Impact of European Bison Manure on Soil Carbon in Białowieża Forest

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Abstract:

European bison (*Bison bonasus*) manure plays an important role in promoting biodiversity among many other ecological functions. Yet, as conservationists in the Białowieża Forest have observed, relatively little literature appears to have attempted to quantify European bison's impacts on nutrient cycles. European bison's locally rare niche of being large ruminants that browse woody material along with herbaceous and gramineous material motivated this study to investigate wild-roaming European bison manure's effects on soil organic carbon. This study modelled, using RothC, the potential effect generated by wild-roaming European bison manure presence on soil organic carbon (SOC) in the Białowieża forest. Bison manure's estimated DPM:RPM decomposability ratios (DR) (Low: 0.33, Medium: 0.41, High: 0.5) were found to have a negative correlation effect on SOC throughout the 100-year forward run. However, the natural low density of bison minimized the effects of their manure on SOC therefore leading to accepting the null hypothesis, that European bison manure had no significant effect on SOC.

1. Introduction:

Climate change and soil degradation are two major global problems exacerbated by anthropogenic activity, monoculture farming, unsustainable land use, fossil fuels, and pollution (Jol & Fussel, 2016; Jones *et al.* 2010; Lal, 2012). The European Environment Agency points out the importance of soil organic carbon (SOC) as an indicator of soil health and as a source for tackling climate change (Jones *et al*, 2010; Schils *et al*, 2008). With biodiversity loss being a huge and frequently irreversible problem affected by these issues (Lal, 2012), solutions that tackle more than one of these problems simultaneously are required.

European bison (*Bison bonasus*), rescued from extinction in the 20th century, are now important ecosystem engineers in wildlife parks around Europe (Pucek, 2004). One of the locations containing the most wild-roaming European bison is the Białowieża Forest shared between Poland and Belarus (Kraskinska, 2013). Despite the methane emissions produced by ruminants like bison which can contribute to GHG emissions (Guyader *et al*, 2016; Kim *et al*, 2018; Kipling *et al*, 2016; Soussana, *et al*, 2010; Stoy *et al*, 2021), studies have shown that ruminants can play a key role in increasing soil organic matter (SOM) (Frank & Groffman, 1998; Harrison & Bardgett, 2008; Soussana *et al*, 2010) which positively correlates with SOC (Falloon & Smith, 2006; Koga *et al*, 2011; Pribyl, 2010; Ramos *et al*, 2006; Smith *et al*, 1996) and improves ecological functions of their environment (Bilotta *et al*, 2007; Teague *et al.* 2016).

Local studies have shown bison waste to increase flora and fauna richness significantly (Jaroszewicz, 2009, 2011, 2012; Eycott *et al*, 2013; Kaminski *et al*, 2015), though, as local conservationists have noted (BPN, personal correspondence, 2023), there is currently limited available literature on the inherent properties of bison waste to enrich soils (Krasinska & Krasinski, 2013; Melis *et al*, 2007).

The potential impact bison play on the nutrient cycles of an ecosystem tie appropriately to the UN's 15th Sustainable Development Goal which focuses on protecting terrestrial biodiversity and the soil in which they inhabit. This creates the possibility of such ruminants to play a key role in soil models focused on terrestrial carbon sinks in pursuit of fighting against climate change and GHG emissions. The potential for positive contributions to nutrient cycles made by European bison are a result of their ability to consume highly lignified material, such as soft wood and hard wood, bark, and leaf matter, along with herbaceous and gramineous material (Gębczyńska & Krasińska, 1974); this implies they may have a more diverse geographic range for food sources and intake than domesticated ruminants, such as sheep and cattle, and could potentially deposit more carbon in the soil due to the importance of lignin in reducing decomposition rate and therefore volatility of ruminant faeces (Jebari *et al.* 2021).

The Białowieża Forest is one of the oldest forests in Europe (Krasinska, 2013). It has been a well-studied environment with free roaming herds of bison that have been increasing in population since 1950's when breeding and protection schemes were further developed (Krasinska, 2013; Pucek, 2004). Although the site is believed to be one of the most historically prominent sources of scientific literature on wild European bison population and physiological dynamics (Krasinska, 2013; Pucek, 2004), measuring their impact on soil carbon fluxes in situ is a relatively resource intensive strategy. Mathematically modelling the dynamics involved in carbon fluxes using estimated inputs for models such as RothC enable researchers to quickly predict the potential effect of changes in environmental inputs, such as the presence of bison on soil richness. All this with largely reduced resource requirements.

The Białowieża Forest serves as a suitable case study for modelling the potential impact wild-roaming European bison could make on soil carbon and soil health in heterogenous forest ecosystems over the coming decades as more countries get involved in tackling SDG 15. The results from this study serve as a contribution to the growing foundation for future predictive and descriptive modelling on the effects of large ruminants like European bison on nutrient cycles in temperate forests, while also contributing to the shared understanding of the factors that provide resilience against climate change and land degradation on a local scale.

Aim / Research question: The aim of the project is to assess, using Rothamsted carbon (RothC) model, to what extent could European bison manure deposition influence soil carbon pools in the Białowieża Forest from 2020-2120.

H_a: Bison manure produce a significant effect on SOC after 100 years of bison presence in the Białowieża forest.

2.Methodology:

2.1.Location:

The Białowieża forest area being studied is as defined by UNESCO's World Heritage Site map in 2014 with extensions made to include more forested area within reasonable proximity, totaling to approximately 1182.5km^2 (Fig. 2). The land studied includes over 80% temperate forested areas with the majority and most ancient trees being deciduous trees in podzolic soils. Grasslands, cropland, and shrub make up most of the remaining minority of land being studied (Fig. 3). Within these lands, a variety of ungulates such as elk, deer, and bison have remained present and free roaming for thousands of years despite excessive hunting at times nearly leading to local extinction such as with the bison (Pucek, 2004) Croplands and grasslands around the area are only sporadically fenced and tend to not be well protected from bison. This is due to the forest's region being located within the Natura 2000 Puszcza Białowieża PLC200004 area (Perzanowska & Korzeniak, 2020; BPN, 2022), making the construction of fences in agricultural areas limited. Therefore, these areas will not be removed from the map entirely and the model is extended to farmlands and grasslands within proximity.

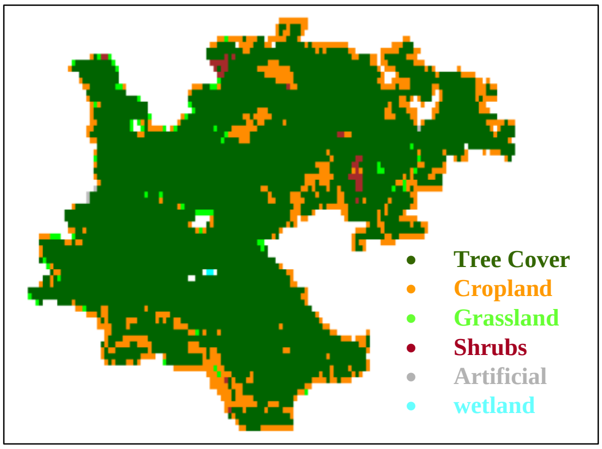

Fig. 1: Land Use types for Białowieża Forest according to FAO (CORINE, 2021). See (Fig. 2) for satellite map.

The study area is divided into 4730 geographic data points, each representing 25 hectares of the Białowieża Forest and each classed based on FAO land use type which will affect decomposability rate (DR) values necessary for integrating into the RothC model (Maet, 2022). Each pixel on the raster (Figure 1 & 4) represents a scenario with climate, soil, and land use layers where the RothC model is run for 100 years.

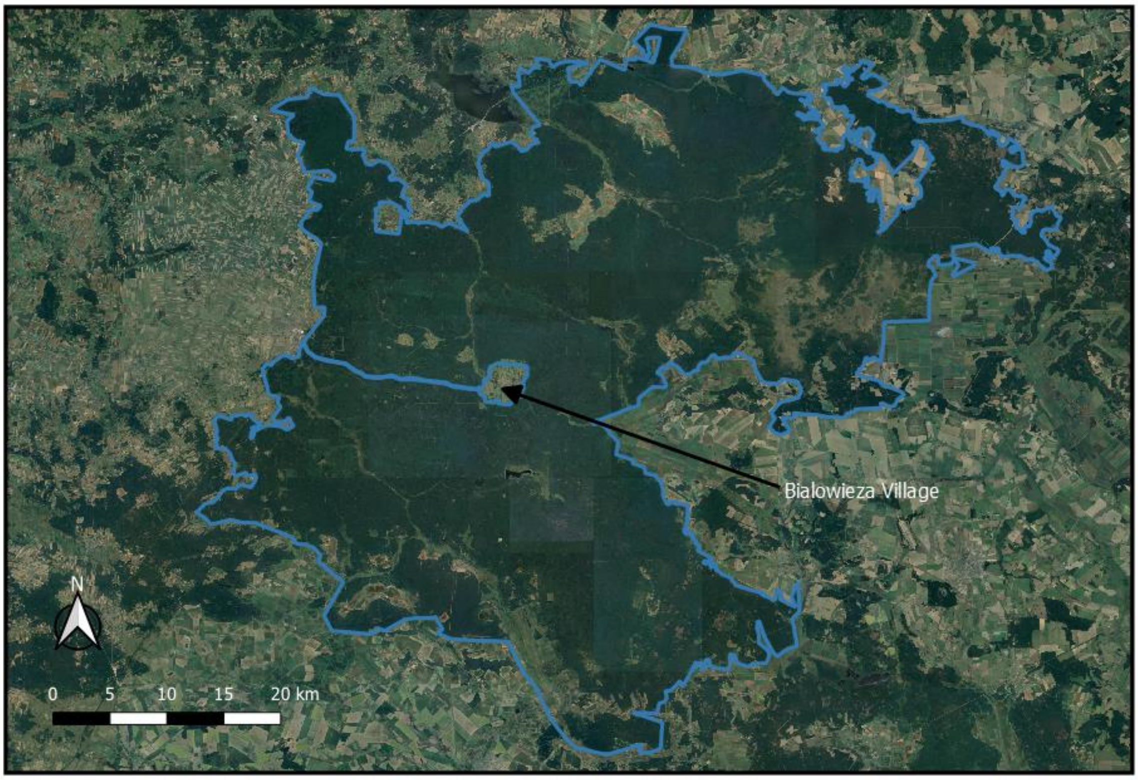

Fig. 2: Satellite map of Białowieża forest, estimated to contain relevant range of bison in the studied area (blue outline). See (Fig. 1) for land use types and (Fig. 3) for SOC of the studied area.

<u>2.2.Model inputs:</u>

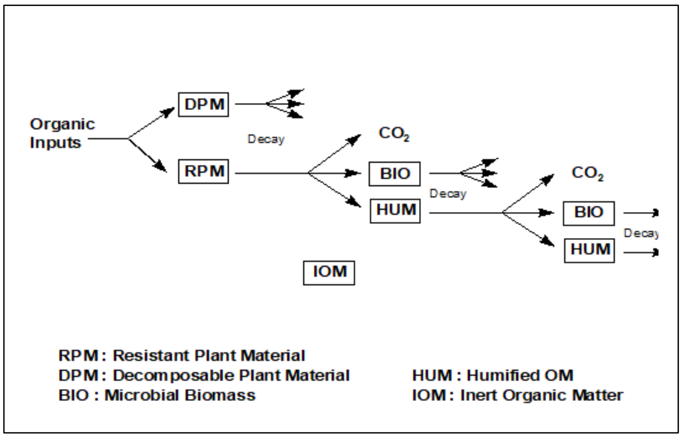

Fig. 3: Structure of the Rothamsted carbon model's soil carbon dynamics in which the 5 carbon pools (RPM, DPM, BIO, HUM, IOM) are initially calculated over the spin up phase using environmental inputs.

RothC is a widely used environmental model for quantifying the turnover of organic carbon (Fig. 1) (full details of model structure: (Coleman & Jenkinson, 1996)). This model, though initially focused on arable land has been expanded to model grassland and forest soils (Dib *et al*, 2014; Jebari *et al* 2021; Mishra *et* al, 2019). Its simplicity when it comes to data requirements compared to other models make it a valuable model for desk-based studies with limited time and resources and can be programmed easily in R (R Core Team, 2023) using a variety of programming libraries and public databases (Peralta *et al*, 2020).

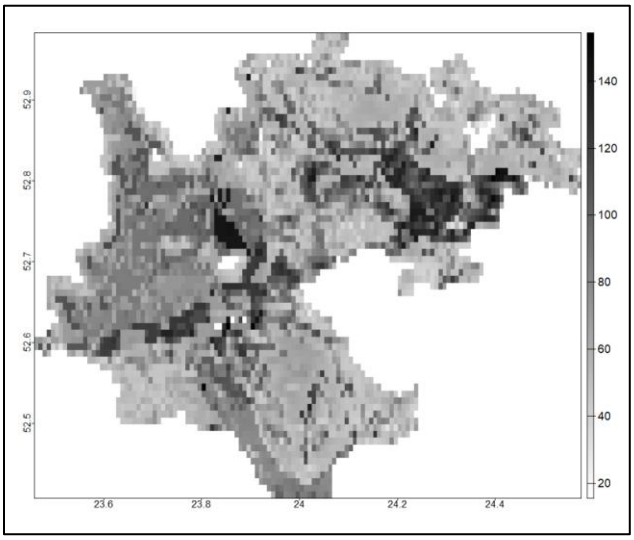

Fig. 4: SOC t C ha^{-1} in 2018 from GSIS showing the great diversity of initial SOC in the Białowieża Forest (x & y axis showing longitudinal and latitudinal coordinates respectively).

The datasets that RothC require include Poland and Belarus's climate, soil, and land use management data. These datasets in this study's model are spun up using data from the years 1980-2000 – series averaged, for 500 years and warmed up, also described as generating the steady state, using data from years 2000-2020 – year to year. Climate data, which includes monthly rainfall, monthly open pan evaporation/evapotranspiration (mm), and average monthly mean air temperature (ºC), from the Climatic Research Unit (*CRU TS v4.03 Data Variables*, 2023). Soil data includes total initial SOC and clay composition which are both collected up to a depth of 30cm. The initial SOC data was be sourced from the Global Soil Information System (GSIS) (FAO, 2023) and the clay percentages were sourced from the International Soil Reference and Information Centre (ISRIC, 2023). For Land use management data, the monthly soil cover (vegetated vs. Bare) and the monthly carbon inputs from plant residue were collected from Europe's CORINE land cover database (CORINE, 2021). Due to the protected nature of the area (Perzanowska & Korzeniak, 2020), land use data is assumed to be consistent with no significant change over the years.

The inputs of European bison were implemented in the warmup phase while the forward phase for each data point of the study area was run for 100 years, 2020-2120, representing 4 main scenarios: 1 run in standard conditions without bison (B-), and 3 runs in standard conditions with bison (B+), each containing high, medium, or low estimation of bison waste decomposability respectively (section 2.3). More runs were done as part of the sensitivity and uncertainty analysis in which environmental inputs needed to be changed for each forward run (section 2.4).

2.3.Properties of Bison waste:

Gębczyńska & Krasińska, (1972) at the Białowieża forest reported data on 5-year-old Bison consuming between 23-32 kg of feed (therefore an assumed average of 27.5 kg). Data from (Krasinska and Krasinski, 2002, 2013) on mean body masses of 5-year-old bison give an average weight of 437 kg – sex ratios and associated masses considered, which then suggests that bison eat 6.3% of their body weight. Further data on population composition suggests adults (≥6-year-old) to make up the vast majority of the population (≥80%) (Krasinska & Krasinski, 2013). From the data collated (Krasinska & Krasinski, 2013), a conservatively estimated body mass of an average bison is then estimated to be 500 kg. Since the quantity of bison waste produced under such a diet is highly variable and difficult to calculate it is assumed for the purposes of this model that bison excrete the same amount of mass as they consume. It is also assumed that the majority of bison waste is comprised of carbohydrates and therefore majority carbon containing material (Gębczyńska & Krasińska, 1972, 1974). This would lead to the estimation of 31 kg C dy^{-1} or 11,350 kg C yr^{-1}. With bison density conservatively a mean of 6 individuals per 10 km^2 (Krasiński, 1978; BPN, personal correspondence, 2023), the average amount of waste being produced per hectare is estimated to be:

$$Bison\,waste\;t\;C\;ha^{-1} = \frac{(0.6_{individuals\;km^{-2}} * 11.3515_{t\;yr^{-1}})}{100} = 0.068$$

This can be assumed as a conservative constant for bison waste production. How it affects inputs into the soil is via the following calculations.

Ruminant waste is estimated to have 30% decomposable plant material (DPM) and 60% resistant plant material (RPM) (decomposability ratio (DR): 0.5) in grassland ecosystems when excluding holocellulose which is not considered in standard RothC inputs (Jebari *et al*, 2021). Jebari *et al*, (2021) has not focused on bison and their forested habitats. Bison's higher consumption and excretion of lignin suggests this estimated ratio to be a rather high value in the context of Białowieża's bison. Therefore, a ratio of 0.5 can be treated as a maximum decomposability ratio due to the higher decomposability rate of grasslands material compared to forests. By incrementally increasing RPM and decreasing DPM by 10 and 20%, high, medium, and low decomposability values can be estimated. The DPM:RPM (DR) ratio values to be implemented in this model are 0.5 (high decomposability), 0.41 (medium decomposability), and 0.33 (low decomposability).

Because bison are herbivores and are expected to filter a fraction of plant annual C input. The bison waste DR is expected to alter the DR of total plant input. Since plant input is estimated using net primary production (NPP) (Bernardi, 2006), The following formula is used:

$$Bison\ waste\ fraction\ of\ plant\ input\ (B_{WF}) = \frac{0.068_{t\ C\ ha^{-1}yr^{-1}}}{NPP_{t\ C\ ha^{-1}yr^{-1}}}$$

$$Plant\ input\ decomposability_{RothC} = B_{WF} * B_{DR} + DR_{habitat} * (1 - B_{WF})$$

Where B_{WF} is Bison waste fraction of plant input, B_{DR} is the decomposability of bison waste, and $DR_{habitat}$ is the default estimated decomposability of the land use type.

Bison populations and density are assumed to be sufficiently constant throughout the model runs thus not requiring an increase or decrease in expected bison waste input throughout the forward phase of the model. Wild roaming bison are also believed to not be highly preferential for where they defecate, their defecation rate being around 30 times a day, allows a sufficiently even random distribution of waste (Eycott *et al*, 2013). Hence the waste will be assumed to accumulate evenly throughout the forest, with dependent coprophilous organisms such as dung beetles helping in faeces nutrient diffusion (Kaminski *et al*, 2015).

2.4.Statistical analysis:

In order to measure the impact of each input parameter on the outcome of the model, a sensitivity analysis is performed on all variable inputs (Abdalla *et al*, 2014). Furthermore, an uncertainty analysis is performed by combining the maximum uncertainties and minimum uncertainties of each input to visualize the extreme outcomes of the model in this given scenario with bison waste defaulted to medium decomposability (Peralta *et al.* 2020).

This study prioritizes the differences between the outcomes of bison absence (B-) and that of bison presence (B+) over the actual accuracy of total SOC values.

3.Results:

3.1.Sensitivity analysis:

Sensitivity analysis (Fig. 5) showed climate variables to be weighted inputs (**evapotranspiration:** 0.53 (+10%) and 0.52 (-10%); **precipitation:** 0.96 (+10%) and 0.93 (-10%); **temperature:** 1.38). Vegetation covers also had an important impact with a reduction in vegetation cover (-10%) having on average 0.07t more C lost than would be gained by increasing veg cover by 10%. Soil inputs are especially weighted when it comes to inert organic matter (IOM) and humified organic matter (HUM) values with HUM values making the biggest difference in SOC after 100 years (3.88 t C ha^{-1} for both +10% and -10% inputs, max and min respectively).

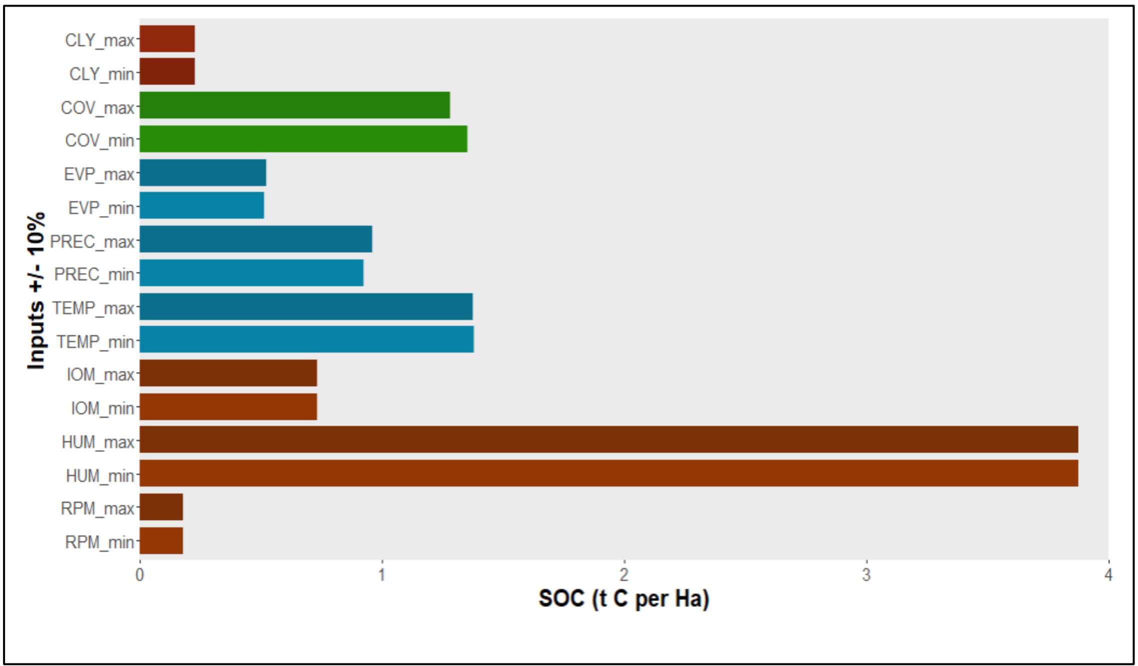

Fig. 5: Sensitivity response of RothC inputs when compared with a model with bison (medium decomposability). Input values were increased (max) and decreased (min) by 10% to visualize the difference each input made on the outcome. Inputs with a sensitivity analysis value ≤ 0.1 t C ha^{-1} were omitted from the chart. This includes, microbial biomass (BIO) C pool, DPM pool, C input, habitat DR, and total SOC.

3.2.Uncertainty analysis:

Increasing all the inputs to their highest and lowest uncertainty value gave minimal differences (≤0.1)(Table. 1) in terms of bison presence (B+) vs. bison absence (B-). However, a difference in the mean SOC after 100 years was noticed to vary overall between maximum, standard, and minimum inputs.

Table 1: Displays the uncertainty analysis results, worst- and best-case scenarios, minimum and maximum respectively, for SOC values after 100 years. Displays the control (B-) without bison as well as the result for Bison (B+) with medium decomposability excreta (0.41) (Standard deviation in parenthesis).

Uncertainty Treatment to model (B+ = bison presence, medium decomposability)	**Mean SOC after 100 years (C t ha^{-1})**	**Total SOC outcome difference in relation to Standard B- (t C)**
Maximum B-	52 (17.9)	38935
Maximum B+	52 (11.8)	39004
Standard B-	43 (17.3)	
Standard B+	43 (17.3)	-0.3
Minimum B-	34 (11.8)	-38582
Minimum B+	34 (11.8)	-38644

3.3.Bison Waste Effect Results

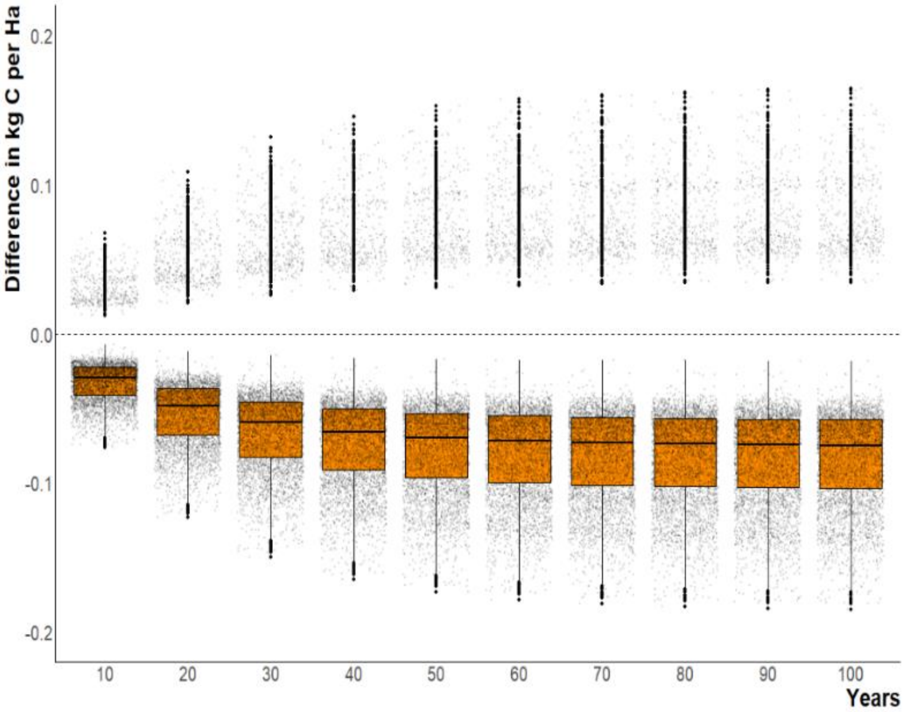

Fig. 6: A boxplot graph showing difference between B- and B+ with Bison DR ratio of 0.41. outliers are displayed as vertically aligned dots (with jitter showing the data points).

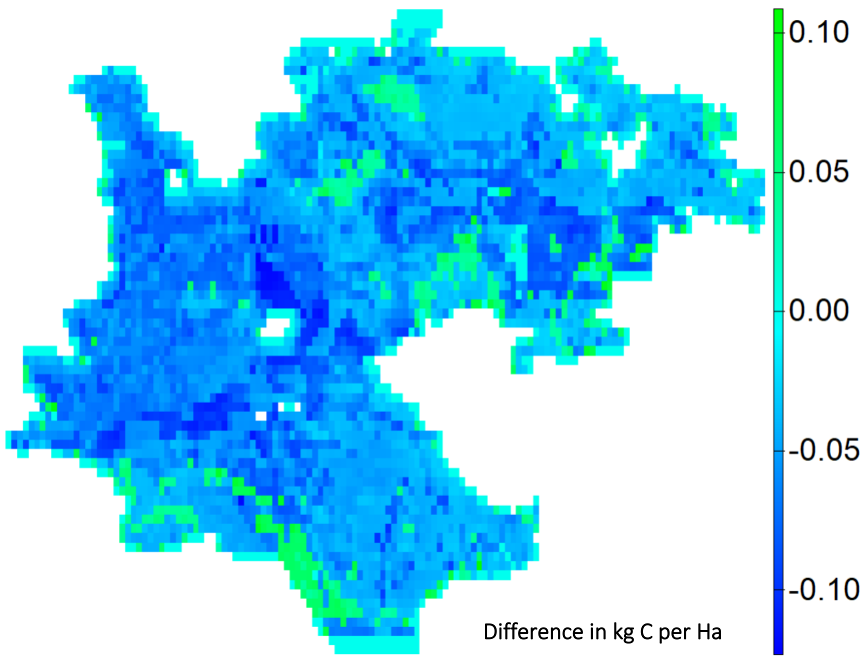

Fig. 7: Raster map of figure 5 values in relation to their geographic position in the Białowieża Forest.

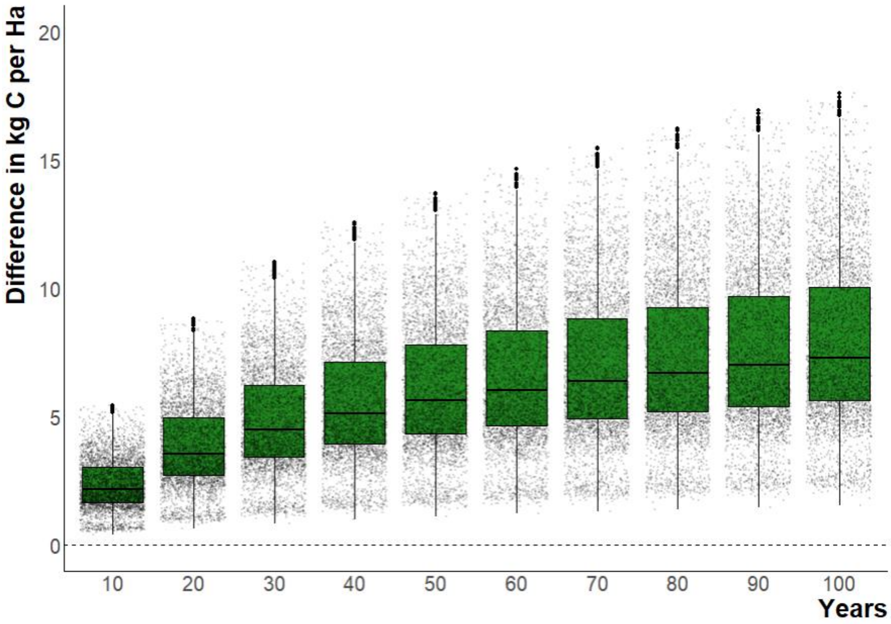

Fig. 8: A boxplot graph showing difference between B- and B+ with Bison DR ratio of 0.33. outliers are displayed as vertically aligned dots (with jitter showing the data points).

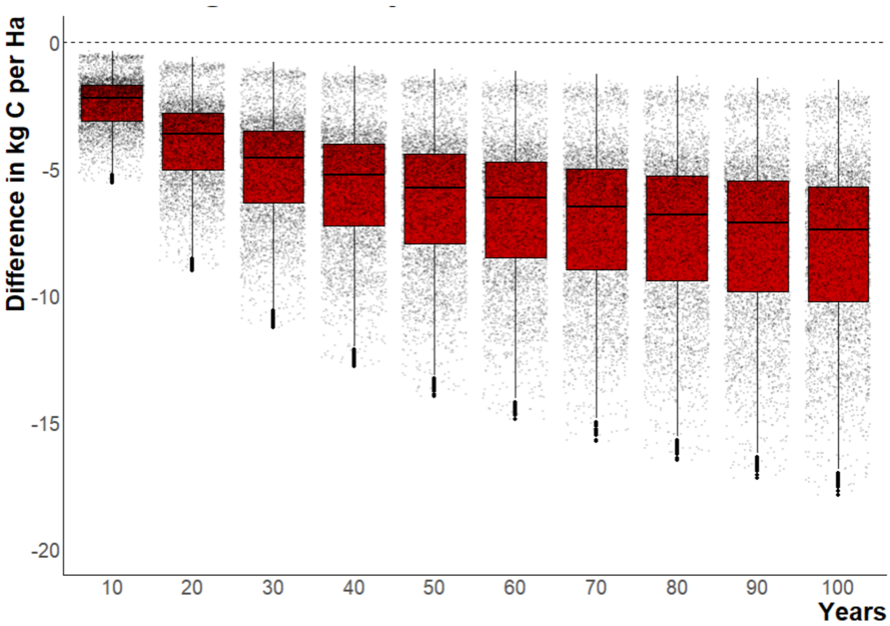

Fig. 9: A boxplot graph showing difference between B- and B+ with Bison DR ratio of 0.5. outliers are displayed as vertically aligned dots (with jitter showing the data points).

The model results show bison waste with a low decomposability (B_{DR} = 0.3; Fig. 8) to increase SOC over 100 years (mean increase: 7.89 kg C ha^{-1}) while in medium and high decomposability (B_{DR}: 0.41 & 0.5 respectively; Fig. 6 & 9), the SOC decreases (mean decrease: 0.06 kg C ha^{-1} and 7.98 kg C ha^{-1} respectively). The variability of the results can be seen to increase (Fig 6, 8, & 9) as time progresses. Nevertheless, the overall trend appears to be clear cut.

Bison waste with a decomposability of 0.41 (Fig. 6) led to a split in the data with the majority decreasing in SOC while a minority of under 17% increasing. This split in trends was found to be exactly correlated with land use types (compare Fig. 3 & 7).

4. Discussion:

Running the model for the three bison waste decomposability scenarios showed a contrast in trends (Section 3.3). High decomposability consistently led to less SOC than soils without bison (B-). Low decomposability did the exact opposite and enriched SOC compared to B-. This suggests a negative correlation between SOC and waste decomposability. With medium decomposability (Fig. 6 & 7), however, grasslands and croplands seem to benefit more readily from the lignin rich excreta than forests, which lost SOC in medium DR scenario. This is likely due to the repartitioning effect of bison, consuming calcitrant material from forests and depositing it in grasslands, which tend to produce less RPM and so have a higher DR, therefore enriching the soils of grasslands at the cost of the forest's rich sources of RPM. With the scale of the trends, visualized above, it can be deduced that due to European bison waste's potential for having high lignin content, and therefore high RPM content; grasslands may gain SOC more readily than forests as grassland soils become enriched with more calcitrant material deposited by bison having consumed lignin rich material.

Despite the trends being clear cut, the model's results display trends that appear on a scale too small to be significant – (kg ha^{-1}) instead of (t ha^{-1}), with most of the uncertainties of the inputs making exponentially more of a difference than the effect of bison waste (section 3.1 & 3.2). As the sensitivity analysis shows (Fig. 5), small changes in certain inputs such as climate data, Hummus C pools, or vegetation cover visibly change the SOC values, further diminishing the effects made by changing the DR of plant inputs in habitats with bison. A distinguishing behaviour of bison that causes the deposition of its waste to have a lower impact than other bovine species is due to the naturally low densities of the population throughout most of the year causing less waste to be deposited overall in each area (Krasiński, 1978). This study's results indicate that bison density, and logically bison waste quantity, to be a more amplifying factor of SOC dynamics than the decomposability of the waste. This all leads to the alternative hypothesis being rejected, and the null hypothesis accepted, in which European bison waste is not found to have a significant effect on SOC in the Białowieża Forest.

RothC's simplicity can be beneficial for getting basic models running however can have a few weaknesses when focusing on such site-specific cases. Plant inputs are a big difference between RothC and other models such as CENTURY (Falloon & Smith, 2006). In RothC, plant input is simplified by a function based on climate inputs and not actual structure and biodiversity of the land being studied (Bernardi, 2006). Direct in situ measurements would lead to better estimations of above and below ground biomass and NPP (Clark *et al*, 2001). Because bison's effect on habitat DRs are estimated in this study in relation to amount of NPP, the methodology used in this study would benefit from further calibrations accounting for the diversity of plants to better understand the root to shoot (RS) ratios that would determine how much above ground biomass is available for bison to forage on. Such methods have been done in site specific studies before, though require a deeper understanding of local plant species composition (e.g., deciduous vs. conifer) in the area (Clark *et al*, 2001; Houghton *et al*, 2008; Scurlock *et al*, 2002).

In relation to NPP and the RothC model in general, the sensitivity analysis showed climate inputs to have a significant effect on the results (Fig. 4). The implications of this are important considerations for assessing the future of SOC pools in habitats under threat of change in climate. Further attempts at modelling dynamics of ecosystems like the forests studied here would benefit from modelling the effects of different climate scenarios on SOC pools (Gottschalk *et al*, 2012; Afzali *et al*, 2019). Such studies could extend to assess potential impacts of climate change on keystone flora and fauna in such systems (Azad, 2019).

Despite RothC's ability to consider clay percentages in soils and their effect on SOC, the model omits further consideration of the soil type and associated behaviours. Podzolic soils like those in Białowieża, have the ability to accumulate organic matter in the B-horizon which can extend to a depth below 30 cm (Buurman & Jongmans, 2005; Freyerová & Šefrna, 2014) – the standard depth used in RothC. In situ measurements of soil depth and estimations on the ability for carbon to percolate down to deeper soil depths would enable more accurate analyses of total SOC as well as accumulated SOC over time by NPP and bison activity.

A factor that affects the ability of different land covers to store carbon is the vegetation cover and the dynamics between the type of vegetation and types of soil. Białowieża's podzolic soil diminishes in presence in croplands and grasslands, due to the lack of trees (Buurman & Jongmans, 2005). Croplands and grasslands, due to their reduced vegetation cover may have difficulty, relative to forests, in retaining enrichment they get from bison manure. This hence complicates the dynamics and suggests a need to study and compare the specific habitats in further detail and resolution than is within scope for this desk-based study.

Future studies would benefit from better understanding the properties of manure on soil C pool dynamics as well as the properties and quantities of bison manure expected to be deposited (Gross & Glaser, 2021). Treating bison waste as plant input with a slightly different DR obscures the complex properties of faeces (Peltre *et al*, 2012) with crude simplifications on the effects of associated microbes on soil C mineralization (Smith *et al*, 1994), and soil hummus being an important C pool affected by such dynamics (Fig. 4 & 5) (Mondini *et al,* 2017). Although there are studies on bison waste lignin content (Gębczyńska & Krasińska, 1974) which could have been used to make an estimation of bison waste decomposability using Van Soest fractions (Jebari *et al,* 2021; Pardo *et al*, 2017), such data was gathered from bison being fed agricultural by-products – hay and barley, which is far from being as lignin rich as the material bison forage for in the forests which comprise the majority of the Białowieża habitat for bison. Studies on bison waste properties in the wild would benefit a shared understanding of the effect of bison on soils of habitats under rewilding schemes internationally and would help align such programmes better with SDG 15 (Frank & Groffman, 1998; Harrison & Bardgett, 2008; Soussana *et al,* 2010).

Despite this study's narrow focus on ruminant waste on nutrient cycles. It must be acknowledged that bison are believed to provide a huge impact that goes beyond the waste they produce. Browsing can reduce NPP in forests (Li & Jiang, 2021) while also altering root exudation rate which alters SOC deposition rate by plants and affects soil food webs significantly (Hamilton *et al,* 2008; Sun *et al*, 2017). Grazing can reduce vegetation cover which can cause soils to dry up more quickly and metabolize more CO2 (Ludvíková *et al,* 2014; van Klink *et al*, 2015), urination can add nitrogen and enrich soils but can also allow more breakdown of carbon (Uchida *et al*, 2011; Li *et al*, 2012; Selbie *et al*, 2014), and soil poaching caused by herds of bison can directly change a landscape and significantly alter SOC in water saturated soils (Ludvíková *et al*, 2014; van Klink *et al*, 2015). As ecosystem engineers, European Bison have the capability to drastically alter plant species richness and therefore fauna biodiversity which can have a variety of cascading effects on carbon pools as well as ecological stability (Jaroszewicz. 2009, 2011, 2012), an important aspect of tackling climate change. The general low density of bison in habitats such as the Białowieża Forest allow for their negative impacts to be minimized while enabling their ecological benefits to persist throughout.

To conclude, although literature shows *Bison bonasus* to have a plethora of ecological functions, European bison manure's impact on soil organic carbon seems minimal due to their low population densities compared to other herding ruminants. Further studies in line with this one would benefit from using in situ measurement techniques or focusing on the other behaviours of bison that could impact nutrient cycles such as soil compaction/poaching, and cascading biological impacts caused by European bison's ability to change forest landscapes and biodiversity.

5. Code and Data inputs:

All the algorithms, code, and visualization procedures written during this study can be found digitally available (Arkaned, 2023).

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Bibliography

Abdalla, M. *et al*, (2014). Simulation of CO2 and Attribution Analysis at Six European Peatland Sites Using the ECOSSE Model. Water, Air, & Soil Pollution, 225(11). doi:https://doi.org/10.1007/s11270-014-2182-8.

Afzali, S.F., Azad, B., Golabi, M.H. and Francaviglia, R. (2019). Using RothC Model to Simulate Soil Organic Carbon Stocks under Different Climate Change Scenarios for the Rangelands of the Arid Regions of Southern Iran. Water, [online] 11(10), p.2107. doi:https://doi.org/10.3390/w11102107.

Arkaned (2023). BisonRothC. [online] GitHub. Available at: https://github.com/Arkaned/BisonRothC.git [Accessed 19 Dec. 2023].

Azad, B. *et al*, (2019). Modeling the effect of vegetation conversion and climate change on the dynamics of soil organic carbon stock in a complex ecosystem. Shiraz University, [online] 9(1), p.83-99. https://doi.org/10.22069/ejsms.2019.13695.1762

Bernardi, M. (2006). The Miami Model of climatic net primary production of biomass.

Bilotta, G.S., Brazier, R.E. and Haygarth, P.M. (2007) 'The impacts of grazing animals on the quality of soils, vegetation, and surface waters in intensively managed grasslands', *Advances in Agronomy*, pp. 237–280. doi:10.1016/s0065-2113(06)94006-1.

BPN (2023). Bialowieski Park Narodowy - European bison Show Reserve. [online] Available at: https://bpn.com.pl/index.php?option=com_content&task=view&id=67&lang=en [Accessed 24 Nov. 2023].

BPN, personal correspondence (Nov, 2023), Bialowieski Park Narodowy [interviewed November, 2023]

Buurman, P. and Jongmans, A.G. (2005). Podzolisation and soil organic matter dynamics. *Geoderma*, 125(1-2), pp.71–83. doi:https://doi.org/10.1016/j.geoderma.2004.07.006.

Clark, D.A. *et al*, (2001). Measuring Net Primary Production In Forests: Concepts And Field Methods. *Ecological Applications*, 11(2), pp.356–370. doi:https://doi.org/10.1890/1051-0761(2001)011[0356:mnppif]2.0.co;2.

Coleman, K. and Jenkinson, D.S. (1996) 'ROTHC-26.3 - a model for the turnover of carbon in soil', *Evaluation of Soil Organic Matter Models*, pp. 237–246. doi:10.1007/978-3-642-61094-3_17.

CORINE land cover (2021) *European Environment Agency*. Available at: https://www.eea.europa.eu/help/faq/what-is-corine-land-cover (Accessed: 28 September 2023).

CRU TS v4.03 Data Variables (2023) *Cru TS v4.03 data variables*. Available at: https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.03/cruts.1905011326.v4.03/ (Accessed: 28 September 2023).

Dib, A.E. *et al.* (2014) 'Simulating effects of changing climate and co2 emissions on soil carbon pools at the Hubbard Brook Experimental Forest', *Global Change Biology*, 20(5), pp. 1643–1656. doi:10.1111/gcb.12436.

Eycott, A. *et al*, (2013). Defecation rate in captive European bison, Bison bonasus. Acta Theriologica, 58(4), pp.387–390. doi:https://doi.org/10.1007/s13364-013-0129-x.

Falloon, P. and Smith, P. (2006) 'Simulating SOC changes in long-term experiments with ROTHC and Century: Model evaluation for a regional scale application', *Soil Use and Management*, 18(2), pp. 101–111. doi:10.1111/j.1475-2743.2002.tb00227.x.

Frank, D.A. and Groffman, P.M. (1998) ‘Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park’, *Ecology*, 79(7), pp. 2229–2241. doi:10.1890/0012-9658(1998)079[2229:uvlcos]2.0.co;2.

Freyerová, K. and Šefrna, L. (2014). Soil organic carbon density and storage in podzols – a case study from Ralsko region (Czech Republic). AUC GEOGRAPHICA, 49(2), pp.65–72. doi:https://doi.org/10.14712/23361980.2014.16.

Gębczyńska, Z. & Krasińska, M. (1972). Bisoniana XLIX. Food preferences and requirements of the European bison. Acta Theriologica, 17, pp.105–117. doi:https://doi.org/10.4098/at.arch.72-10.

Gębczyńska, Z. & Krasińska, M. (1974) ‘Bisoniana lv. A comparison of the digestibility of nutrients by European bison and cattle’, *Acta Theriologica*, 19, pp. 283–289. doi:10.4098/at.arch.74-22.

Gottschalk, P., Smith, J.U., Wattenbach, M., Bellarby, J., Stehfest, E., Arnell, N., Osborn, T.J., Jones, C. and Smith, P. (2012). How will organic carbon stocks in mineral soils evolve under future climate? Global projections using RothC for a range of climate change scenarios. Biogeosciences, [online] 9(8), pp.3151–3171. doi:https://doi.org/10.5194/bg-9-3151-2012.

Gross, A. and Glaser, B. (2021). Meta-analysis on how manure application changes soil organic carbon storage. Scientific Reports, 11(1). doi:https://doi.org/10.1038/s41598-021-82739-7.

Guyader, J. *et al.* (2016) ‘Forage use to improve environmental sustainability of ruminant production12’, *Journal of Animal Science*, 94(8), pp. 3147–3158. doi:10.2527/jas.2015-0141.

Hamilton, E.W., Frank, D.A., Hinchey, P.M. and Murray, T.R. (2008). Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. *Soil Biology and Biochemistry*, 40(11), pp.2865–2873. doi:https://doi.org/10.1016/j.soilbio.2008.08.007.

FAO (2023) *data.apps.fao.org*. Available at: https://data.apps.fao.org/glosis/?share=f-6756da2a-5c1d-4ac9-9b94-297d1f105e83&lang=en (Accessed: 28 September 2023).

Harrison, K.A. and Bardgett, R.D. (2008) ‘Impacts of grazing and browsing by large herbivores on soils and soil biological properties’, *Ecological Studies*, pp. 201–216. doi:10.1007/978-3-540-72422-3_8.

ISRIC (2023) *Soilgrids Web Portal*, *SoilGrids web portal*. Available at: https://www.soilgrids.org/ (Accessed: 28 September 2023).

Jebari, A. *et al.* (2021) ‘Estimating soil organic carbon changes in managed temperate moist grasslands with Rothc’, *PLOS ONE*, 16(8). doi:10.1371/journal.pone.0256219.

J.-M. Bollag (2017). *Soil Biochemistry*. Routledge.

Jol, A. and Fussel, H.-M. (2016) *Climate change, impacts and vulnerability in Europe*. rep. European Environment Agency.

Jones, A. *et al.* (2010) *The State of Soil in Europe*. rep. European Environment Agency.

Kamiński, M.J., Byk, A. and Tykarski, P. (2015). Seasonal and Diel Activity of Dung Beetles (Coleoptera: Scarabaeoidea) Attracted to European Bison Dung in Białowieża Primeval Forest, Poland. *The Coleopterists Bulletin*, 69(1), pp.83–90. doi:https://doi.org/10.1649/0010-065x-69.1.83.

Kim, S.Y. *et al.* (2018) 'Cattle manure composting: Shifts in the methanogenic community structure, chemical composition, and consequences on methane production potential in a rice paddy', *Applied Soil Ecology*, 124, pp. 344–350. doi:10.1016/j.apsoil.2017.12.002.

Kipling, R.P. *et al.* (2016) 'Modeling European ruminant production systems: Facing the challenges of climate change', *Agricultural Systems*, 147, pp. 24–37. doi:10.1016/j.agsy.2016.05.007.

Koga, N. *et al.* (2011) 'Estimating net primary production and annual plant carbon inputs, and modelling future changes in soil carbon stocks in arable farmlands of northern Japan', *Agriculture, Ecosystems & Environment*, 144(1), pp. 51–60. doi:10.1016/j.agee.2011.07.019.

Krasińska, M. and Krasiński, Z.A. (2002). Body mass and measurements of the European bison during postnatal development. Acta Theriologica, 47(1), pp.85–106. doi:https://doi.org/10.1007/bf03193569.

Krasinska, M. (2013) *European bison: The nature monograph*. Heidelberg: Springer.

Krasiński, Z.A. (1978). Bisoniana LXVII. Dynamics and structure of the European bison population in the Białowieża Primeval Forest. *Acta Theriologica*, 23, pp.3–48, plates 1-2. doi:https://doi.org/10.4098/at.arch.78-1.

Lal, R. (2012) 'Climate change and soil degradation mitigation by sustainable management of soils and other natural resources', *Agricultural Research*, 1(3), pp. 199–212. doi:10.1007/s40003-012-0031-9.

Li, F.Y. *et al*, (2012). Effects of nitrogen load variation in animal urination events on nitrogen leaching from grazed pasture. *Agriculture, Ecosystems & Environment*, 159, pp.81–89. doi:https://doi.org/10.1016/j.agee.2012.07.003.

Li, B.V. and Jiang, B. (2021). Responses of forest structure, functions, and biodiversity to livestock disturbances: A global meta-analysis. *Global Change Biology*, 27(19), pp.4745–4757. doi:https://doi.org/10.1111/gcb.15781.

Ludvíková et al, (2014). Long term defoliation by cattle grazing with and without trampling differently affects soil penetration resistance and plant species composition in Agrostis capillaris grassland. *Agriculture, Ecosystems & Environment*, [online] 197, pp.204–211. doi:https://doi.org/10.1016/j.agee.2014.07.017.

Maet, T.D. (2022). *ESA/CCI viewer*. [online] maps.elie.ucl.ac.be. Available at: https://maps.elie.ucl.ac.be/CCI/viewer/download.php

Mishra, G., Jangir, A. and Francaviglia, R. (2019) ‘Modeling soil organic carbon dynamics under shifting cultivation and forests using ROTHC model’, *Ecological Modelling*, 396, pp. 33–41. doi:10.1016/j.ecolmodel.2019.01.016.

Mondini, C., María Luz Cayuela, Sinicco, T., Flavio Fornasier, Gálvez, A. and Sánchez-Monedero, M.Á. (2018). Soil C Storage Potential of Exogenous Organic Matter at Regional Level (Italy) Under Climate Change Simulated by RothC Model Modified for Amended Soils. Frontiers in Environmental Science, 6. doi:https://doi.org/10.3389/fenvs.2018.00144.

Muhammad, N., Dai, Z., Xiao, K., Meng, J., Brookes, P.C., Liu, X., Wang, H., Wu, J. and Xu, J. (2014). Changes in microbial community structure due to biochars generated from different feedstocks and their relationships with soil chemical properties. *Geoderma*, 226-227, pp.270–278. doi:https://doi.org/10.1016/j.geoderma.2014.01.023.

Pardo, G., Moral, R. and del Prado, A. (2017). SIMSWASTE-AD - A modelling framework for the environmental assessment of agricultural waste management strategies: Anaerobic digestion. Science of The Total Environment, 574, pp.806–817. doi:https://doi.org/10.1016/j.scitotenv.2016.09.096.

Peltre, C. *et al*, (2012). RothC simulation of carbon accumulation in soil after repeated application of widely different organic amendments. Soil Biology and Biochemistry, 52, pp.49–60. doi:https://doi.org/10.1016/j.soilbio.2012.03.023.

Peralta, G. *et al.* (2020) *Technical Manual Global Soil Organic Carbon ... - github pages, Technical Manual Global Soil Organic Carbon Sequestration Potential Map GSOCseq*. Available at: https://fao-gsp.github.io/GSOCseq/index.html (Accessed: 28 September 2023).

Perzanowska, J. and Korzeniak, J. (2020). Red list of Natura 2000 habitat types of Poland. *Journal for Nature Conservation*, 56, p.125834. doi:https://doi.org/10.1016/j.jnc.2020.125834.

Pribyl, D.W. (2010) ‘A critical review of the conventional SOC to SOM conversion factor’, *Geoderma*, 156(3–4), pp. 75–83. doi:10.1016/j.geoderma.2010.02.003.
Pucek, Z. (2004) *European bison*. Gland, Switzerland: IUCN.

Ramos, M.C., Quinton, J.N. and Tyrrel, S.F. (2006) ‘Effects of cattle manure on erosion rates and runoff water pollution by faecal coliforms’, *Journal of Environmental Management*, 78(1), pp. 97–101. doi:10.1016/j.jenvman.2005.04.010.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. [online] R Foundation for Statistical Computing. Available at: https://www.r-project.org/.

Scurlock, J.M.O., Johnson, K. and Olson, R.J. (2002). Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology*, 8(8), pp.736–753. doi:https://doi.org/10.1046/j.1365-2486.2002.00512.x.

Schils, R. *et al.* (2008) ‘Review Of Existing Information On The Interrelations Between Soil And Climate Change’, *Climsoil Final Report* [Preprint]. doi:10.30852/p.4344.

Scholefield, D. and Hall, D.M. (1985) ‘A method to measure the susceptibility of pasture soils to poaching by cattle’, *Soil Use and Management*, 1(4), pp. 134–138. doi:10.1111/j.1475-2743.1985.tb00976.x.

Selbie, D. R., Cameron, K. C., Di, H. J., Moir, J. L., Lanigan, G. J. and Richards, K. G. (2014) “The effect of urinary nitrogen loading rate and a nitrification inhibitor on nitrous oxide emissions from a temperate grassland soil,” *The Journal of Agricultural Science*. Cambridge University Press, 152(S1), pp. 159–171. doi: 10.1017/S0021859614000136.

Smith, J., Halvorson, J. and Boltonjr, H. (1994). Spatial relationships of soil microbial biomass and C and N Mineralization in a semi-arid shrub-steppe ecosystem. Soil Biology and Biochemistry, 26(9), pp.1151–1159. doi:https://doi.org/10.1016/0038-0717(94)90137-6.

Smith, J., Smith, P. and Addiscott, T. (1996) ‘Quantitative methods to evaluate and compare soil organic matter (SOM) models’, *Evaluation of Soil Organic Matter Models*, pp. 181–199. doi:10.1007/978-3-642-61094-3_13.

Soussana, J.F., Tallec, T. and Blanfort, V. (2010) ‘Mitigating the greenhouse gas balance of ruminant production systems through carbon sequestration in Grasslands’, *Animal*, 4(3), pp. 334–350. doi:10.1017/s1751731109990784.

Stoy, P.C. *et al.* (2021) ‘Methane efflux from an American bison herd’, *Biogeosciences*, 18(3), pp. 961–975. doi:10.5194/bg-18-961-2021.

Sun, G., Zhu-Barker, X., Chen, D., Liu, L., Zhang, N., Shi, C., He, L. and Lei, Y. (2017). Responses of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine meadow: An implication for pasture management. *Plant and Soil*, 416(1-2), pp.515–525. doi:https://doi.org/10.1007/s11104-017-3236-7.

Teague, W.R. *et al.* (2016) ‘The role of ruminants in reducing agriculture’s carbon footprint in North America’, *Journal of Soil and Water Conservation*, 71(2), pp. 156–164. doi:10.2489/jswc.71.2.156.

TUOHY, P. *et al.* (2014) ‘The effects of treading by two breeds of dairy cow with different live weights on soil physical properties, poaching damage and herbage production on a poorly drained clay-loam soil’, *The Journal of Agricultural Science*, 153(8), pp. 1424–1436. doi:10.1017/s0021859614001099.

Tuñon, G. *et al.* (2013) ‘Spring and autumn animal treading effects on pre-grazing herbage mass and tiller density on two contrasting pasture types in Ireland’, *Grass and Forage Science*, 69(3), pp. 502–513. doi:10.1111/gfs.12055.

Uchida, Y., Clough, T.J., Kelliher, F.M., Hunt, J.E. and Sherlock, R.R. (2011). Effects of bovine urine, plants and temperature on N2O and CO2 emissions from a sub-tropical soil. *Plant and Soil*, 345(1-2), pp.171–186. doi:https://doi.org/10.1007/s11104-011-0769-z.

van Klink, R., Schrama, M., Nolte, S., Bakker, J.P., WallisDeVries, M.F. and Berg, M.P. (2015). Defoliation and Soil Compaction Jointly Drive Large-Herbivore Grazing Effects on Plants and Soil Arthropods on Clay Soil. *Ecosystems*, 18(4), pp.671–685. doi:https://doi.org/10.1007/s10021-015-9855-z.