

Coupling a physiological grazer population model with a generalized model for vegetation dynamics



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ABSTRACT

Large grazers have played a fundamental role in grassland and savannah ecosystems since these vegetation types formed in the late Miocene, but the feedback loops between vegetation and large grazers are still not well understood. Modern dynamic global vegetation models (DGVMs) lack the explicit impact of herbivory, but are calibrated to benchmarks including herbivory. We coupled a generalized model for the population dynamics of large mammalian grazers, based on animal physiology, with a plant-physiological model for vegetation dynamics and ecosystem processes, applicable at local to global scales (LPJ-GUESS). To our knowledge, this is the first attempt to combine process-based grazer population and vegetation modelling in a single generalized modelling framework, applicable at regional to continental scales. The capability of the coupled model to reproduce real-world grazer densities was tested by comparing modelled biomass densities with empirical data from African game parks, where semi-natural grazer populations still exist. The model reproduced inter-park differences in long-term average grazer biomass densities and yielded similar dependencies between major environmental drivers (e.g. precipitation, annual net primary productivity (NPP), dry season length) and grazer population densities as found in other more empirical studies. Amongst the potential environmental drivers, modelled NPP and dry season length were most strongly correlated with empirical and modelled biomass densities. Major discrepancies between modelled and empirical densities occurred for individual parks, but this was expected because the model did not include all factors that influence grazer populations (e.g. nutrient dynamics and poaching). The generalized flexible framework of the coupled model makes it possible to apply the model to other regions, to include further processes (if data for parameterizing them is available) and to parameterize other types of grazers. It could become a useful tool for investigating interactions between grazers and vegetation in a process-based framework.

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Abbreviations: A_{HFT} , adult grazer body mass; b, c , scaling factors; B , number of offspring; B_{Cond} , body condition; β , intake velocity of a grazing species; CPC%, crude protein fraction; d_{Living} , digestibility of functional grass biomass; d , digestibility of consumed grass; E_D , daily energy expenditure by grazer; E_M , monthly energy expenditure by grazer; F_j , current fat depot; F_{Max} , maximum age-specific grazer fat depot; G_d , proportion of functional grass in grazer forage; HFT, Herbivore functional type; I_D , daily intake by grazer; I_M , monthly intake by grazer; I_{Max} , maximum daily intake by grazer; IOM, Illius and O'Connor model; j , age class; L_{phen} , functional leaf carbon; m , metabolic coefficient; ME, metabolisable energy; M_j , age specific grazer body mass; M_0 , birth weight; N , number of breeding grazers; NE, net energy; p , fraction of female individuals in a cohort; σ , standard deviation from the mean fat depot in a cohort; u_g , gut scaling factor; $V_{Consume}$, consumable grass biomass; V_{Dead} , dead grass biomass; V_{Living} , functional grass biomass; V_{total} , total grass biomass provided by LPJ-GUESS.

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1. Introduction

Large mammalian grazers (>10 kg) have been an integral part of dryland and savannah ecosystems since the rise of grasslands in the late Miocene (Cerling et al., 1997; Webb, 1983). Today, the livelihoods of many people depend on their grazing herds in rangelands. Even though the interactions between vegetation, grazers and ecosystem functioning have been heavily debated for decades (Farnsworth et al., 2002; Frank et al., 1998; McNaughton, 1985; Valeix et al., 2011; Wilmshurst et al., 1999), a unified theory has not emerged. A number of factors have been proposed as main drivers of grazer population densities, namely environmental stochasticity, which may prevent herbivore population growth to levels at which grazers can exert a strong influence on vegetation and thus be controlled by population density-dependent effects (Ellis and Swift, 1988; Gillson and Hoffman, 2007; Higgins et al., 2007; Sullivan and Rohde, 2002), annually integrated or dry-season forage availability (Illius and O'Connor, 2000; Ogotu and Owen-Smith, 2003) and predators (Fay and Greeff, 2006; Grange et al., 2004). However, it

is still unclear under which circumstances or to which extent one driver prevails over the others.

Mathematical models can be used for deriving hypotheses concerning the relative importance of these different drivers, but most population dynamic models for large grazers that have been developed thus far lack generality as they are parameterized for particular systems (e.g. Dunham et al., 2004) or are statistical models (e.g. Georgiadis et al., 2003). Furthermore, the representation of vegetation and forage dynamics in grazer population dynamics models is often rather simple, e.g. by using rainfall as proxy for vegetation growth or a constant vegetation growth factor (e.g. Basset et al., 1997; Owen-Smith, 2004). Recent advances in dynamic vegetation modelling (e.g. Prentice et al., 2007) have, as far as we are aware, not been utilized in population dynamic modelling of grazers. Also, vegetation models are believed to lack realism in certain systems because the effects of large grazers are neglected (e.g. Bond and Keeley, 2005).

In this study we implemented a generalized model for grazers, based on animal physiology (Illius and O'Connor, 2000) within a generalized framework for modelling vegetation and ecosystem processes that is applicable at local to global scales (LPJ-GUESS, Smith et al., 2001). The two models were linked through above-ground productivity of herbaceous biomass, which represents the available forage for grazers and thus limits thereby the population growth of grazers. Productivity of herbaceous biomass in the vegetation model is influenced by climate, CO₂-concentrations in the atmosphere, soil texture, fire and competition from trees. We parameterized three herbivore functional types (HFTs), corresponding to zebra (*Equus spec.*), wildebeest (*Connochaetes sp.*), and African buffalo (*Syncerus caffer*, excluding the subspecies *nanus*). Here, we present a first test of the model using multi-year average grazer biomass from African game parks and a time series for the Serengeti. We also explore potential drivers of grazer population dynamics in the empirical data and in the model results.

2. Materials and methods

In the coupled vegetation herbivore model (Fig. 1), simulated monthly above-ground herbaceous (C₃ and C₄ photosynthesis type) biomass drives the growth of grazing individuals and

their population dynamics (monthly mortality and annual breeding). Consumption of herbaceous biomass by grazers affects the herbaceous biomass, productivity, competition with trees, biogeochemical cycles and fire dynamics.

2.1. The LPJ-GUESS global vegetation model

LPJ-GUESS is a flexible, modular modelling platform for simulating vegetation dynamics and biogeochemical cycles at local to global scales. It includes the widely used Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM; Sitch et al., 2003), but vegetation dynamics (tree establishment and mortality, as well as tree size distribution, canopy structure and disturbance) can also be represented in more detail, adopting a forest gap model approach (Shugart and West, 1980). The more detailed mode is commonly referred to as LPJ-GUESS, or in earlier publications as the General Ecosystem Simulator (GUESS, Smith et al., 2001). Here, the detailed LPJ-GUESS mode was used, including the hydrological cycle by Gerten et al. (2004), disturbance through wildfires (Thonicke et al., 2001) and the global parameterization of version 2.1 (Ahlström et al., 2012). Savannah vegetation was represented by four plant functional types (PFTs): tropical rain-green trees (which shed their leaves during the dry season), tropical evergreen trees, and herbaceous plants with C₃ or C₄ photosynthesis. In one park, also the temperate broad-leaved evergreen tree PFT occurred. The global version of the model, which includes further PFTs, reproduces known global patterns of vegetation distribution, net primary productivity, carbon storage and the hydrological cycle (e.g. runoff).

A location in the model is represented as a stand, i.e. an area with identical environmental conditions, defined by soil texture and a set of climatic variables. The spatial extent of a stand is flexible and simply given by the spatial resolution of environmental driver variables, here a grid of 0.5° × 0.5° longitude and latitude (see Section 2.3.2). For each stand, vegetation is simulated in a number of replicate patches (without a specific location within the stand), in which individual tree establishment, mortality and patch-replacing disturbances are simulated stochastically (as commonly done in forest gap models). The size of a patch roughly corresponds to the maximum range of influence of one adult tree, here 1000 m². The output from the patches is then averaged to characterize the average

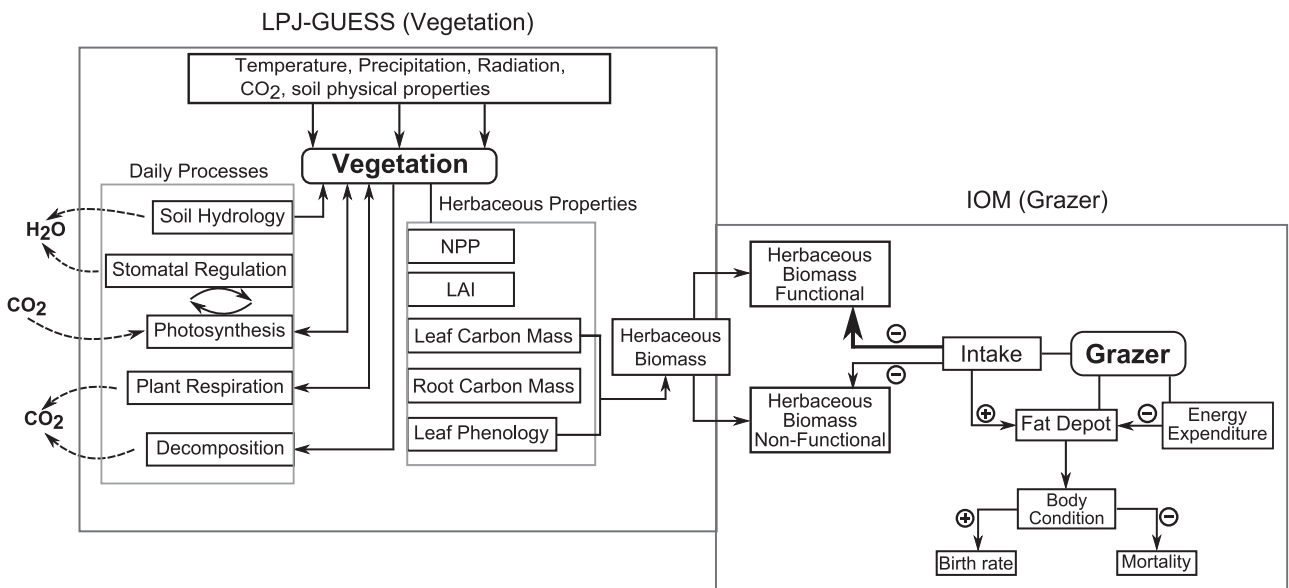


Fig. 1. Model scheme of LPJ-GUESS with the example of a herbaceous plant functional type (PFT, left) and the grazer submodel (right). Straight arrows indicate influence on compartments and interactions, dotted arrows show exchange with the environment. In the IOM part, plus indicates positive feedbacks, minus negative feedbacks. The abbreviations are net primary productivity (NPP) and leaf area index (LAI). The LPJ-GUESS scheme was partly adopted from Benjamin Smith (unpublished).

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