulated and measured evapotranspiration after the GLEAMv33a dataset (Miralles et al., 2011). All figures used model output between 1980-2014. Each marker shows the average of a grid cell over the 34-year timespan. The markers colour indicates the grid cell's yearly average near surface temperature and precipitation sum.



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Figure 7: Linear fit of simulated and measured vegetation carbon mass for four datasets. The non-cropland & non-pasture dataset is based on the ESA aboveground biomass (Santoro and Cartus, 2023) and the ESA land cover datasets (ESA Land Cover Climate Change Initiative (Land_Cover_cci): Global Land Cover Maps, Version 2.0.7, 2024). AGB was converted into total vegetation carbon mass.



285 A general issue with the above comparisons is that we compare data derived from measurements that include human-influenced land covers with simulations of natural vegetation. For many variables such as GPP or NPP (and to some degree also LAI) croplands and forests do not necessarily differ hugely such that the comparison is qualitatively useful, in particular since the purpose is to demonstrate that the coupling with herbivory does not push the model into an unrealistic state.

For carbon mass, the products we use here are for forests only and include also managed forests (Figure 7). Overestimation of these data with our simulations is thus expected, as seen in particular in the comparison to (Saatchi et al., 2011) for the forest vegetation carbon mass in Africa. For European forests, the dataset from (Pugh et al., 2023) matches the modelled vegetation carbon best for both model versions. Compared to the non-cropland and non-pasture aboveground biomass (AGB) levels, based on the ESACCI from (Santoro and Cartus, 2021), the coupled model system and the stand-alone version of LPJ-GUESS both show a overestimation in areas with low aboveground biomass and an underestimation in areas with high aboveground biomass. Overall, the coupled model system shows lower carbon mass when compared to stand-alone LPJ-GUESS.

4 Discussion

A high abundance of herbivores often results in reduced vegetation biomass (Dangal et al., 2017; Jia et al., 2018; Schmitz et al., 2014; Staver et al., 2021). In the current version of the coupled LPJ-GUESS/Madingley model system, no other effects like the acceleration of the nutrient cycles (Enquist et al., 2020) or shifts in plant species distribution through selective feeding (Schmitz et al., 2014; Staver and Bond, 2014) are parameterised. Thus, the general trends we see in vegetation and process-responses are caused by the monthly removal of green biomass. This removal in principle should reduce canopy photosynthesis, although the effect may be partially compensated by more light reaching into lower layer of the canopy. We therefore expected a reduction of plant biomass as a response to the herbivore introduction. While the overall effects across the modelled domains are small, spatial variation in the impacts are visible, which indicate biome specific dynamics. Nevertheless, the overall response is showing a negative trend in productivity, vegetation biomass, autotrophic respiration and LAI as we expected.

Human impacts, such as from timber harvest and grazing, and in general altering natural trophic chains (Ripple et al., 2015; Wardle and Bardgett, 2004), are expected to be included directly and/or indirectly in large-scale empirical datasets we used here for evaluation. Therefore, when comparing our simulation results to empirical data, we expect an overestimation in particular regarding forest vegetation carbon masses, in both the coupled and the uncoupled versions. Confidence in overall model performance arises to some degree from the good fit against the estimates by Pugh et al (2023), which are derived for areas with relatively little direct human impact. Still, the Pugh et al. (2023) estimates are strongly model-based, including the use of LPJ-GUESS (with an adjusted natural disturbance function compared to our model version), which explains in part the good agreement. Nevertheless, the simulations by Pugh et al. are only ca. 30% lower than the Thurner et al. (2014) estimates. However, in a pre-human world without anthropogenic influence, (Pearce et al., 2023) found that light woodland



and open vegetation could cover more than 50% of the European land surface – in contrast to the traditional assumption of a dense, close-canopy forest of a human-free world.

The data from Thurner et al. (2014) and Pugh et al. (2023) fits best to our simulation results. Generally, vegetation datasets for Europe match the simulation results better than dataset for Africa. In contrast to the degradation of savanna biomes due to impacts of human activity (Osborne et al., 2018), management across the forested areas of Europe (which are dominated by northern temperate and boreal forests) may not reduce total biomass drastically compared to natural vegetation. This was also confirmed by (Lindeskog et al., 2021) who simulated forest above-ground carbon with and without wood harvest in LPJ-GUESS.

The spatial patterns we found in our simulations show that under boreal climate conditions, the impact of leaf damage on photosynthesis may be more noticeable than in warmer climates due to the shorter growth season with fewer days that allow high photosynthesis rates. In boreal ecosystems, the combination of a reduced photosynthesis rate leads to a reduction of GPP despite of increased light transfer to deeper layers of the canopy, which is also reflected in the reduced NPP and thus the vegetation carbon mass. The increased light transfer to the underlying vegetation layer is visible in the increase of carbon mass and LAI of herbaceous PFTs and the resulting shifts in vegetation composition in the boreal regions. A similar trend was previously described in studies investigating general empirical relationships between herbivores and ecosystem productivity and structure: (Schmitz et al., 2014) stated that in boreal ecosystems, leaf damage caused by moose can cause declines in CO₂ uptakes and storage directly by browsing on photosynthetic tissue and indirectly through suppressing of tree growth. In other boreal forests, moose were reported to lower primary productivity of tree species (Bonan, 1992; Kielland and Bryant, 1998; Schmitz et al., 2003). Another aspect of the herbivory response in central and northern Europe is that broadleaf summergreen PFTs are becoming more prominent. In reality, evergreen plants grow leaves that are less nutritious than leaves of deciduous plants and animals chose their nutrition source depending on the nutrient content (Villalba and Provenza, 2009). In contrast, animals modelled by the Madingley model attempt to meet their metabolic cost through consuming evergreen and deciduous plants without taking leaf C:N ratios into consideration. The impact observed through e.g., moose selectively browsing on deciduous vegetation is not yet included. Still, our modelled responses broadly go into the right direction although at the moment we expect animals to overprioritize evergreen vegetation in our coupled model system.

For the African continent, both LPJ-GUESS versions are overestimating productivity, LAI and vegetation carbon mass. (Erb et al., 2018) found reductions in aboveground biomass stock in used tropical and subtropical forests and savannas, to be substantially larger compared to reductions in used boreal forests - and also larger when compared to managed temperate forest, even though the differences were less pronounced. In Africa the human pressure on dry forests and savannas is high due to the dependence of people on savanna ecosystem goods and services like timber for construction, fuelwood and charcoal, land surface for livestock grazing and wildlife tourism (Osborne et al., 2018). Overall, human pressure exerted on savanna ecosystems (Osborne et al., 2018; Otieno et al., 2019; Thiollay, 2006) is high and likely explains in part the model system's overestimation of the ecosystem's carbon stocks throughout the African continent. Besides humans, large grazer



350 populations, especially wildebeest and impala, also exert a significant amount of pressure on grassland ecosystems directly
through biomass removal and indirectly via grazer-grass-fire-interactions (Staver and Bond, 2014). The effects of grazers
tempering wildfires by removing potential fuel is often described alongside the control over the amount of organic matter
biomass and nutrients entering the soil pool (Schmitz et al., 2014). (Pachzelt et al., 2015), who also used LPJ-GUESS in
355 biomass, tree biomass and burned area. The found herbivory-induced responses in vegetation mass is similar to the responses
found in our simulations. The importance of grazers is also highlighted by (Kiffner and Lee, 2019), who showed that
herbivore grass consumption can triple browse consumption, as reported in Lake Manyara Nation Park in Tanzania.
However, the coupled model system so far does not differentiate herbivores into grazers and browsers.
Nevertheless, our study results show that by including herbivory via the coupled model system still upholds LPJ-GUESS's
360 ability to produce realistic biome species distributions and carbon fluxes.

5 Limitations and Outlook

The bi-directional coupling of LPJ-GUESS and Madingley is a further step towards exploring how plants and animals
interact in natural and human-modified ecosystems and regulate biogeochemical cycling. A number of important processes
are still lacking that prevent us from doing this holistically. For example, this version of the coupled models is lacking
365 explicit C:N cycling through animals. Implementing C:N stoichiometry into the process descriptions would enable
herbivores to (i) choose their diet, which would affect quantity and type of biomass consumed and (ii) return animal-based
litter with the relatively enriched N content found in nature, which is expected to affect nitrogen cycling in soils. A related
development is the need to differentiate between grazers and browsers in Madingley and to incorporate proper sub-annual
allocation of carbon and nitrogen to tissue growth in LPJ-GUESS.

370 The presented simulations are mimicking a pristine world without human impact. LPJ-GUESS is part of the Land-SyMM
framework (www.landsymm.earth), which enables simulations of human land management and related land cover and land
use change. In the future, we aim to include the implemented coupling between the Madingley model and LPJ-GUESS into
Land-SyMM framework and so begin to explore mechanistically interactions between humans and ecosystems of interacting
plants and animals.

375 6 Code and data availability

The LPJ-GUESS model code is available under the open access repository (<https://doi.org/10.5281/zenodo.11401444>). The
original Madingley model code is managed by the UN Environment Programme World Conservation Monitoring Centre
(UNEP-WCMC) at the University of Cambridge, England. The intellectual property right for the translated version we used
in this study is hold by the Radboud University in Nimwegen, Netherlands. Therefore, a DOI for the Madingley model code



380 cannot be provided publicly. The source can be made available under a collaboration agreement under the acceptance of
certain conditions. The input data used for the simulations are publicly available and cited in the manuscript.
Output data from the simulations are available under the open access repository (<https://zenodo.org/records/12788281>).

7 Author Contribution

Jens Krause: Conceptualization, Methodology, - Writing, Original draft, Visualization.

385 Mike Harfoot: Conceptualization, Methodology, Software, Writing – Review & Editing.

Peter Anthoni: Software, Validation - Review & Editing.

Moritz Kupisch: Conceptualization, Methodology

Almut Arneth: Validation, Writing – Review & Editing, Supervision, Funding acquisition.

8 Competing Interests

390 The contact author has declared that none of the authors has any competing interests.

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