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Integrating Herbivore Population Dynamics Into a Global Land Biosphere Model: Plugging Animals Into the Earth System**Notes/Citation Information**

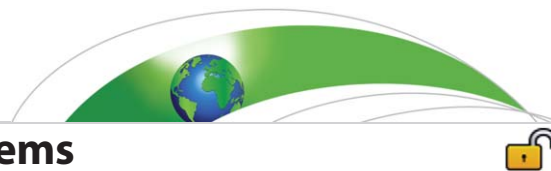
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RESEARCH ARTICLE

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Integrating Herbivore Population Dynamics Into a Global Land Biosphere Model: Plugging Animals Into the Earth System

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Key Points:

- Mammalian herbivore population dynamics has been represented in the Dynamic Land Ecosystem Model (DLEM 3.0)
- Simulation results indicate that herbivores have a significant impact on terrestrial carbon dynamics and hence carbon-climate feedbacks
- Animal as an essential component of ecosystems needs to be taken into account in the earth system modeling framework

Supporting Information:

- Supporting Information S1

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Abstract Mammalian herbivores are an essential component of grassland and savanna ecosystems, and with feedbacks to the climate system. To date, the response and feedbacks of mammalian herbivores to changes in both abiotic and biotic factors are poorly quantified and not adequately represented in the current global land surface modeling framework. In this study, we coupled herbivore population dynamics in a global land model (the Dynamic Land Ecosystem Model, DLEM 3.0) to simulate populations of horses, cattle, sheep, and goats, and their responses to changes in multiple environmental factors at the site level across different continents during 1980–2010. Simulated results show that the model is capable of reproducing observed herbivore population dynamics across all sites for these animal groups. Our simulation results also indicate that during this period, climate extremes led to a maximum mortality of 27% of the total herbivores in Mongolia. Across all sites, herbivores reduced aboveground net primary productivity (ANPP) and heterotrophic respiration (Rh) by 14% and 15%, respectively ($p < 0.05$). With adequate parameterization, the model can be used for historical assessment and future prediction of mammalian herbivore populations and their relevant impacts on biogeochemical cycles. Our simulation results demonstrate a strong coupling between primary producers and consumers, indicating that inclusion of herbivores into the global land modeling framework is essential to better understand the potentially large effect of herbivores on carbon cycles in grassland and savanna ecosystems.

1. Introduction

Mammalian herbivores are an essential component of the terrestrial biosphere and therefore affect the exchanges of energy, water, carbon, and greenhouse gases between land and the atmosphere (Herrero et al., 2009; Steinfeld & Gerber, 2010; Tian et al., 2016). Changes in herbivore abundance can lead to dramatic direct and indirect effects on plant composition, aboveground and belowground primary productivity, nutrient cycling, and other ecosystem processes (Augustine & McNaughton, 1998; Piñeiro et al., 2010; Steinfeld & Wassenaar, 2007). The overall impact of herbivores on forage productivity and diversity has been mixed, with results ranging from positive (increase) to negative (decrease) effects of herbivores on net primary production (Hoshino et al., 2009; Schönbach et al., 2011). A better understanding of herbivore population dynamics and their impact on ecosystem processes is essential to enhance our knowledge of how herbivores regulate ecosystem-climate feedback mediated by changes in carbon, nitrogen, and water cycles across different scales. However, animal as an essential component of ecosystems has been often forgotten in the current global land surface or biosphere-modeling framework.

Biotic factors such as species composition, plant morphology, productivity, and forage quality may affect the population size and spatial distribution of mammalian herbivores (Bailey et al., 1996). In areas with stable forage resources, mammalian herbivores are regulated in a density-dependent manner (Illius & O'Connor, 1999, 2000). As the herbivore population exceeds ecological carrying capacity, increased competition among herbivores for forage resources may lead to a reduction in herbivore productivity (Vetter, 2005), provided that supplemental feeding from stored forage resources are not considered. However,

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when herbivore populations are below carrying capacity, mortality during unfavorable years is reduced due to availability of greater forage and body fat reserves (Vetter, 2005). Thus, the availability of forage resources, both in terms of quality and quantity, may directly influence herbivore population dynamics.

Abiotic factors such as climate, topography, soil characteristics, and distance to water can directly (i.e., feed intake, water intake, growth, and reproduction) or indirectly (i.e., feed supply, parasites and diseases, and shelter) influence mammalian herbivore populations (Morignat et al., 2015; Rao et al., 2015; Reeves & Bagne, 2016; Williamson & Payne, 1978). Seasonal variation in precipitation creates alternating wet and dry periods, which forces herbivores to migrate (Owen-Smith et al., 2010) or lose weight (Illius & O'Connor, 2000) during periods of low resource availability. Likewise, extreme climatic conditions, such as drought and severe cold can indirectly affect herbivore productivity by limiting both forage availability and accessibility (Begzsuren et al., 2004; Rao et al., 2015). The effect of extreme climatic conditions on herbivores may vary depending on the type of herbivore, foraging behavior, and distribution patterns.

We also have a limited understanding about how mammalian herbivores affect ecosystem processes. Existing results indicate both positive and negative effects of herbivores on forage productivity, plant species composition, and soil organic matter input (Augustine & McNaughton, 2006; Bardgett & Wardle, 2003; Iri-sarri et al., 2016). Some empirical and modeling studies suggest that herbivory reduces primary productivity and decreases nutrient cycling rates (Dangal et al., 2016; Pastor & Cohen, 1997; Schönbach et al., 2011), while other studies indicate that herbivory can stimulate primary productivity and promote nutrient cycling (Frank et al., 2002; McNaughton et al., 1997). Likewise, herbivores may influence soil processes by altering the quantity and quality of resource inputs (i.e., exudation and litter inputs) and functional composition of vegetation, which may enhance or reduce litter quality and soil decomposition (Bardgett & Wardle, 2003). While previous experimental and modeling studies have quantified the effect of herbivores on individual carbon components, such as ANPP, soil organic carbon, and methane emission (Dangal et al., 2016; Herrero et al., 2013; Milchunas & Lauenroth, 1993), these studies do not account for population dynamics of herbivores, and therefore cannot quantify the feedback among climate, herbivores, and ecosystem processes.

Ecosystem models with explicit representation of herbivore population dynamics serve as an important tool to quantify the tradeoffs and synergies related to herbivory and forage productivity across broad temporal and spatial scales (Freer et al., 1997; Pachzelt et al., 2013; Rotz et al., 2005). Most population dynamics models lack generality, as they are parameterized for particular systems and specific herbivore types. For example, individual-based modeling simulates individual herbivores as a function of intake rates and energetics (Turner et al., 1993), while statistical models simulate herbivore dynamics as a function of the previous year herbivore size, rainfall, and mean annual temperature (Ogutu & Owen-Smith, 2003). While individual-based modeling approach is critical when biological data about the herbivores (i.e., specific behavior, activity, development, and interactions) are available (Grimm & Railsback, 2005), it is simply not feasible to simulate all individual herbivores at large scales. In addition, the level of information required to simulate individual herbivores may further constrain the applicability of the individual-based modeling approach (Hellweger et al., 2016). Similarly, statistical models can only be applied to particular species or for particular systems (Austin, 2002). It is therefore important to use a cohort-based approach, where a closed group of individuals with at least one similar attribute are aggregated into a single animal functional type.

Other complex models such as GRAZPLAN (Freer et al., 1997) and Growth, Metabolism and Mortality (GMM) model (Owen-Smith, 2002) have been used to model herbivore population dynamics with detailed animal physiology. For example, GRAZPLAN includes detailed animal and plant physiology, with pasture submodel operating at a daily time step, but it can only be applied to sheep or cattle (Gill et al., 2010; King et al., 2012; Moore et al., 1997). Similarly, the GMM model does not explicitly consider resource and climatic constraints on different age classes of herbivores (Owen-Smith, 2002). Therefore, it is imperative to improve current population dynamics models by including explicit representation of different herbivore types for quantifying herbivore dynamics in response to changes in both biotic and abiotic factors.

The purpose of this study is to explicitly integrate herbivore population dynamics into the global land modeling framework and to evaluate the impact of herbivores on ecosystem dynamics and ultimately, the biogeochemistry. In this study, we simulated the population dynamics of domestic herbivores but did not include wild herbivores because of inherent differences in their dynamics and stocking rates (Archibald & Hempson, 2016; Sheehy et al., 2010). In particular, we attempt to model the growth, mortality, and

reproduction of specific herbivore types as a function of available forage, climate, and other environmental factors. The herbivore population dynamics model was coupled with a global land ecosystem model (the Dynamic Land Ecosystem Model, DLEM 3.0) to quantify the effects of herbivores on carbon, nitrogen, and water cycles through aboveground biomass and the associated feedback of herbivores on vegetation and soil. Our primary objectives are to (1) simulate global mammalian herbivore population dynamics as a function of resource and environmental constraints; (2) evaluate model performance and quantify herbivore population dynamics across multiple sites in Asia, Africa, and North America; (3) quantify climate and environmental controls over herbivore population dynamics at the study sites; and (4) examine the impact of herbivores on aboveground net primary productivity (ANPP), net ecosystem productivity (NEP), heterotrophic respiration (Rh), and evapotranspiration. We hypothesize that the incorporation of herbivore population dynamics into the global land modeling framework will have a significant impact on terrestrial biogeochemistry, and the magnitude and direction of this impact will depend on the relative abundance of herbivores at a given location.

2. Materials and Methods

2.1. The Dynamic Land Ecosystem Model (DLEM)

The DLEM is a highly integrated global land ecosystem model that simulates the interactions and feedbacks among multiple ecosystem components to estimate the stocks and fluxes of carbon, nitrogen, and water at the landscape, regional, continental, and global scales (Pan et al., 2014, 2015; Tian et al., 2010, 2015a). The DLEM is driven by changes in atmospheric chemistry (i.e., nitrogen deposition, tropospheric ozone concentration, and atmospheric CO₂ concentration), climate, land-use and land cover (LULC), and disturbances (i.e., fire and timber harvest). The model has been extensively used to quantify carbon stocks (i.e., vegetation carbon and soil carbon) and fluxes (i.e., net primary productivity and net ecosystem productivity) and the exchange of methane and nitrous oxide between multiple terrestrial ecosystems and the atmosphere (Lu & Tian 2013; Pan et al., 2017; Ren et al., 2012; Tian et al., 2015a, 2015b; Yang et al., 2015). Detailed descriptions of the processes for simulating vegetation dynamics and biogeochemical cycles are available in our previous studies (Pan et al., 2014; Tian et al., 2010, 2011a, 2011b).

The basic simulation unit in the DLEM is a grid cell, which is covered by a mixture of vegetation cover, impervious surface, lake, stream, bare land, and glacier. At all the study sites, we ran the model at a resolution of $0.5^\circ \times 0.5^\circ$, which is approximately equal to $55 \text{ km} \times 55 \text{ km}$ at the equator. The vegetation cover in the DLEM includes five plant functional types (PFTs), of which four are reserved for natural vegetation and one for crops. The grid is assumed to have identical environmental conditions including climate, soil, and topography.

In this study, we simulated forage productivity for three major PFTs (i.e., C3 grassland, C4 grassland, and savanna) within a grid assuming that steppe and savanna biomass are the most preferred resources for mammalian herbivores at the study sites. In the new version of the DLEM (DLEM 3.0), we included the fifth core component (The Animal Dynamics Module; Figure 1). The Animal Dynamics Module includes four major processes: (1) energy intake, (2) energy expenditure, (3) reproduction, and (4) mortality including both base mortality (age-related mortality) and starvation-related mortality, which occurs as an indirect consequence of extreme climatic conditions (i.e., drought and freezing winter conditions). We simulated the dynamics of cattle, horses, sheep, and goats during the course of this study. The detailed processes that regulate natality, mortality, and reproduction of different herbivore types are described in section 2.2.

2.2. Modeling Herbivore Population Dynamics

The representation of herbivore population dynamics in the DLEM 3.0 is based on several previous modeling studies (Freer et al., 1997; Illius & O'Connor, 2000; Konandreas & Anderson, 1982; Figure 2). The basic simulation unit for herbivore population dynamics is a grid, in which the maximum of four different herbivore types can coexist at a time. Although we attempted to simulate the population dynamics of four herbivores at the site level in this study, the simulation scheme makes the model applicable to any herbivore types and at regional to global scales. Using the DLEM 3.0, we simulated the population dynamics of cattle, horses, sheep, and goats in Mongolia, Africa, and the United States. We were particularly interested in browsing by goats versus grazing by sheep and cattle. We assumed that grazers feed on vegetation biomass at surface level while browsers feed on intact foliage, buds, and stems of woody trees and shrubs

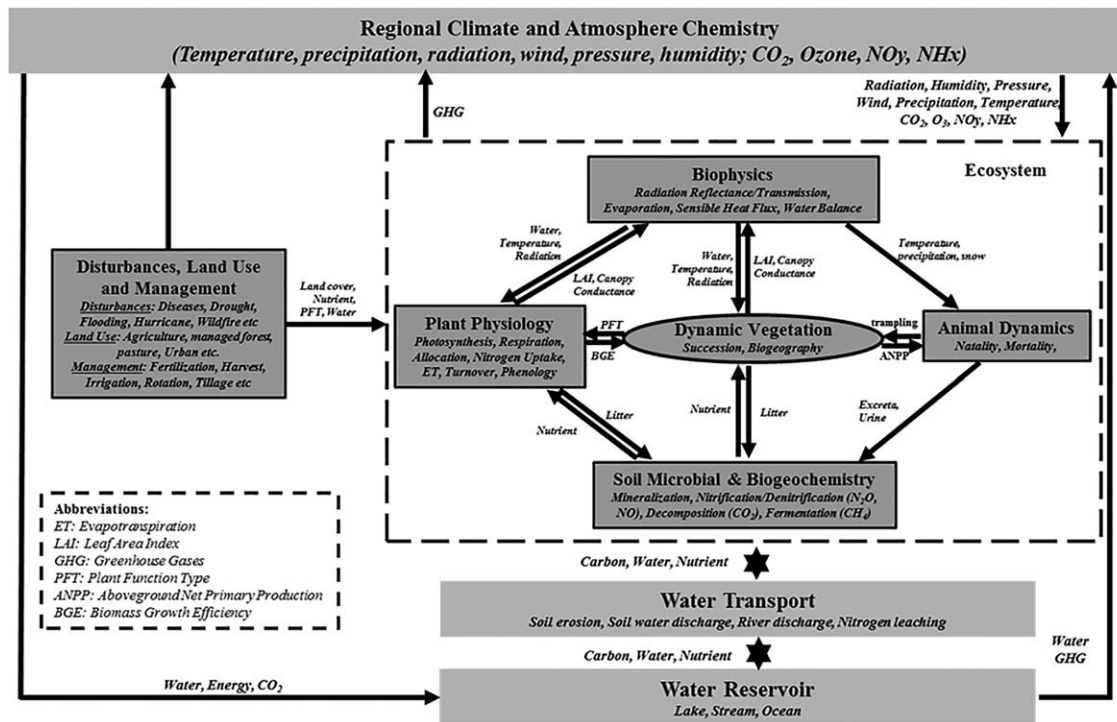


Figure 1. The simplified framework of the Dynamic Land Ecosystem Model (DLEM 3.0) coupled with herbivore population dynamics.

(Askins & Turner, 1972). Goats are mixed feeders, which rely on plant parts with higher digestibility such as buds, leaves, fruits, and flowers that contain less fiber and more protein. In case of limited supply of highly digestible plant parts, goats shift toward grasses. For instance, Malechek and Leinweber (1972) found that goats selected 60% shrubs, 30% grasses, and 10% forbs, while sheep selected 20% shrubs, 50% grasses, and 30% forbs. In the DLEM 3.0, we assumed that goats prefer shrubs over grasses, and leaves and reproductive parts over stems within grasses. This assumption allows us to capture the inherent differences in the grazing behavior of grazers and browsers. Below we describe the detailed model structure and algorithms through which we model energy intake, energy expenditure, reproduction, and mortality among different herbivore types within each grid cell.

2.2.1. Forage Intake and Digestibility

2.2.1.1. Maximum Forage Intake by Herbivores

The daily maximum forage intake (I_{max}) is defined as the potential intake by a single herbivore on a daily basis given unlimited forage biomass. In the DLEM 3.0, potential forage intake is related to animal size and food digestibility (measured in proportion) and is expressed as the maximum daily net energy intake (MJ/d)

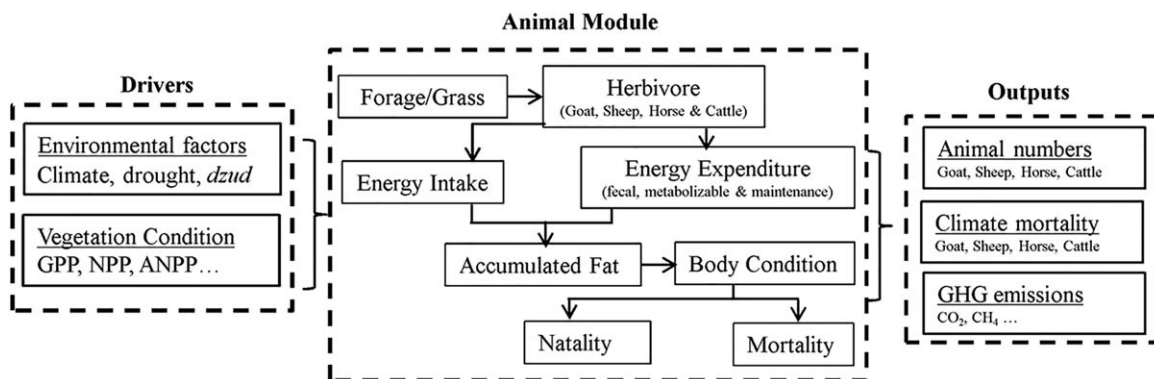


Figure 2. Modeling framework showing the input drivers, herbivore dynamics, and outputs from the coupled herbivore-land model (DLEM 3.0).

based on the relationship among physical and chemical properties of food, animal mass, and type of digestive system (Illius & Gordon, 1991, 1992; Shipley et al., 1999). The maximum intake rate (MJ/d) for different herbivore types (ruminants versus hindgut) were regressed against the body weight (kg) to derive the following equation:

$$I_{max} = i \times \exp^{j \times d} \times A_{It}^{(k \times \exp(d) + 0.73)} \times u_g \quad (1)$$

where i, j, k are the parameters that control the potential intake rates for different herbivore types; d is the biomass digestibility (measured in fraction) based on equation (4); A_{It} is the mature body mass of each herbivore type (kg); and u_g is a scalar to define the gut capacity of different herbivore types by age classes and is expressed as

$$u_g = \left(\frac{W}{A_{It}} \right)^{0.75} \quad (2)$$

where W is the body mass (kg) of different herbivore types by age classes.

The expression $i \times \exp^{j \times d}$ allows for the conversion of body mass (kg) to energy intake (MJ/kg of body weight) such that for hindgut herbivores i is 0.108, while for ruminant herbivores i is 0.034. The higher conversion coefficient (i) of hindgut herbivores assumes higher potential intake rate per unit body weight compared to ruminant herbivores. For example, comparison of ruminant and hindgut herbivores of similar body weights indicated that the ratio of horse to cattle dry matter intake averaged 1.73 and metabolizable energy intake averaged 1.48 (Johnson et al., 1982).

2.2.1.2. Forage Digestibility

The digestibility of the consumable forage ($V_{consume}$) in the DLEM is separated into the proportion of living and dead forage, with their respective digestibility rate (fraction). The digestibility of the dead forage is assumed to be 0.4 (Illius & O'Connor, 2000), while the digestibility of the living forage is a function of the quantity of available live forage at any time period and is modeled similar to Pachzelt et al. (2013):

$$d_{living} = 0.4605 + 0.239106 \times V_{living}^{-0.1697} \quad (3)$$

where d_{living} is the digestibility of live forage on offer (fraction) and V_{living} is the live aboveground forage (g DM/m²).

Equation (3) is derived by combining the dependence of digestibility on crude protein content of forage (Prins, 1996) and the exponential decrease of crude protein content with increasing biomass (van Wijngaarden, 1985), such that the coefficient 0.239106 allows for the conversion of living biomass (g DM/m²) to digestibility (fraction). The negative power (−0.1697) assumes that the digestibility of living biomass decreases with increasing biomass availability (van Wijngaarden, 1985).

The overall digestibility of the total available forage (both dead and living) is modeled as

$$d = d_{living} \times B_d + 0.4 \times (1 - B_d) \quad (4)$$

where B_d and $1 - B_d$ represent the proportion of functional (live) and nonfunctional biomass, respectively. B_d in the DLEM is based on Illius and O'Connor (2000), and is expressed as

$$B_d = \left(\frac{V_{living}}{V_{total}} \right)^{0.2} \quad (5)$$

The exponent 0.2 is used to describe diet selection during progressive defoliation by herbivores or annual variation in living biomass availability (Chacon & Stobbs, 1976). Illius and O'Connor (2000) showed that the standard error for the exponent was 0.032, with the correlation coefficient (r) of 0.79.

2.2.1.3. Relative Intake by Herbivores

The proportion of the potential intake that a herbivore can ingest depends on two attributes of forage supply: (1) relative availability and (2) relative ingestibility (Freer et al., 1997). In the DLEM, relative availability of the forage is measured as a function of model simulated aboveground biomass ($V_{consume}$), while relative ingestibility is a saturating function of available plant biomass (Illius & O'Connor, 2000). Thus, daily forage intake (MJ/d) is modeled as a function of maximum daily intake rate (MJ/d) based on equation (1) and the saturating function of available aboveground biomass:

$$I_{daily} = I_{max} \times \left(\frac{V_{consume}}{\beta + V_{consume}} \right) \quad (6)$$

where I_{daily} is the actual daily intake rate (MJ/d), $V_{consume}$ is the total forage biomass available for different herbivore types (kg DM/ha), and β is the half maximum intake rate (kg/ha/d).

2.2.2. Energy Intake and Expenditure

2.2.2.1. Metabolizable Energy Intake by Herbivores

Metabolizable energy is the energy remaining after urinary and gaseous energies during fermentation are subtracted from the total digestible energy. The total metabolizable energy intake in the DLEM 3.0 is a function of forage intake and its digestibility and is mathematically expressed based on Freer et al. (1997):

$$MEI_f = (17.2 \times d - 1.71) \times I_f \quad (7)$$

where MEI_f is the metabolizable energy intake from forage (MJ/d) and I_f is the daily forage intake (kg DM/d).

Equation (7) was estimated by regression based on 55 roughage feeds in Givens and Moss (1990), such that the expression $(17.2 \times d - 1.71)$ allows for the conversion of dry matter intake (kg DM/d) to metabolizable energy (MJ/d). However, we did not attempt to quantify the metabolizable energy intake for supplemental feeds and milk in this study.

To obtain the amount of grass (kg DM) necessary for daily energy intake, the intake energy (I_{daily}) is divided by the net grass energy content. Mathematically,

$$I_f = \frac{I_{daily}}{N_e} \quad (8)$$

where N_e is the grass net energy content (MJ/kg DM), which depends on the total metabolizable energy content (MJ/kg) of grass, and is estimated based on ARC (1980) as

$$N_e = ME(0.503 + 0.019 \times ME) \quad (9)$$

where ME is the metabolizable energy content of the grass (MJ/kg DM), which is estimated based on ARC (1980) as

$$ME = 15.6 \times d \quad (10)$$

Equation (10) assumes that the digestible organic matter of forages has 15.6 MJ ME/kg DM.

2.2.2.2. Maintenance Energy of Herbivores

In the DLEM 3.0, total energy costs are simulated as the sum of energy required for maintenance, grazing, and travel (Freer et al., 1997). The metabolic energy required for maintenance is based on Corbett et al. (1985), which considers the effect of different feeding levels on metabolic energy requirements. The metabolic energy is expressed as

$$E_{daily} = \left(\frac{E_{metab} + E_{graze}}{K_m} + E_{lw} \times MEI_f \right) \quad (11)$$

where E_{daily} is the metabolic energy required for maintenance by different herbivore types (MJ/d), E_{metab} is the basal metabolic energy required by different herbivore types (MJ/d), E_{graze} is the metabolic energy required for maintenance of grazing and travel by different herbivore types (MJ/d), and E_{lw} is the fraction of metabolic energy intake required for maintenance of daily liveweight gain (unit less). E_{lw} is set to 0.09 for all herbivore types based on Freer et al. (1997). K_m is the efficiency of use of metabolic energy for maintenance (unit less).

The basal metabolic energy requirement (E_{metab}) is a function of body weight, age, sex, and milk intake and is expressed based on Freer et al. (2012):

$$E_{metab} = B_s \times S_s \times M_s \times W_s \times W^{0.75} \times \max(\exp(A_s \times age), 0.84) \quad (12)$$

where B_s is the basal metabolism scalar for metabolic energy requirement (unit less), S_s is the effect of sex on metabolic energy requirement (unit less), M_s is the effect of milk production on metabolic energy requirement (unit less), W_s is the effect of weight on metabolic energy requirement (unit less), W is the weight of different herbivore types by age classes (kg), A_s is the effect of age on basal metabolism (day^{-1}), and age is the age of different herbivore types (days).

The effect of sex on the metabolic energy requirement (S_s) is obtained from Wheeler (2015). We used an S_s value of 1.075 for a mixture of male and female herbivores.

The effect of milk production on the metabolic energy requirement (M_s) is based on Freer et al. (1997) and is estimated as

$$M_s = 1 + B_{milk} \times P_{milk} \quad (13)$$

where B_{milk} is the basal metabolism for milk intake (unit less) and P_{milk} is the proportion of diet as milk (unit less).

The energy required for grazing is a function of distance walked by different herbivore types, which is reduced to zero when herbivores are not grazing. Mathematically,

$$E_{graze} = C_c \times W \times I_f \times (C_e - DMD_f) + E_{move} \quad (14)$$

where C_c is the chewing cost of herbivores (MJ/kg²), C_e is the chewing efficiency (unit less), DMD_f is the dry matter digestibility of consumed forage (unit less), and E_{move} is the energy required for movement (MJ) and is expressed as

$$E_{move} = E_h \times D_c \times W \quad (15)$$

where E_h is the energy cost of walking (MJ/km/kg) and D_c is the horizontal distance equivalent travelled (km).

The horizontal distance equivalent travelled (D_c) is estimated as the product of horizontal distance travelled and the steepness of the land (L_{steep}):

$$D_c = \begin{cases} L_{steep} \times \frac{\min\left(1.0, \frac{S_{thres}}{S_{actual}}\right)}{(0.000057 \times V_{living} + 0.16)} & V_{living} \geq 100 \text{ kg DM/ha} \\ L_{steep} \times \frac{\min\left(1.0, \frac{S_{thres}}{S_{actual}}\right)}{(0.000057 \times V_{dead} + 0.16)} & V_{living} < 100 \text{ and } V_{dead} \geq 100 \text{ kg DM/ha} \\ 0 & V_{dead} < 100 \text{ kg DM/ha} \end{cases} \quad (16)$$

where D_c is the distance covered as its horizontal equivalent (km) and L_{steep} is the steepness score of the land on a scale of 1–2 with a value of 1 indicating that the land is flat, while the value of 2 indicating that the land is steep. In the DLEM 3.0, the slope of the grid is scaled in the range of 1–2 to obtain the steepness score. S_{thres} is the threshold stocking rate of different herbivore types (head/ha) and S_{actual} is the actual stocking rate of different herbivore types (head/ha).

The value of 0.000057 implies the average distance (km) travelled by herbivores per unit of biomass availability (kg DM). Overall, equation (16) assumes that the distance travelled decreases with increasing biomass availability.

2.2.3. Growth and Reproduction of Herbivores

In the DLEM 3.0, growth of herbivores is calculated at a daily time step as a difference between the amount of energy gained and the amount of energy lost by herbivores (Illius & O'Connor, 2000; Pachzelt et al., 2013). The net change in daily energy flux is further used to update the fat reservoir, which is given by

$$\frac{df}{dt} = \frac{(I_{daily} - E_{daily})}{m} \quad (17)$$

where m is the metabolic coefficient for the conversion between energy (MJ/d) and fat (kg/d). The value of m is based on Blaxter (1989), such that $m = 39.5$ MJ net energy/kg for $I_{daily} < E_{daily}$ (catabolism) and $m = 54.6$ for $I_{daily} > E_{daily}$ (anabolism).

Daily change in fat (df/dt) in equation (17) is used to update the fat pool, which determines the overall body condition (B_{con}) of the herbivores.

$$B_{con} = \frac{F}{F_{max}} \quad (18)$$

where F is the net fat storage at the end of the year (kg) and F_{max} is the maximum fat reserves for each age class of herbivores (kg).

Body condition (B_{con}) in the previous year is then used to determine the number of offspring born in the current year. The number of newly born offspring is based on the number of mature herbivores and their body condition. Mathematically,

$$B_h = \frac{N \times p}{l * (1 + \exp(-b(B_{con} - c)))} \quad (19)$$

where B_h is the birth rate of different herbivore types (numbers/yr), N is the number of mature individuals for different herbivore types in previous year (heads), p is the population maximum annual intrinsic rate of increase (proportion), l is the length of birth season (fraction of a year), which is set to 1.0 in case of large herbivores (horse and cattle) and 0.8 in case of small herbivores (goat and sheep), and b and c are the constants that control the effect of body reserves on reproductive rate (unit less).

The value of p in equation (19) is set to 0.8, which implies a male to female ratio of 1:4, with every female having the possibility of giving birth to one offspring. B_{con} is based on the net changes in body fat condition within the mature age class of herbivores, such that a B_{con} of 0.3 would result in 50% of the female breeding while a B_{con} of 0.5 would result in 95% of the female breeding.

The length of the breeding season l allows the model to capture differences in breeding rates among different herbivore types. The l of 1.0 ensures that every female has the possibility of giving birth to one offspring per year, while the l of 0.5 results in a birth of 2.0 offspring per year.

2.2.4. Mortality

In the DLEM 3.0, we account for two potential causes of herbivore mortality. One is a daily mortality that occurs under normal conditions (base mortality). The other is mass herbivore mortality as a result of extreme climatic conditions, such as summer drought or freezing winter conditions (Begzsuren et al., 2004; Rao et al., 2015), which increases the risk of starvation-related mortality.

2.2.4.1. Mortality of Herbivores

The mortality of herbivores is predicted daily as a function of basal rate and body condition, which varies based on specific herbivore type (Freer et al., 1997; Pepper et al., 1999). The model assumes that there is a greater risk of death in herbivores, if the body condition is below a threshold. The model estimates age-related (base) mortality, starvation-related mortality, and mortality associated with low fat depot (starvation) based on Pepper et al. (1999):

$$MR = \begin{cases} M_{base} + 0.3 \times \left(1 - \frac{BC}{BC_{crit}}\right) & BC < BC_{crit} \ \& \ W_{daily} < 0.2\delta N \\ M_{base} & \text{else} \end{cases} \quad (20)$$

where MR is the mortality rate of herbivore (fraction), M_{base} is the basal mortality constant for specific herbivore type (fraction), W_{daily} is the daily weight gain (kg/d), BC is the relative body condition and is expressed as a ratio of base weight (kg) of herbivores to normal weight (kg) of herbivores, BC_{crit} is the threshold body condition below which death is assumed to occur at a higher rate, δN is the normal weight gain for different herbivore types by current age (kg/d), and BC_{crit} in the DLEM is expressed as

$$BC_{crit} = 1 - 0.2 \times (1 + Z) \quad (21)$$

where Z is given by

$$Z = \min\left(1, \frac{\delta N}{A_{lt}}\right) \quad (22)$$

where A_{lt} is the reference mature body weight (kg).

The normal body weight gain (δN) is expressed as a function of mass, age, and weight at birth of processed herbivore type (Freer et al., 1997) and is given by

$$\delta N = A_{lt} - (A_{lt} - W_{birth}) \times \exp\left(-0.0157 \times \frac{age}{A_{lt}^{0.27}}\right) \quad (23)$$

where W_{birth} is the weight at birth (kg).

2.2.4.2. Methane Emissions From Herbivores

Methane (CH_4) emissions is a function of daily gross energy expenditure, forage digestibility, and liveweight of different herbivore types (IPCC, 2006). IPCC (2006) requires estimate of gross energy content, which is defined as the sum of net energy for maintenance and growth. Mathematically, we first calculate the gross energy requirement of different herbivore types based on daily net energy expenditure and the percentage of digestible energy in the diet:

$$GE = \frac{\frac{NE_m}{REM} + \frac{NE_g}{REG}}{d} \quad (24)$$

where GE is the gross energy (MJ/d) and NE_m is the daily net metabolic energy expenditure for maintenance obtained as

$$NE_m = \frac{E_{metab} + E_{graze}}{K_m} \quad (25)$$

NE_g is the daily net metabolic energy expenditure for growth obtained as

$$NE_g = E_{lw} \times MEI_f \quad (26)$$

REM is the ratio of net energy available for maintenance in a diet to digestible energy consumed, and is estimated as

$$REM = \left[1.123 - (4.092 \times 10^{-3} \times (d \times 100)) + [1.126 \times 10^{-5} \times d^2] - \frac{25.4}{d} \right] \quad (27)$$

REG is the ratio of net energy available for growth in a diet to digestible energy consumed and is estimated as

$$REG = \left[1.164 - (5.160 \times 10^{-3} \times (d \times 100)) + [1.308 \times 10^{-5} \times d^2] - \frac{37.4}{d} \right] \quad (28)$$

where d is the digestible energy expressed in fraction and is estimated based on equation (4).

Equations (27) and (28) are obtained from IPCC (2006, see equations (10) and 10.15). Overall the equation assumes that as the digestibility of forage increases, the biomass intake of the herbivore decreases and vice versa.

We then calculate the methane emissions factor for each herbivore type, which is multiplied by the total number of herbivores to estimate total methane emissions within each grid cell. Mathematically,

$$E_f = \frac{GE \times Y_m}{55.65} \quad (29)$$

where E_f is the emissions factor (kg CH_4 /head/yr) and Y_m is the methane conversion factor, which refers to the percent of gross energy in feed converted to CH_4 . The CH_4 conversion factor is set to 6.5% for all livestock types based on IPCC (2006). The energy content of methane is 55.65 MJ/kg CH_4 .

It should be noted that equation (29) provides estimates of methane emissions for mature herbivore types, which likely differs for lower age classes. In the DLEM 3.0, we obtain methane emissions of lower age class individuals by scaling the emissions obtained for mature herbivore types as a function of their body weights.

2.3. Modeling Plant Production and the Feedback of Herbivores

The representation of primary productivity in the DLEM is based on several previous studies (Bonan, 1996; Collatz et al., 1991; Farquhar et al., 1980; Sellers et al., 1996). The detailed description of biophysical, plant physiological, and soil microbial processes is available elsewhere (Pan et al., 2014; Tian et al., 2010, 2011a,

2011b, 2015a). Here we only describe the major plant production processes that affect herbivore dynamics and the feedback of herbivores to carbon, nitrogen, and water cycles.

2.3.1. Primary Production

Gross primary production (GPP) is modeled using a modified Farquhar's model (Farquhar et al., 1980), where the whole plant canopy is divided into sunlit and shaded layers. For each of the two layers, GPP (g C/m²/d) is calculated by scaling leaf level assimilation rates to the whole canopy. Mathematically,

$$GPP_{sun} = 12.01 \times 10^{-6} \times A_{sun} \times plai_{sun} \times dayl \times 3600 \quad (30)$$

$$GPP_{shade} = 12.01 \times 10^{-6} \times A_{shade} \times plai_{shade} \times dayl \times 3600 \quad (31)$$

$$GPP_{total} = GPP_{sun} + GPP_{shade} \quad (32)$$

where GPP_{sun} and GPP_{shade} are GPP of sunlit and shaded canopy, respectively (g C/m²/yr). A_{sun} and A_{shade} are leaf level assimilation rates of sunlit and shaded canopy, respectively (μmol CO₂/m²/s). $plai_{sun}$ and $plai_{shade}$ are projected leaf area index of sunlit and shaded canopy, respectively (fraction). $dayl$ is daytime length (second) in a day. 12.01×10^{-6} is a constant to change the unit from μmol CO₂ to g C.

The carbon assimilation rate is a minimum function of three limiting factors: (a) photosynthetic enzyme (rubisco); (b) photosynthetically active radiation (light); and (c) photosynthetic product utilization (export). In the case of C4 species, the export limitation (c) refers to the phosphoenolpyruvate (PEP) carboxylase limited rate of assimilation. Mathematically,

$$A = \min(w_c, w_j, w_e) \times Index_{gs} \quad (33)$$

$$w_c = \begin{cases} \frac{(c_i - \Gamma_*) V_{max}}{c_i + K_c(1 + o_i/K_o)} & \text{for C}_3 \text{ plants} \\ V_{max} & \text{for C}_4 \text{ plants} \end{cases}$$

$$w_j = \begin{cases} \frac{(c_i - \Gamma_*) 4.6 \phi \alpha}{c_i + 2\Gamma_*} & \text{for C}_3 \text{ plants} \\ 4.6 \phi \alpha & \text{for C}_4 \text{ plants} \end{cases} \quad (34)$$

$$w_e = \begin{cases} 0.5 V_{max} & \text{for C}_3 \text{ plants} \\ 4000 V_{max} \frac{c_i}{P_{atm}} & \text{for C}_4 \text{ plants} \end{cases}$$

where w_c , w_j , and w_e are rubisco, light, and export (for C3) or PEP carboxylase (for C4) limited assimilation rates, respectively; c_i is the internal leaf CO₂ concentration (Pa); o_i is the O₂ concentration (Pa); Γ_* is the CO₂ compensation point (Pa); K_c and K_o are Michaelis-Menten constants for CO₂ and O₂, respectively; α is the quantum efficiency; ϕ is the absorbed photosynthetically active radiation (W m⁻²); and V_{max} is the maximum rate of carboxylation, which varies as a function of temperature, foliage nitrogen concentration, and soil moisture (Bonan, 1996) and is expressed as

$$V_{max} = V_{max25} a_{vmax} \frac{T_{day} - 25}{10} f(N) f(T_{day}) \beta_t \quad (35)$$

where V_{max25} is the rate of carboxylation at 25°C, a_{vmax} is the temperature sensitivity parameter, $f(T_{day})$ is the function of temperature related metabolic processes, $f(N)$ is the adjustment of photosynthetic rate for foliage nitrogen, and β_t is the soil moisture and temperature effects on stomatal resistance and photosynthesis (unit less).

The net primary production (NPP) in the DLEM is estimated as the net carbon gain after carbon losses through plant respiration, and is expressed as

$$NPP = GPP - Mr - Gr \quad (36)$$

where NPP is the net primary production (g C/m²/d), Mr is the maintenance respiration of plants (g C/m²/d), and Gr is the growth respiration of plants (g C/m²/d).

In the DLEM, Gr is calculated by assuming that the fixed portion of assimilated C will be used to construct new tissue (for turnover or plant growth). During these processes, 25% of assimilated carbon is used in growth respiration. However, maintenance respiration is a function of surface air temperature and biomass carbon content, and is expressed as

$$Mr_i = \min(rf_i \times f(T), r_{\max}) \times C_i \quad (37)$$

where i is the carbon pool of different plant parts including leaf, sapwood, fine root, and coarse root, Mr_i is the maintenance respiration ($\text{g C/m}^2/\text{d}$) of different pools, rf_i is the maintenance respiration coefficient for different plant parts. r_{\max} is the maximum respiration rate of different carbon pools and C_i is the carbon content (g C/m^2) of vegetation pool i .

The aboveground NPP (ANPP; $\text{g C/m}^2/\text{d}$) in the DLEM 3.0 is estimated as a ratio of aboveground carbon pools to the total carbon pools and is expressed as

$$ANPP = \frac{\text{leaf}C + \text{reprod}C + \text{stem}C}{\text{leaf}C + \text{reprod}C + \text{stem}C + \text{root}C} \times NPP \quad (38)$$

The ANPP calculated in equation (38) represents the consumable forage (V_{consume}) for herbivores explained in section 2.2.1.2.

Heterotrophic respiration (Rh ; $\text{g C/m}^2/\text{d}$) is estimated as the sum of net carbon fluxes from different soil pools and is expressed as

$$Rh = rh_{AOM1} + rh_{AOM2} + rh_{DOM} + rh_{SMB1} + rh_{SMB2} + rh_{SMR} + rh_{NOM} + rh_{PSOM} \quad (39)$$

where rh_{AOM1} is the carbon flux from slowly decomposable pool ($\text{g C/m}^2/\text{d}$), rh_{AOM2} is the carbon flux from easily decomposable pool ($\text{g C/m}^2/\text{d}$), rh_{DOM} is the carbon flux from dissolved organic matter pool ($\text{g C/m}^2/\text{d}$), rh_{SMB1} is the carbon flux from autochthonous (slow growth) soil microbial biomass pool ($\text{g C/m}^2/\text{d}$), rh_{SMB2} is the carbon flux from zymogenous (fast growth) soil microbial biomass pool ($\text{g C/m}^2/\text{d}$), rh_{SMR} is the carbon flux from soil microbial residue pool ($\text{g C/m}^2/\text{d}$), rh_{NOM} is the carbon flux from native organic matter (humus) pool ($\text{g C/m}^2/\text{d}$), and rh_{PSOM} is the carbon flux from passive organic matter pool ($\text{g C/m}^2/\text{d}$).

2.3.2. Herbivore Impacts on Grassland/Savanna Ecosystems

The impact of herbivores on carbon, nitrogen, and water cycles is simulated as a function of relative supply and demand of forage resources at a daily time step (Dangal et al., 2016). The maximum dry matter demand per unit area is dependent on the number of herbivores and the amount of food required by herbivores on a daily basis and is estimated as

$$C_{\text{demand}} = 0.05 \times I_f \times N_{it} \quad (40)$$

where C_{demand} is the maximum amount of dry matter required by herbivores (g C/d), I_f is the daily forage intake (kg DM/d) based on equation (8), N_{it} is the herbivore density expressed as the standardized units (sheep/ha), and 0.05 is a factor to convert kg/ha/d to $\text{g C/m}^2/\text{d}$.

The demand of forage by herbivores is restricted by the amount of forage produced per unit area. Thus, the dry matter supply is modeled as a function of grazing efficiency and the amount of forage available from a unit area of land. Mathematically,

$$C_{\text{supply}} = 0.95 \times (C_{\text{leaf}} + C_{\text{stem}} + C_{\text{reprod}}) \quad (41)$$

where 0.95 is a factor to limit the grassland biomass supply to 95% of the available biomass. C_{leaf} , C_{stem} , and C_{reprod} are carbon in leaf, stem, and reproduction pool, respectively.

Combining equations (40) and (41), the daily impact of herbivores on primary production is estimated as

$$\text{Intake}_{\text{daily}} = f_{\min}(C_{\text{demand}}, C_{\text{supply}}) \quad (42)$$

The biomass consumed by herbivores is then further separated into different parts using an energy flow approach. These parts include carbon losses during respiration, assumed to be 50% (Minonizio et al., 1998), and carbon losses through excretory processes, assumed to be 30% (Schimel et al., 1986). The amount of carbon and nitrogen lost through excreta is further separated into urine and feces assuming that the

Table 1
Key Parameters Controlling the Herbivore Population Dynamics in the DLEM

Parameters	Horse	Cattle	Sheep	Goat	Remarks	References
A_{it}	400	400	65	65	Mature mass (kg)	FAO and Illius and O'Connor (2000)
β	240	240	308	308	Half saturation intake rate (kg/ha)	Wilmshurst et al. (2000)
b, c	$b = 15, c = 0.3$				Parameters controlling effect of body reserves on birth	Illius and O'Connor (2000)
i, j, k	0.034, 3.565, 0.077				Ruminant intake const	Shiple et al. (1999)
i, j, k	0.108, 3.284, 0.08				Hindgut intake const	Shiple et al. (1999)
p	0.8				Intrinsic rate of increase	Illius and O'Connor (2000)
C_e	0.7	0.9	0.9	0.9	Chewing efficiency	Freer et al. (2012) for cattle and goats
C_c	0.02	0.025	0.02	0.02	Chewing cost (MJ/kg)	Freer et al. (2012) for cattle and goats
S_{thres}	5	5	40	40	Threshold stocking rate (heads/ha)	Freer et al. (2012) for cattle and goats
M_{base}	0.00003	0.00003	0.00003	0.00003	Basal rate of mortality (frac)	Pepper et al. (1999) for Sheep
F_{max}	0.3	0.3	0.3	0.3	Maximum body fat (fraction of mature weight)	Illius and O'Connor (2000)

nitrogen in urine is readily available for plant use (Dangal et al., 2016). However, we do not consider the flows of carbon and nitrogen associated with the death of herbivores in the current herbivore module.

2.4. Model Parameterization and Calibration

In this study, we parameterized and calibrated both vegetation and herbivore components of the model (Table 1). Based on existing and previous studies, we first determined the reasonable range of key model parameters that control the growth and productivity of both vegetation (White et al., 2000) and herbivores (Freer et al., 1997; Illius & O'Connor, 2000; Pachzelt et al., 2013). Within these ranges, we allow DLEM parameters to vary such that the parameters were optimized to fit the simulated carbon, nitrogen, and water fluxes with observations for specific plant functional types (PFTs). In this study, PFT refers to a group of biome (single plant type) that responds similarly to changes in environmental parameters. We grouped all grasses into C3 and C4 categories, and all shrubs into evergreen and deciduous categories. In the case of herbivores, we tuned the parameters such that the parameters were optimized to fit observed populations for specific herbivore types. During the start of simulation, we assumed that the total number of herbivores for each cohort is evenly distributed across all the age classes. The DLEM, however, updates the number of herbivores in each class annually assuming that small herbivores have a maximum of three age classes, while large herbivores have a maximum of four age classes.

2.5. Simulation Protocol

2.5.1. Input Data Sets

The model input data include daily climate data sets (daily mean temperature, maximum temperature, and minimum temperature and daily precipitation), monthly atmospheric CO₂ concentrations, annual land cover and land use (LCLU) maps, nitrogen deposition (Dentener, 2006), tropospheric ozone concentrations (Felzer et al., 2004), soil properties (texture, pH, and bulk density), and topographical information (e.g., elevation, slope, and aspect). Due to limited climate data, we generated daily data differently in each study region. In Mongolia, we used site level monthly climate data from National Statistics of Mongolia, Institute of Meteorology and Hydrology. These monthly climate data were allowed to follow the daily precipitation pattern based on CRUNCEP by restricting the total precipitation during a month using monthly meteorological observations. In Africa, we extracted daily climate data for the sites based on CRUNCEP global data sets. In the United States, we downloaded daily meteorological data from NOAA National Centers for Environmental Information (<https://www.ncdc.noaa.gov>). LCLU map for each site was extracted from the global LCLU maps, which was constructed by combining Synergetic Land Cover Product (SYNMAP; Jung et al., 2006) and HYDE 3.1 land use data (Klein Goldewijk et al., 2011). Monthly atmospheric CO₂ concentration data were derived from Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MsTIMP, <http://nacp.ornl.gov/MsTIMP.shtml>). Soil property data including soil texture, pH, and bulk density were extracted from Global Soil Data Task (www.daac.ornl.gov). The site level elevation, slope, and aspect were extracted from Global 30 Arc-Second Elevation product (GTOPO30; <https://lta.cr.usgs.gov/GTOPO30>).

2.5.2. Model Simulation and Implementation

The model simulation follows a three-step procedure: an equilibrium run, a spin-up, and a transient simulation. The model simulation begins with an equilibrium run driven by a 30 year (1980–2009) average climatic conditions, 1980 levels of atmospheric CO₂, and vegetation cover, assuming no herbivores exist in the system. The equilibrium run is carried out for a maximum of 10,000 years or until the net carbon exchange between the atmosphere and the site is less than 0.1 g C m⁻², the change in soil water pool is less than 0.1 mm, and the change in total nitrogen content is less than 0.1 g N m⁻² during two consecutive 20 year periods. The purpose of the equilibrium run is to get the initial conditions for the spin-up and transient simulations. After the model spin-up, we carry out a transient simulation using daily climate data, monthly atmospheric CO₂ concentrations, and time series LCLU maps.

For the simulation of herbivore population dynamics in Mongolia, we developed a scalar that accounted for anthropogenic changes associated with policy shifts (Chen et al., 2015). After the collapse of former Soviet Union in the early 1990s, Mongolia transitioned to private herd ownership, which resulted in a dramatic increase in herbivore populations (Johnson et al., 2006). At present, 95% of herbivores are privately owned with the largest proportions of sheep and goats since 1990 due to rapid growth of cashmere industry (Arulpragasam et al., 2004; Berger et al., 2013). In the DLEM 3.0, the transition from a centralized to market economy is represented by developing a scalar, which accounts for the rapid increase in number of herbivores and changes in herd composition during the post-Soviet Union period. The scalar is derived as a ratio of 30 year average (1961–1990) herbivore populations to annual herbivore populations for each herbivore type, which is directly applied to the respective herbivore pool following economic transition in Mongolia. However, in Africa and the United States, the scalar that accounts for policy shifts and economic transitions was set to 1.0. Applying a similar approach, Shabb et al. (2013) used different parameters developed through optimization to simulate herbivore populations by separating the study area into seven different time periods during 1970–2011. The time periods were categorized into socialist, postsocialist, *dzud* (severe winter), and drought years, such that each time period assumed a separate set of parameters to simulate herbivore populations. The *dzud* is a local term in Mongolia, which refers to a severe winter condition that causes herbivore mortality, primarily due to starvation.

In this study, we performed two different simulations. The first simulation was carried out in the absence of feedback of herbivores to ecosystems in order to quantify the population dynamics of herbivores in response to climate, forage availability, and local environmental conditions. In the second simulation, we introduced the feedback of herbivores to terrestrial ecosystems to quantify the impact of herbivores on carbon and water cycles at the study sites. We simulated the population dynamics of horses, cattle, sheep, and goats in Mongolia. However, in Africa and North America, we only simulated the population dynamics of cattle, sheep, and goats because census data for model evaluation of horses were not available.

Model evaluation in the DLEM 3.0 follows a two-step procedure: (1) evaluation of simulated carbon pools and fluxes and (2) evaluation of simulated herbivore density against observations at the study sites. Our study sites in Mongolia, Ethiopia, South Africa, Zimbabwe, and the United States were dominated by C3 grassland, C4 grassland, and savanna (Table 2). The detailed description of the study sites used to evaluate

Table 2
Site Information Used for Model Evaluation During 1980–2010 in Mongolia, Africa, and the United States

Site location	lon, lat	Elev (m)	Climate		Dominant	
			Tair (°C)	Prec (mm)	PFT	Herbivore
Arxangai, MN	101.5°E, 47.5°N	1,865	0.91	335.95	C3 grassland	Sheep
Bulgan, MN	103.6°E, 48.8°N	1,176	-0.6	329.54	C3 grassland	Sheep
Zavxan, MN	96.60°E, 47.7°N	2,547	-1.65	211.91	C3 grassland	Sheep
Selenge, MN	105.3°E, 49.1°N	926	-0.64	325.84	C3 grassland	Sheep
Ethiopia	39.1°E, 9.1°N	1,263	16.63	1,131.2	Savanna	Cattle
Zimbabwe	31.1°E, 20.2°S	941	19.1	667.9	Savanna	Cattle
South Africa	29.2°E, 30.5°S	1,203	13.6	795.4	Savanna	Sheep
Texas, US	99.9°W, 32.8°N	504	17.3	673.8	C3 grassland	Goat
Kansas, US	98.8°W, 38.4°N	330	17.6	659.5	C4 grassland	Cattle

carbon fluxes is available in supporting information Text S1. The comparison of simulated carbon fluxes with observation was performed in the absence of herbivory. After the evaluation of carbon fluxes against observations, we simulated the herbivore population dynamics as a function of DLEM-estimated ANPP and prevailing climatic and environmental conditions. The simulated herbivore density was then compared with observations at the study sites. The detailed description of study sites used to evaluate herbivore populations performance is available in supporting information Text S2.

To quantify the CH₄ fluxes from the fermentation of different herbivores, the model first estimated the CH₄ emission factor based on IPCC tier II approach for each herbivore type, which was then multiplied by the total number of herbivores at the specific sites to obtain the net CH₄ emissions. The model simulated emissions factor using an IPCC tier II approach was compared with the IPCC tier I approach in Mongolia, Africa, and the United States (supporting information Table S1).

2.6. Statistical Analysis

In this study, we used the mean and one standard deviation of the mean to estimate annual primary production, carbon and water fluxes, and herbivore population dynamics. To test for a statistically significant trend between 1980 and 2010, we performed linear regression at 5% level of significance. In addition, we used Welch's *t* test to test the statistically significant difference between model outputs with and without herbivores. We also used coefficient of variation and regression slope to evaluate the model performance against observations. Spearman correlation coefficient was used to quantify the relationship between environmental factors and model simulated outputs.

3. Results

3.1. Evaluation of DLEM-Simulated Carbon Fluxes

In Inner Mongolia, there is reasonable agreement between DLEM-simulated ANPP and observed ANPP (observed = 1.11 × simulated; $p < 0.05$; $R^2 = 0.87$; supporting information Figure S1). In Kansas, comparisons of daily gross primary production (GPP), ecosystem respiration (ER), and net ecosystem productivity (NEP) are all in reasonable agreement with eddy covariance (EC) measurements ($p < 0.05$; supporting information Figure S2). Overall, DLEM overestimated daily GPP and ER by 4% and 4.6%, respectively. In Africa, we found both simulated GPP and NEP to be significantly, though weakly, correlated with observations ($R^2 = 0.26$ for GPP and $R^2 = 0.20$ for NEP; $p < 0.05$; supporting information Figure S3). Overall, DLEM tends to underestimate daily GPP by 7.7%, but overestimate NEP by 0.38 g C/m²/d when compared to observations.

3.2. Evaluation of DLEM-Simulated Herbivore Density

The DLEM-simulated herbivore density is in reasonable agreement with observations across all sites (Figure 3 and supporting information Figure S5). In general, the DLEM simulation captured the mean herbivore populations across all sites in Mongolia, Africa, and North America ($R^2 = 0.72$; observed = 1.01 × simulated; $p < 0.05$). In Mongolia, the simulated herbivore density was in good agreement with observations ($R^2 = 0.95$; observed = 1.08 × simulated; $p < 0.05$; supporting information Figure S4a). Model tends to underpredict herbivore density by 8%. In the United States, overall model simulated results were in reasonable agreement with observations ($R^2 = 0.96$; observed = 0.89 × simulated; $p < 0.05$; supporting information Figure S4b), with slight overprediction (8%). In Africa, however, model simulated mean herbivore density overpredicts, but simulated herbivore density was not significantly different from observations ($R^2 = 0.83$, observed = 0.70 × simulated; $p < 0.05$; supporting information Figure S4c).

As market/policy changes have a substantial impact on herbivore dynamics, we also compared the DLEM-simulated herbivore density with and without the market/policy changes against observations. Simulation results show that herbivore density after the inclusion of policy changes were closer to observations compared to simulations without policy changes (Figure 4). We also found that the simulated herbivore density with policy changes were not significantly different from simulation without policy changes for sheep, cattle, and horses. However, simulation results show a significant difference in goat density between the simulation with and without policy changes ($p < 0.05$), indicating that policy changes strongly affect the abundance of herbivores. Overall, simulation results show that policy changes resulted in an increase in horses, cattle, sheep, and goat density by 10%, 5%, 1%, and 83%, respectively.

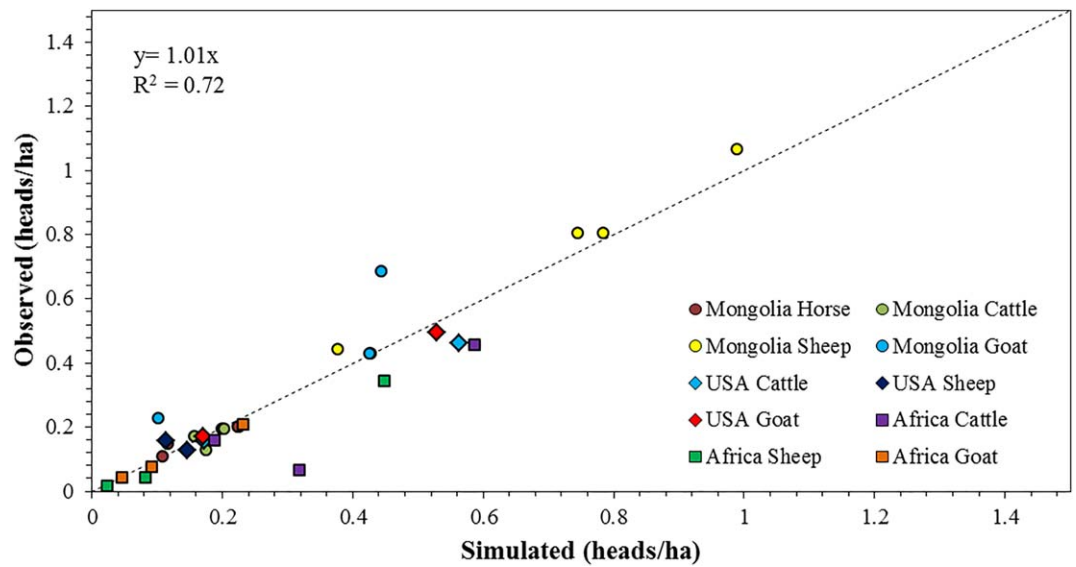


Figure 3. Comparison of simulated and observed population of horse, cattle, sheep, and goat across all sites in Mongolia, the United States, and Africa.

3.3. Herbivore Response to Resource Availability

Simulation results show that the temporal change in mean herbivore density across sites was correlated with annual ANPP; however, the effect was not statistically significant ($p = 0.28$; Figure 5). Interestingly, model results also indicate that individual herbivore density of horses, cattle, sheep, and goats were significantly correlated with annual ANPP ($p < 0.05$). Changes in annual ANPP explained 23% of the variation in the density of horses, while ANPP explained $< 10\%$ of the variation in case of other herbivores (cattle, sheep, and goats).

3.4. Herbivore Mortality During Extreme Climatic Conditions

In Mongolia, simulation results show maximum mortality of 27% of the herbivores due to a combination of drought and *dzud* (Figure 6). The temporal pattern of total mortality during 1980–2010 indicates that the total herbivore mortality in Mongolia has been increasing significantly at a rate of 0.003 heads/ha ($p < 0.05$). In Africa and North America, herbivores experienced a maximum mortality of 17% and 13%, respectively (Figure 6). The DLEM simulations show a base mortality of 8.7% across all sites during 1980–2010.

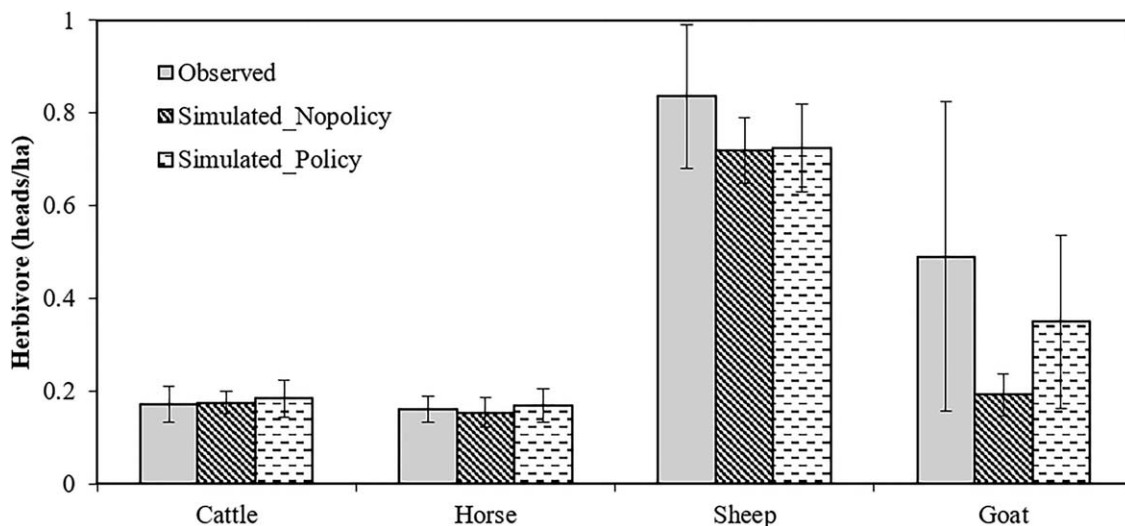


Figure 4. Comparison of simulated and observed population of different herbivores with and without policy changes in Mongolia.

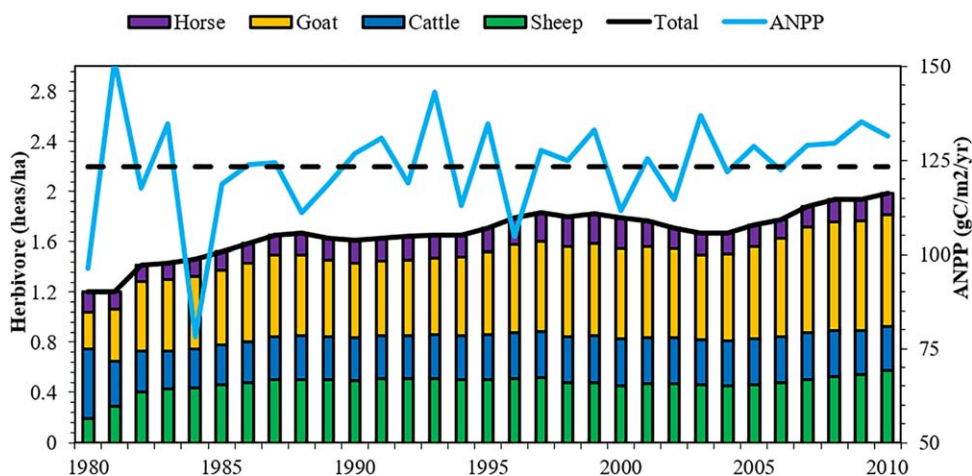


Figure 5. Temporal pattern of herbivore and ANPP change in the study area. The dashed lines represent the long-term mean ANPP during 1980–2010.

Interestingly, DLEM simulations did not show a significant increase in herbivore mortality in Africa and North America during 1980–2010 ($p > 0.1$) suggesting high biomass availability during the growing season led to low starvation-related mortality at these sites. For example, model simulated ANPP was 31% and 50% higher in North America and Africa, respectively, compared to Mongolia.

3.5. Herbivore Feedback to Carbon and Water Fluxes

The DLEM simulations show that the inclusion of herbivores in the model resulted in a significant decline in ANPP and Rh by 14% and 15%, respectively ($p < 0.05$; Figures 7a and 7b). When investigating NEP, model simulation indicate that herbivores increased NEP by 12%, although the effect was not statistically significant ($p = 0.85$; Figure 7c). Likewise, herbivores did not significantly alter ET across our study sites ($p = 0.95$; Figure 7d), although herbivores tend to reduce transpiration and increase evaporation.

3.6. Herbivore Effect on CH₄ Fluxes Through Enteric Fermentation

Model simulations show that herbivores had a significant impact on biogeochemistry through CH₄ emissions. Cattle were the largest source of CH₄ emissions (56%), followed by horses (32%), sheep (8%), and goats (4%; Figure 8). In Mongolia, DLEM simulations with herbivores show a significant increase in CH₄ emissions at the rate of 0.5 kg CH₄/ha/yr ($R^2 = 0.32$; $p < 0.05$). Similarly, CH₄ emissions increased at the rate of 0.2 kg CH₄/ha/yr ($R^2 = 0.36$; $p < 0.05$) and 0.3 kg CH₄/ha/yr ($R^2 = 0.25$; $p < 0.05$) in Africa and the United States, respectively.

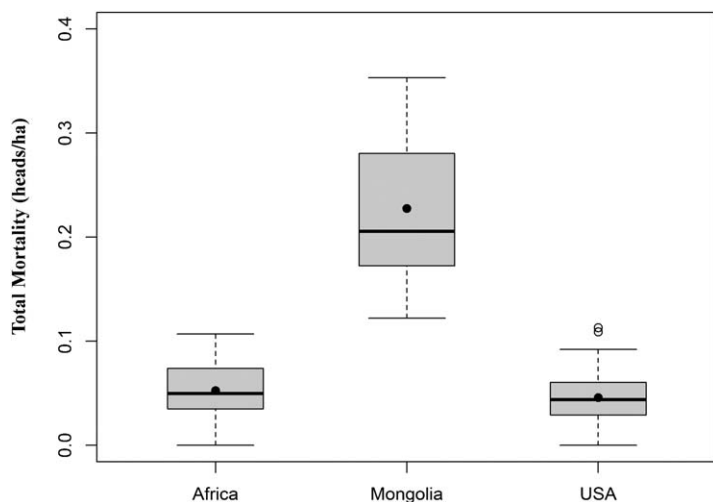


Figure 6. DLEM simulated total herbivore mortality in Africa, Mongolia, and the United States. Total mortality in the model refers to mortality due to aging (basal) and resource limitation (starvation).

4. Discussion

4.1. Simulation of Herbivore Density in Mongolia, Africa, and North America

The population dynamics model developed here captured the annual variation in herbivore density reasonably well across all sites in Mongolia, Africa, and North America (Figure 3 and supporting information Figures S5 and S6). We did not expect the model to exactly reproduce the variability in the observations because we only simulated herbivore density as a function of climate and environmental conditions. We did not include other factors such as predation and diseases in Mongolia and market-policy changes, demand and supply of herbivore products, and predation and diseases in Africa and North America. For example, we found that the transition from a centralized to market-based economy in 1993 resulted in a rapid increase in herbivore numbers in Mongolia (Johnson et al., 2006). Unlike Mongolia, low

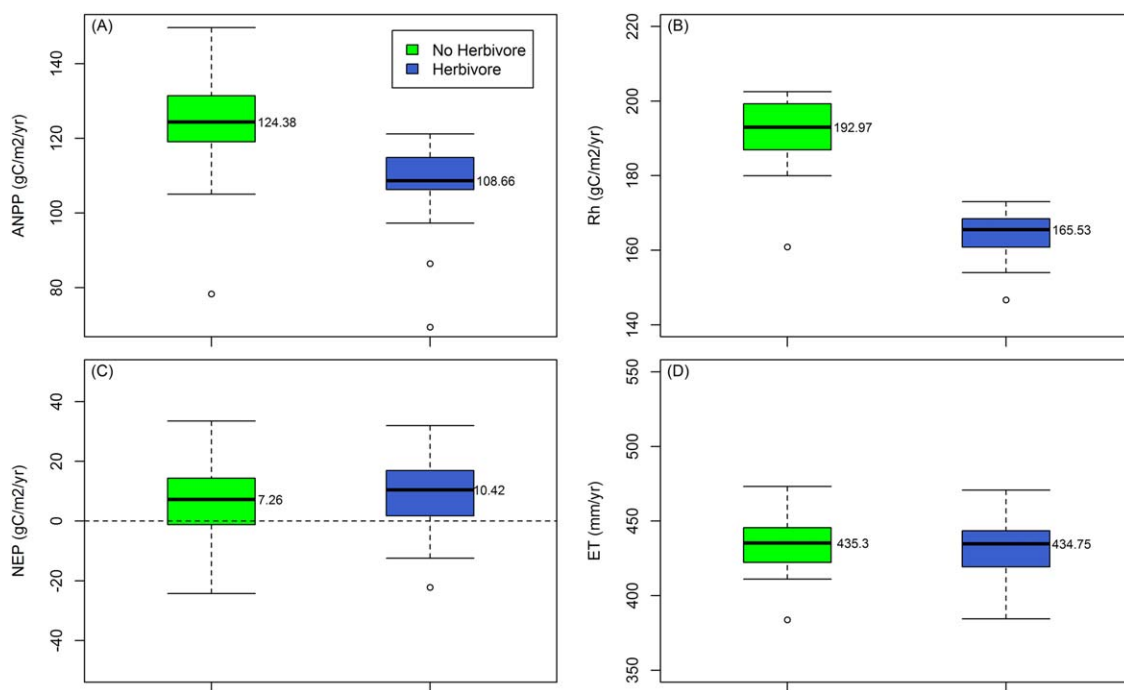


Figure 7. Effect of herbivores on (a) ANPP, (b) Rh, (c) NEP, and (d) ET across all sites in Mongolia, Africa, and North America. The values on the graph represent the median values for ANPP, Rh, NEP, and ET.

demand of wool products due to increased availability of synthetic fibers (Jones, 2004) resulted in a decline in sheep populations in the United States.

To account for the shortcomings associated with market/policy changes, we tested the effect of the transition from centralized to market-based economy in Mongolia on herbivore populations (see section 2.5.2). Simulation results indicate that the transition from a centralized to market-based economy resulted in an increase in horse, cattle, sheep, and goat density by 10%, 5%, 1%, and 83%, respectively. The largest increase in goat populations was due to increasing demand for cashmere (Berger et al., 2013). Overall, market/policy changes had a significant impact on goat density ($p < 0.05$), but no significant impact on cattle, sheep and horse density. Our study, therefore, indicated that market/policy changes have the potential to significantly influence herbivore density. However, such an effect not only is region-specific but also depends on the forage demand/supply for the type of herbivores.

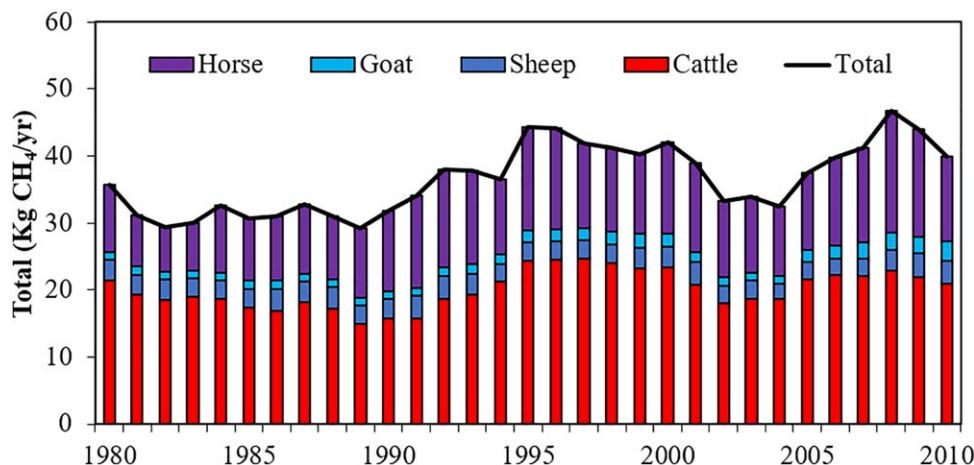


Figure 8. Methane emissions from herbivores across all sites in Mongolia, Africa, and North America.

4.2. Comparison of Simulated Carbon Fluxes and Herbivore Density With Observations

The DLEM-simulated carbon fluxes (GPP, ANPP, ER, and NEP) were close to the observed values in North America. However, the DLEM simulation did not capture the low respiration (ER) of 2011 at Konza Prairie, likely due to variation among root classes not adequately represented in the model. For example, using a PnET-CN vegetation model, Thorn et al. (2015) overestimated the contribution of root respiration to ER at the Konza Prairie site, and associated that to metabolic variation among different root classes. In the DLEM, we broadly categorize roots into two major classes (fine and coarse roots). It is possible that DLEM overestimates the contribution of roots to ecosystem respiration likely due to different root classes not included in the model. Likewise, DLEM-simulated a daily NEP close to zero, compared to observations of $0.3 \text{ g C/m}^2/\text{d}$ at Konza Prairie. Overall, DLEM tends to underestimate NEP during high-precipitation years (2009–2011). Simulation results show that during high-precipitation years, increased runoff and leaching enhanced nitrogen limitation associated with a decrease in plant available nitrogen (Felzer et al., 2011; LeBauer & Treseder, 2008). Burke et al. (2002) found that nitrogen, particularly in the form of nitrates is vulnerable to leaching with maximum leaching rates during wet seasons. Our results indicate that nitrogen limit NEP at Konza Prairie, possibly due to increased leaching during wet years. Similarly, DLEM overestimated NEP by $0.38 \text{ g C/m}^2/\text{d}$ when compared to observations in Africa. The overestimation is likely due to factors not included in the model, such as fire and herbivore diversity. At Skukuza site, there are 14 species of large mammalian herbivores which translates into a herbivore flux (both from respiration and decomposition of dung) of $0.03 \text{ g C/m}^2/\text{d}$ (Archibald et al., 2009). However, we did not include the effect of different herbivores while simulating carbon fluxes because data on different herbivore types and their exact number were not available. Another important factor not included is fire, which releases carbon at a rate of $0.11 \text{ g C/m}^2/\text{d}$ in Skukuzu (Archibald et al., 2009).

The DLEM-simulated herbivore densities were close to observations across all sites, although the model has a tendency to underpredict at some sites. For example, DLEM underpredicted herbivore density by 8% in Mongolia. The slight underprediction is likely because we have not included the impact of extreme climate on metabolic and physiological adjustment and their relevant effect on herbivore mortality. For example, Bishop-Williams et al. (2015) found that every one unit increase in heat stress indices increases on-farm mortality rates of dairy cows by 1.03 times. In the United States, DLEM overpredicted herbivore density by 8%. This is likely due to reported decline of sheep density in Texas and Kansas. Although climatic conditions and forage productivity were favorable at the study sites, which resulted in an increase in the number of cattle and goats during the observation period, we found no link between climate and sheep population in the United States. A previous study indicated that sheep numbers in Texas and Kansas have declined by 61% and 59%, respectively since 1975 (Jones, 2004). A decline in sheep numbers has been attributed to low demand of wool products from sheep due to availability of less expensive synthetic fibers (Jones, 2004). In the current version of DLEM, we have not included how demand and supply of wool products from sheep could affect sheep productivity in the United States. However, in Africa, DLEM-simulated herbivore density was higher than observation by 44%. This overprediction is because we did not include predation (Ogada et al., 2003; Patterson et al., 2004) in the model, which has been suggested to reduce herbivore populations annually by up to 2.4% in southeastern Kenya (Patterson et al., 2004), 5% in Zimbabwe's community lands (Butler, 2000), and 8% in South Africa (Van Niekerk, 2010).

4.3. Herbivore Response to Resource Availability

The response of herbivores to forage availability has been the subject of ongoing debate over the last few decades (Fernandez-Gimenez & Allen-Diaz, 1999; Illius & O'Connor, 1999; Sullivan & Rohde, 2002; Vetter, 2005). The debate focuses on two important aspects of rangeland ecology, i.e., density-dependent and density-independent interactions. Density-dependent interactions are affected by competition and predation among herbivores, while density-independent interactions are affected by abiotic factors including climate and soil properties. While the model does not account for the effect of predation on herbivores, competition among herbivores during period of low carrying capacity limits the growth and productivity of herbivores (Illius & O'Connor, 2000). Likewise, abiotic factors such as temperature and precipitation changes indirectly affect herbivore dynamics through changes in biomass availability (Ellis & Swift, 1988). Our simulated results indicate that the mean herbivore density (heads/ha) was not significantly related to biomass availability ($p = 0.28$). This is likely because we aggregated herbivore as a sum of individual herbivore densities (Figure 5). We did not consider the differences among body weights and intake rates while aggregating

the density (heads/ha) across different herbivore types. However, our simulated results also indicate that the density of individual herbivores was significantly correlated with biomass availability ($p < 0.05$), where biomass availability explained 23% of the variation in horse density and less than 10% of the variation in the density of cattle, sheep, and goats. With the mechanistic modeling approach, we found that hindgut herbivores show a different dependencies on biomass availability compared to ruminants. Interestingly, simulation results show that ANPP (an indicator of carrying capacity of land) increased with low-precipitation, intermediate-precipitation, and high-precipitation levels (supporting information Figure S7). Although herbivore density increased with an increase in carrying capacity of the land during wet years, extreme climatic events in some years led to an overall decline in herbivore density as an indirect consequence of limited forage availability.

4.4. The Role of Extreme Events on Herbivore Mortality

In Mongolia, DLEM-simulated results indicate that summer drought and extreme winter conditions led to a maximum mortality of 27% of the total herbivores. In Africa and the United States, herbivore experienced a mortality of 17% and 15%, respectively. Our simulation results are consistent with previous studies, which report that the consecutive drought and extreme winter (*dzud*) event of 1999–2002 resulted in a mass mortality of 30% of the herbivores in Mongolia (Fernandez-Gimenez et al., 2012). The highest mortality rates during consecutive drought and *dzud* events are due to prior summer drought and upcoming winter snowfall, which reduces the carrying capacity of land and increases the risk of starvation-related mortality (Begzsuren et al., 2004; Rao et al., 2015). Similarly, high mortality rates of cattle population in the range of 37–42% have been reported in semiarid Ethiopia during drought (Alemayehu & Fantahun, 2012; Desta & Coppock, 2002). In the United States, a decrease in herbivore productivity and an increase in mortality rate due to increasing heat waves and maximum temperatures have been reported (Key et al., 2014; Nienaber & Hahn, 2007). Extreme events, such as maximum temperatures and drought, can either result in high herbivore mortality or lead to a reduction in their productivity through adjustments in metabolic rate to cope with maximum temperatures (Coulson et al., 2001; Nardone et al., 2010; Walthall et al., 2012). Climate-related mass mortality of herbivores has been strongly linked to summer droughts in Mongolia, Africa, and the United States (Key et al., 2014; Kgosikoma & Batisani, 2014; Megersa et al., 2014; Nardone et al., 2010; Rao et al., 2015). Similarly, extreme winter conditions have also been linked to mass herbivore mortality, particularly in countries like Mongolia (Begzsuren et al., 2004; Fernandez-Gimenez et al., 2012; Rao et al., 2015). Winter weather disasters associated with deep snow and severe cold limits forage accessibility increasing the risk of starvation-related mortality (Rao et al., 2015). But mortality could vary depending on herbivore type as, for example, their feeding behavior and recovery rate following extreme winters may vary (Nardone et al., 2010). In the DLEM 3.0, extreme events related herbivore mortality is a function of annual changes in body fat. For example, decline in forage resources (ANPP) due to extreme climatic conditions reduces the accumulation of body fat, which ultimately alters the growth, reproduction, and survival of herbivores. Overall, DLEM simulations indicate that drought is the primary cause of starvation-related mortality in Africa and the United States, while both drought and winter snowfall are responsible for starvation-related mortality in Mongolia.

4.5. Herbivore Feedback to Carbon and Water Fluxes

Analysis of model simulated impacts of herbivores on carbon and water fluxes suggests that herbivores have a significant negative impact on ANPP and Rh ($p < 0.05$). However, herbivores have no significant impact on NEP and ET. Previous studies indicate that herbivores have a substantial impact on the flow of energy and nutrients (Augustine & McNaughton, 2006; Bardgett & Wardle, 2003; McNaughton et al., 1997), but the magnitude and direction of this effect varies widely across ecosystems (Augustine & McNaughton, 1998; Milchunas & Lauenroth, 1993). In many ecosystems, herbivores have been found to reduce ANPP, but there are also reports of an increase in ANPP following herbivory (McNaughton, 1979; Milchunas & Lauenroth, 1993). The differences among studies are likely due to differences in herbivore density and how they affect litter inputs and nutrient cycling in different ecosystems (Asner et al., 2004). For example, Irisarri et al. (2016) found that doubling grazing intensity resulted in a reduction in ANPP by 25%, while our simulation results indicate an overall reduction in ANPP by 14%. Similarly, enclosure experiments in Mongolia, Africa, and the United States have indicated that herbivores reduce ANPP in areas with low rainfall, regardless of nutrient availability (Augustine & McNaughton, 2006; Irisarri et al., 2016; Schönbach et al., 2011). Our

simulation results are consistent with the findings that herbivores have a negative impact on ANPP, but the magnitude of this impact largely depends on the density and type of herbivores and the ecosystem considered.

Likewise, DLEM simulations also indicate that herbivores reduce Rh by 15% across the study sites. In semi-arid grasslands, Kang et al. (2013) found that herbivory resulted in a significant reduction in Rh by 33%, which is higher than our estimate. Kang et al. (2013) used a moderate herbivore density to quantify the effect of grazing on Rh, while we used a dynamic approach to simulate herbivore density and its effect on Rh. The reduction in Rh in the DLEM is due to reduced litter input (Savadojo et al., 2007). The reduction in litter pool suppress soil organic matter decomposition, due to reduction in substrate availability necessary for soil microbial activity (Piñeiro et al., 2010; Raiesi & Asadi, 2006). In addition to reduction in litter pools, herbivores can reduce canopy photosynthesis and slow down the translocation of carbon to the rhizosphere, resulting in an overall reduction in annual soil respiration by 18% (Bremer et al., 1998). The DLEM 3.0 accounts for changes in leaf area index (LAI; a measure of one sided leaf area per unit of ground surface area) following herbivory, which ultimately drives canopy photosynthesis. Changes in allocation of carbohydrates also occur due to a grazing-induced reduction in canopy photosynthesis, which affect Rh at the study sites.

Model simulations also indicate that herbivores increased NEP by up to 12%, but the effect was not statistically significant. The change in NEP following herbivory depends on several factors such as soil water content, soil temperature, and properties (Potts et al., 2006; Zhao et al., 2011), biomass, and litter inputs including other vegetation characteristics (Frank, 2002; Risch & Frank, 2006). In a recent study in semiarid steppe, Kang et al. (2013) found that moderate grazing increased NEP significantly, shifting the ecosystem from negative to positive carbon balance. This was likely due to a slight increase in GPP combined with a significant reduction in Rh. Meanwhile, other studies report no significant effect of herbivory on NEP (Hou et al., 2016; Lecain et al., 2000, 2002), although the general trend was an increase in NEP due to reduction in ecosystem respiration, open canopy structure and the presence of young, photosynthetic leaves that enhance carbon uptake (Owensby et al., 2006). Our study is consistent with the finding that a decrease in Rh is responsible for an increase in NEP, but model simulation also indicate a significant decrease in ANPP following herbivory ($p < 0.05$). While both ANPP and Rh decreased, the reduction in Rh was larger than the reduction in ANPP, which resulted in an increase in NEP in this study.

Increase in herbivores abundance since 1990, particularly in Mongolia suggest an overall increase in CH₄ emissions (Figure 8), but the increasing trends can be modified by the type of herbivores, their body weight and the quality of forage resources (Dangal et al., 2017; Herrero et al., 2013; Steinfeld et al., 2012). The DLEM simulations show that cattle were the largest source of CH₄ emissions, followed by horses, sheep, and goats. Higher emissions from cattle and horses occur because of higher body weight compared to sheep and goats. For example, Chang et al. (2015) found that live body weight is an important factor affecting CH₄ emissions. In addition to live body weight, fermentation of food products and their quality also played an important role in determining net emissions (Moss et al., 2000). In the current modeling framework, we used Intergovernmental Panel on Climate Change (IPCC) tier II guidelines for estimating the CH₄ emission factor, which relies on estimating different components of energy expenditure (lactation, feeding, work, wool, and pregnancy) and digestibility of forage as simulated by the DLEM to quantify the CH₄ emissions.

Analysis of model simulated ET further showed that herbivores does not significantly alter ET at the study sites. The amount of water lost through ET depends on soil surface roughness, which affects surface evaporation and the type of vegetation, which affects plant transpiration (Bhattarai et al., 2016; Frank & Inouye, 1994; Pan et al., 2015; Parton et al., 1981). In grassland ecosystems, reduction in plant surface area and LAI following herbivory resulted in a decline in transpiration rates (Bremer et al., 2001; Naeth & Chanasyk, 1995). Meanwhile, herbivores also increases bare soil surface area, which could ultimately lead to an increase in surface evaporation (Bremer et al., 2001). The net effect of herbivores on ET depends on the balance between lower transpiration rates due to reduction in vegetation cover and LAI, and higher soil evaporation rates due to an increase in bare surface area (Naeth & Chanasyk, 1995). In a recent study, Wang et al. (2012) found that the direct effect of reduced LAI on ET following herbivory was not significant in semiarid ecosystems because increased soil evaporation compensated for most of the losses in plant transpiration. Likewise, in a modeling study with different herbivore density, Zhao et al. (2010) showed that moderate herbivore density had no significant effect on water budget components. But high herbivore density

resulted in a significant reduction in transpiration by 39% (47 mm) and increase in evaporation by 45% (40 mm). When transpiration and evaporation were aggregated together, herbivores led to a reduction in ET by 3%, which is comparable to DLEM simulated changes in ET of 0.3%. This implies that herbivores/herbivory has the potential to alter individual components (evaporation and transpiration) of the water fluxes. However, when the water fluxes (evaporation and transpiration) are aggregated together, decreases in plant transpiration are compensated by an increase in evaporation resulting in no substantial changes in evapotranspiration.

4.6. Implications of Coupling Herbivore Feedbacks Into the Global Land Ecosystem Model

By incorporating herbivore dynamics in the global land ecosystem model, we quantified the response of herbivores to climate variability and resource availability, as well as herbivore effects on carbon, water, and greenhouse gas fluxes. Regarding similar work, Pachzelt et al. (2013) coupled LPJ-GUESS with the grazer model to simulate the population of large ungulates in African savanna. However, the version of LPJ-GUESS considers natural grazer population dynamics and does not account for carbon-nitrogen coupling. Likewise, Madingley model used mechanistic approach to simulate ecosystem structure and function of both terrestrial and marine ecosystems (Harfoot et al., 2014), but the model does not account for the impact of human activity on herbivore dynamics and the complex plant-herbivore interactions. Other models use detailed animal physiology (Kooijman, 2010) and competition for resources (Shabb et al., 2013); however, the models are not explicitly linked to plant physiology. Here we present a global land ecosystem model that explicitly accounts for both herbivore and plant physiology and simulates the impact of climate and other environmental factors on herbivore growth and productivity. By linking the DLEM plant model with the herbivore dynamics, we demonstrate that herbivores have a significant impact on ANPP, Rh, and CH₄ emissions, but no significant impacts on NEP and ET. In addition, model results suggest that the magnitude of herbivore impact on biogeochemical cycles varies by ecosystem type and prevailing climatic conditions. In the absence of herbivore dynamics and their effect on biogeochemical processes, current land models may overestimate ANPP and Rh by up to 14% and 15%, respectively. In addition, current land model may underestimate NEP by up to 12%. But the extent to which model simulated site level responses would scale up to regional and global level remains a subject of future investigation.

5. Uncertainty and Future Needs

This study incorporated a simplified herbivore dynamics model into a global land ecosystem model (DLEM) to simulate the herbivore populations in response to climate and other environmental factors at the site level. Although we attempted to include major processes that affect herbivore populations and how they alter carbon, nitrogen, and water cycles, there are several limitations that need to be addressed in the future work. The largest uncertainty in the model comes from how market-based economic activity (change in demand and supply of products) affects population dynamics of herbivores. While we have shown the effect of market/policy changes in Mongolia, we did not attempt to quantify the effect of market-based economic activity in Africa and North America. Our model can be used to examine how extensive the effect of market/policy changes will be on herbivore populations (see section 4.1), but future work is needed to accurately estimate the effect of policy and market-based economic changes on herbivore populations. In addition, forage digestibility is strictly a function of available biomass. We did not attempt to differentiate digestibility associated with the morphological (dicots and monocots) differences in plants. For example, Codron et al. (2007) found higher fiber digestibility of grass compared to browse, indicating that inherent differences in diet quality may play an essential role in herbivore diversification. Likewise, we have only included four herbivores (horse, cattle, sheep, and goat) in Mongolia, while three herbivores (cattle, sheep, and goat) in Africa and the United States but did not consider the dynamics of wild herbivores. Our study also recognizes that mortality associated with climate extremes is not adequately represented in the current modeling framework. For example, thermal discomfort due to extreme heat waves and drought enhances herbivore mortality (Crescio et al., 2010; Morignat et al., 2014; Vitali et al., 2015). However, we only considered starvation-related mortality due to drought and freezing winter but did not include the impact of thermal discomfort associated with increasing heat waves on herbivore dynamics. We need more experimental studies to model the complexity associated with summer heat waves, and its subsequent impact on herbivore population.

6. Conclusions

In this study, we integrated a mammalian herbivore population model into the global land ecosystem model (DLEM) and quantified the effects of both biotic and abiotic factors on herbivore growth and productivity in various sites across Mongolia, Africa, and the United States. In addition, we simulated the impact of herbivores on carbon, water, and greenhouse gas fluxes. The generalized model was able to capture the observed values of herbivore populations at all sites. Likewise, our simulation results demonstrate that herbivores have a significant impact on ANPP, Rh, and CH₄ emissions. Our simulation results also indicate that climate extremes (droughts and extremely cold winters) resulted in a cumulative mortality of 27% in Mongolia, while drought resulted in mortality of up to 17% and 15% in Africa and the United States, respectively.

Our simulation results demonstrate a strong coupling between primary producers and consumers, indicating that the inclusion of herbivores in the current land surface or biosphere models is essential to better understand the impacts of herbivores on carbon and water cycles in grassland and savanna ecosystems. Animal as an essential component of ecosystem needs to be taken into account in the earth system modeling framework. To the best of our knowledge, this study is the first attempt to couple herbivore population dynamics with a global land ecosystem model, particularly incorporating a detailed animal physiology and the influence of market/policy changes on herbivore populations. Although the current work focused on model development and its application at the site level, with adequate parameterization, the model could be applied at regional and global scales to simulate herbivore population dynamics and its impacts on biogeochemical and hydrological cycles.

Acknowledgments

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