

# JGR Biogeosciences

## RESEARCH ARTICLE

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### Key Points:

- Animals rewire ecosystem food webs and thereby qualitatively change the dominant control over carbon cycling
- Animal-mediated top-down control of the carbon cycle quantitatively changes key ecosystem processes, increasing carbon sequestration
- Leveraging animal-driven carbon capture may lead to more accurate ecosystem carbon budgets, enhancing nature-based climate change solutions

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Rewiring the Carbon Cycle: A Theoretical Framework for Animal-Driven Ecosystem Carbon Sequestration

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**Abstract** Most carbon cycle models do not consider animal-mediated effects, focusing instead on carbon exchanges among plants, microbes, and the atmosphere. Yet, a growing body of empirical evidence from diverse ecosystems points to pervasive animal effects on ecosystem carbon cycling and shows that ignoring them could lead to misrepresentation of an ecosystem's carbon cycle. We develop a new theoretical framework to account for animal effects on ecosystem carbon cycling. We combine a classic ecosystem compartment modeling approach with a classic carbon model to account for carbon flux and storage among plant, animal, and soil microbial trophic compartments. We show, by way of numerical analyses of steady state conditions across three competing scenarios, that animal presence alters the dominant pathways of control over carbon storage and capture. This altered control arises via direct, consumptive effects and especially via indirect, non-consumptive pathways by instigating faster nutrient recycling. This leads to a quantitative change in the ecosystem's carbon balance, enhancing the amount of carbon captured and stored in the ecosystem. Further, the indirect pathways appear especially important in enabling these effects because of their sensitivity to the structure of the ecosystem's food chain. The modeling shows that animals could play a larger role in ecosystem carbon cycle than previously thought. Our framework provides further guidance for empirical research aimed at quantifying animal-mediated control of carbon cycling and to inform the development of nature-based climate change solutions that leverage animal influence on the carbon cycle to help mitigate climate change.

**Plain Language Summary** The mathematical tools that scientists use to account for the amount of carbon captured and stored in ecosystems rarely consider the effects of animals. This stems from the assumption that because animals are much rarer than plants and microbes in ecosystems their potential influence ought to be minimal. Yet, field studies have begun to show that this assumption may not be accurate. Here, we report on modeling analyses that incorporate insights from field research about the different ways that animals can affect carbon uptake and storage in ecosystems through their interactions with plants and microbes. Our analyses show that animal presence fundamentally changes the relationships between plants, microbes, and the environment. In turn, this leads to large changes in the amount of carbon captured and stored in ecosystems relative to conditions that exclude animals. Hence, animals can be allies in fighting climate change as a key addition to the growing portfolio of nature-based climate change solutions.

## 1. Introduction

The carbon cycle involves a series of biogeochemical processes that move carbon through plant, animal, and microbial trophic compartments within ecosystems, and between ecosystems and the atmosphere. The series of processes fundamentally includes photosynthetic capture and assimilation of atmospheric carbon into plant biomass, consumptive transfer and assimilation of carbon into animal (herbivore and carnivore) biomass, assimilation of detrital plant and animal biomass carbon into microbial biomass, and autotrophic (plant) and heterotrophic (microbial and animal) respiratory release of carbon to the atmosphere (Keenan & Williams, 2018; Middelburg, 2019). Thus, all plants, animals, and microbes contribute toward regulating biomass carbon storage in ecosystems (Middelburg, 2019; Schmitz & Leroux, 2020; Steinberg & Landry, 2017). Yet the predominant models of the carbon cycle only account for carbon movement and storage among plant and microbial trophic compartments and the atmosphere (Piao et al., 2013; Zaehle et al., 2014).

Such model formalism is based on two tacit assumptions: (a) ecosystem carbon capture and storage is controlled only by nutrient and water limitations—that is, ecosystem processes are bottom-up controlled; and (b) animal contributions are negligible, or at least are so minuscule that they can be safely subsumed by effects of larger

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biomass compartments, for example, animal respiration is overwhelmed by microbial respiration (Rastetter et al., 2022; Schmitz & Leroux, 2020). However, such assumptions can mischaracterize how ecosystem carbon cycling is controlled, in turn, potentially leading to large under- or over-estimates of the amount of carbon storage in ecosystems (Schmitz & Leroux, 2020; Schmitz et al., 2023).

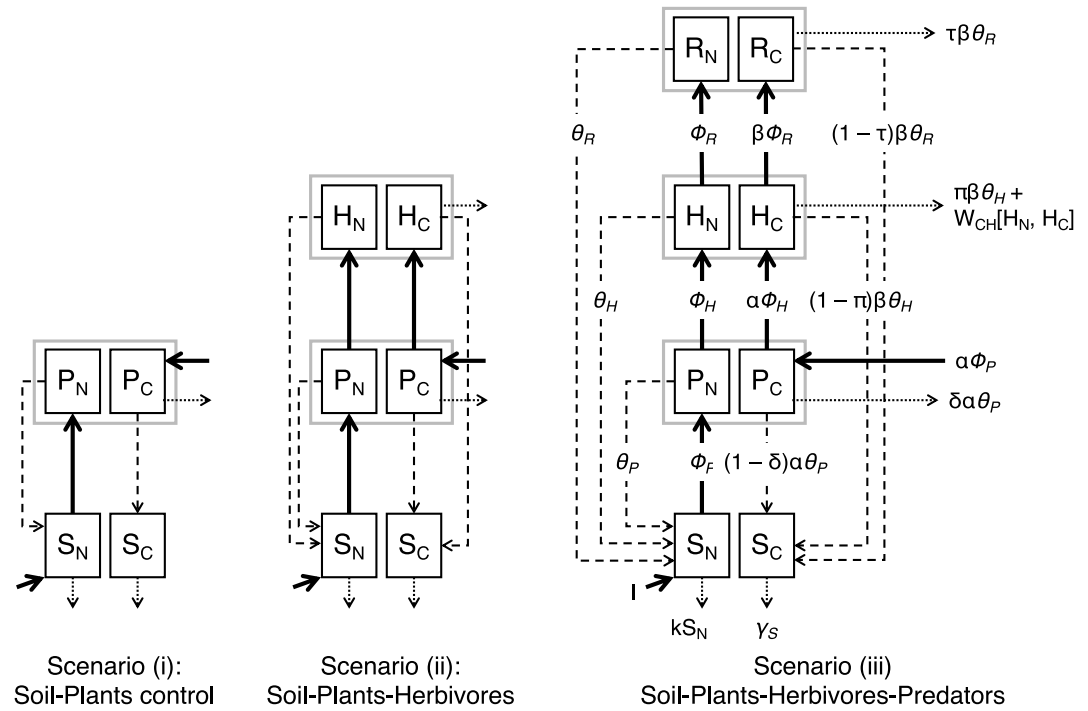
Here we illustrate how including animal feedback controls (i.e., top-down control of ecosystem processes) in a carbon cycle model can fundamentally change the importance of different pathways and rates of carbon movement (fluxes) among trophic compartments and the atmosphere, relative to a model that excludes animal controls. The inclusion of animals in carbon cycle models is rare, but growing (Dangal et al., 2017; Huntley et al., 1991; Leroux et al., 2012; Leroux & Schmitz, 2015; Metcalfe et al., 2014; Rastetter et al., 2022). However, these earlier models are typically designed to characterize specific empirical systems, thereby limiting generalization. We instead designed our models to provide a scaffolding for more generalizable analyses (*sensu* Ives et al., 2005; Leroux & Schmitz, 2015). As such, our process-based modeling does not contain the details needed to depict any specific, real-world system, because such empirical details, while growing, are still lacking for most systems (Pringle et al., 2023; Schmitz & Leroux, 2020). The model does, however, contain the salient principles of animal control over biogeochemical processes (aka, zoogeochimistry; Schmitz et al., 2018) that apply broadly across ecosystems. Furthermore, the structure of the model does enable the substitution of functions for parameters to mechanistically characterize processes and interactions that apply to a given real-world system. By doing this, we aim to inspire new quantitative empirical measurements of animal effects in all kinds of ecosystem types. Considering animal effects on ecosystem processes will be important because, as we show, animal effects could be disproportionately larger than expected based merely on their biomass representation within ecosystems, thereby counterbalancing bottom-up control. This arises because animals cause direct and indirect feedback effects that alter the abundance, elemental content and biogeochemical functioning of the larger, plant and microbial biomass pools.

## 2. Model Structure

Our model (Equations 1–8) combines a classic ecosystem compartment model (DeAngelis, 1992; Holt, 1997; Loreau, 2010) with a classic carbon budget model (Ballantyne et al., 2021; Chapin et al., 2006). The modeling uses principles of elemental flux and storage among different trophic levels in an ecosystem, based on known processes for their action (Leroux & Loreau, 2010). The ecosystem trophic compartment structure—which includes soil elemental pools, plants, and animals (i.e., herbivores, predators; Figure 1)—is typically used when examining organismal effects on ecosystem functioning (Bassar et al., 2012; Hall et al., 2007; Leroux et al., 2012; Leroux & Loreau, 2010; Loreau, 2010). We use a stoichiometric approach that focuses on fluxes and pool sizes of nitrogen (N) and carbon (C) to account for rate limitation of carbon cycling by an essential nutrient. We focus on C and N because they (a) share a strong stoichiometric relationship captured by the C:N ratio which describes the stoichiometry of an individual or trophic/functional group and allows for tracking both C and N (Schmitz & Leroux, 2020; Sterner & Elser, 2002), (b) are fundamental actors in existing carbon models (Zaehle et al., 2014), and (c) are routinely measured in organisms as part of empirical studies (Meunier et al., 2017; Welti et al., 2017). Nonetheless, this model formalism does not preclude the inclusion or substitution of other nutrients (e.g., phosphorus) that may limit carbon cycling rate.

Our model capture the essential features of elemental cycling in general (DeAngelis, 1992; Loreau, 2010) and carbon cycling specifically (Schmitz & Leroux, 2020), including elemental uptake by plants from the abiotic environment (i.e., C uptake from the atmosphere and N uptake from the soil elemental pool) and elemental transfer to and loss from all compartments through trophic interactions, respiration, excretion, egestion, and leaching out of the ecosystem. As such, the model depicts an open system, that is, elements are not solely recycled within the confines of the ecosystem. Nevertheless, we formulate the model to obey fundamental mass balance requirements (Loreau, 2010) such that, at equilibrium, elemental inputs to the ecosystem equal elemental losses from the ecosystem plus storage.

We use this model to explore how animal presence and absence influence ecosystem nutrient cycling, productivity, and carbon capture and storage focusing on three scenarios: (i) an ecosystem with soil and plants but no animals, (ii) an ecosystem with soil, plants, and herbivores, and (iii) an ecosystem with soil, plants, herbivores, and predators. The following set of ordinary differential equations describes the full ecosystem model:



**Figure 1.** Conceptual diagram of the model and the three scenarios tested. Left: scenario (i) acts as control, modeling the dynamics of nitrogen (N) and carbon (C) in an ecosystem with a bi-trophic food chain comprising soil ( $S_N, S_C$ ) and plants ( $P_N, P_C$ ). Middle: scenario (ii) maintains the basic structure of scenario (i) but additionally introduces herbivores ( $H_N, H_C$ ) into the system. Right: modeling scenario (iii) builds on the previous two by also comprising predators ( $R_N, R_C$ ) at the top of the food chain. In each diagram, solid black boxes represent trophic compartments, solid gray boxes represent the C:N ratio of each trophic compartment, solid black lines represent resource uptake by a trophic level from the one below it (e.g., herbivory, predation) or the environment (e.g., photosynthesis), dashed black lines represent recycling pathways from aboveground trophic compartments to the soil compartment, and dotted black lines represent losses of N and C from the system (e.g., respiration, leaching). Table 1 describes the mathematical expressions overlaid upon scenario (iii) and Table 2 details the units of measurement and value ranges for the model's state variables and parameters.

$$\frac{dS_N}{dt} = I - kS_N - \Phi_P + \theta_P + \theta_H + \theta_R \quad (1)$$

$$\frac{dS_C}{dt} = (1 - \delta)\alpha\theta_P + (1 - \pi)\beta\theta_H + (1 - \tau)\beta\theta_R - \gamma_S \quad (2)$$

$$\frac{dP_N}{dt} = \Phi_P - \Phi_H - \theta_P \quad (3)$$

$$\frac{dP_C}{dt} = \alpha(\Phi_P - \Phi_H - \theta_P) \quad (4)$$

$$\frac{dH_N}{dt} = \Phi_H - \Phi_R - \theta_H \quad (5)$$

$$\frac{dH_C}{dt} = \alpha\Phi_H - \beta\Phi_R - (\beta\theta_H + W_{CH}[H_N, H_C]) \quad (6)$$

$$\frac{dR_N}{dt} = \Phi_R - \theta_R \quad (7)$$

$$\frac{dR_C}{dt} = \beta(\Phi_R - \theta_R) \quad (8)$$

**Table 1**  
Model Functions Descriptions and Parameter Definitions

Functions	Description	Formula	Parameters and definitions
$\Phi_P$	N flux from soil to plant compartment	$a_P P_N S_N S_C$	$a_P$ , plant uptake rate
$\Phi_H$	N flux from plant to herbivore compartment	$a_H P_N H_N$	$a_H$ , herbivore uptake rate
$\Phi_R$	N flux from herbivore to predator compartment	$a_R H_N R_N$	$a_R$ , predator uptake rate
$\theta_i$	recycling flux from trophic compartment $i$ to the soil	$r_i i_N$	$r_i$ , N-recycling rate of trophic level $i$ , where $i \in [P, H, R]$
$\gamma_S$	inorganic loss rate of C from soil compartment	$q_S S_N S_C$	$q_S$ , C loss rate from soil compartment
$W_{CH}[H_N, H_C]$	herbivore differential assimilation rate of C	$(\alpha - \beta) a_H P_N H_N$	$\alpha$ , plant C:N ratio; $\beta$ , herbivore C:N ratio

Note. See Table 2 for units of measurement, as well as further parameter definitions and value ranges. N, nitrogen; C, carbon; S, soil; P, plants; H, herbivores; R, predators. See Appendix B for the derivation of the  $W_{CH}[H_N, H_C]$  term.

Specifications for the functions for the terms  $\Phi_i$  and  $\theta_i$  (where  $i \in [S, P, H, R]$ ), as well as  $\gamma_S$ , in Equations 1–8 can be found in Table 1. In addition, we assume the herbivore is N-limited and the function  $W_{CH}[H_N, H_C]$  in Equation 6—which partitions C flow to respiration and recycling depending on the balance of C and N taken up by the herbivore (Daufresne & Loreau, 2001b; Leroux et al., 2012)—is presented in Table 1 with full mathematical derivation of the function in Appendix B. Table 2 describes the model's state variables and parameters, their units of measurement, and value ranges. Note that the modeling framework described by Equations 1–8 simplifies below-ground C dynamics to focus on above-ground animal effects. Introducing additional complexity to the below-ground component (e.g., as done in Cherif & Loreau, 2013) could be a promising avenue for future research and offer additional insights on how interactions between above- and below-ground ecosystem components may shape ecosystem C accounting.

The model described by Equations 1–8 represents scenario (iii), an ecosystem with a food chain comprising four trophic compartments. Setting parameters  $a_R$  and  $r_R = 0$  in the expressions for  $\Phi_R$  and  $\theta_R$  (Table 1) recovers scenario (ii), where the ecosystem comprises a tri-trophic food chain without predators. Likewise, by additionally setting  $a_H$  and  $r_H = 0$  in  $\Phi_H$ ,  $\theta_H$  (Table 1), we can recover scenario (i), in which the ecosystem contains only soil and plants.

**Table 2**  
Variables and Parameters of the Model Shown in Figure 1

Variables and parameters	Symbol	Units	Range	Notes
Soil pool of nutrient $j$	$S_j$	$g$	$>0$	where $j \in [N, C]$
Plant pool of nutrient $j$	$P_j$	$g$	$>0$	where $j \in [N, C]$
Herbivore pool of nutrient $j$	$H_j$	$g$	$>0$	where $j \in [N, C]$
Predator pool of nutrient $j$	$R_j$	$g$	$>0$	where $j \in [N, C]$
Soil inorganic input rate of N	$I$	$g \times t^{-1}$	$>0$	
Soil inorganic loss rate of N	$k$	$g \times t^{-1}$	$>0$	
Soil inorganic loss rate of C	$\gamma_S$	$g \times t^{-1}$	$>0$	
C:N ratio of plants	$\alpha$	unit-less	$>0$	Under N-limitation, $\alpha > \beta$
C:N ratio of herbivores and predators	$\beta$	unit-less	$>0$	Under N-limitation, $\alpha > \beta$
Proportion of plants' C that is respired	$\delta$	unit-less	$[0, 1]$	$1 - \delta$ is the proportion of C recycled back into the soil
Proportion of herbivores' C that is respired	$\pi$	unit-less	$[0, 1]$	$1 - \pi$ is the proportion of C recycled back into the soil
Proportion of predators' C that is respired	$\tau$	unit-less	$[0, 1]$	$1 - \tau$ is the proportion of C recycled back into the soil
Trophic compartment uptake rate	$a_i$	$g \times t^{-1}$	$>0$	where $i \in [P, H, R]$ ; see Table 1
N-specific recycling rate of trophic level $i$	$r_i$	$g \times t^{-1}$	$>0$	where $i \in [P, H, R]$ ; see Table 1
C loss rate from the soil	$q_S$	$g \times t^{-1}$	$>0$	see Table 1

Note. N, nitrogen; C, carbon.

### 3. Numerical Analyses

We solved Equations 1–8 for equilibria (mass balance) in Mathematica (v. 13.2; Wolfram Research, 2022). Each modeling scenario has one equilibrium where all state variables are positive and thus biologically meaningful (see Appendix A). We use these equilibria to perform further numerical analyses for each modeling scenario in R (v. 4.3.1; R Core Team, 2023) aimed at assessing how different magnitudes of model parameter values influence (a) trophic compartment C stocks (i.e., where C is stored), (b) net primary productivity (i.e., net C capture by plants), and (c) net ecosystem carbon balance (i.e., the total net amount of C stored in the ecosystem; *sensu* Chapin et al. (2006); Schmitz and Syl en (2023)). We further characterized the sensitivity of the models to changes in model structure and parameters. Following Leroux and Schmitz (2015), we used a Latin hypercube sampling design to generate 10,000 sets of random parameter values for all parameters in the models, using function `randomLHS` from the `lhs` R package (Carnell, 2022). We used the same parameter sets across all three modeling scenarios. We scaled the random parameter values assigned to parameters  $\alpha$  and  $\beta$ , representing the C:N ratio for plants and herbivores, respectively, to fit in the empirical C:N ranges reported in Buchkowski et al. (2019). As well, we scaled values assigned to respiration rates of plants, herbivores, and predators (parameters  $\delta$ ,  $\pi$ , and  $\tau$ , respectively) to be  $\in [0, 1]$ . Of the 10,000 iterations, we retained only those model solutions that satisfied the feasibility conditions of each equilibrium (reported in Appendix A). Finally, our results arise from conducting numerical estimates of ecosystem functions that produce large sample sizes of output due to an ensemble of parameter selections. We therefore refrain from comparing scenarios (i)–(iii) using frequentist statistical tests on the data because the massive amount of data would produce artificially low  $p$ -values and risk committing a Type II statistical error (White et al., 2014). Instead, we follow recommendations to report effect sizes of differences across scenarios and use graphical means to explore and compare the results arising from our analyses of modeling scenarios (White et al., 2014).

#### 3.1. Ecosystem Structure Analyses

We performed a global sensitivity analysis (Bellmore et al., 2014; Harper et al., 2011) to evaluate how each parameter (Table 2) influences the dynamics of C and N in each trophic compartment, for each modeling scenario. In a global sensitivity analysis (GSA), all parameter values vary simultaneously, thereby accounting for parameter interactions when quantifying each parameter's influence on the models' results (Harper et al., 2011). Using a GSA allows us to (a) investigate changes in the relative influence of parameters in the three model scenarios and (b) quantify each parameter's effect in shaping the three ecosystem functions we use to investigate animal-mediated effects on ecosystem functioning and C sequestration (see below). We use function `randomForest` in R to fit a random forest algorithm to the feasible parameter sets (see above) used in our numerical analyses. We use as response variables the values of each state variable at equilibrium and for each ecosystem function of interest when fitting the random forest algorithm. Function `randomForest` computes the residual sum of squared errors (SSE) for each parameter; from which we calculate a normalized index of relative importance by dividing each parameter's SSE by the total SSE. We repeated this process for all three modeling scenarios. Finally, we visually assessed how each parameter influences the model's results in each scenario (see the Supplementary Code document available in Rizzuto et al., 2023).

#### 3.2. Ecosystem Function Analyses

We investigate the effects of animal presence and absence on three components of ecosystem carbon accounting: biomass and stock C accumulation, primary productivity, and net ecosystem carbon balance (NECB; Chapin et al., 2006; Schmitz et al., 2023). For each modeling scenario, we use the equilibrium values of the model's state variables (Table 2) as estimates of equilibrium soil stock and plant, herbivore, and predator C biomass accumulation (in grams). Following Loreau (2010), we estimate ecosystem primary productivity at equilibrium by substituting the values of  $S_j^*$  and  $P_j^*$  in the expressions for plant growth ( $\alpha\Phi_p$ ; Table 1, Equation 4). We estimate NECB by explicitly accounting for the productivity of each above-ground trophic compartment present in the model, depending on the scenario analyzed (see below for details). We compared the values of these three components of ecosystem carbon accounting at equilibrium among all three modeling scenarios to systematically investigate the effects of adding herbivores and predators to the model ecosystem. Finally, we use partial derivatives with respect to the uptake ( $a_i$ ) and nutrient recycling ( $r_i$ ) rates of each above-ground trophic compartment ( $i \in [P, H, R]$ ) to evaluate the influence of plant- and animal-mediated trophic processes on ecosystem sequestration of atmospheric C.

### 3.3. Net Ecosystem Carbon Balance Derivation

Net Ecosystem Carbon Balance (NECB) measures ecosystem carbon storage in terms of the net difference between an ecosystem's anabolic and catabolic processes, that is, the balance between net rate of carbon accumulation in ecosystems due to carbon fixation by plants (primary productivity), heterotrophic production, heterotrophic respiration, as well as additional losses including CH<sub>4</sub> emissions directly from animals and soils and sediments of ecosystems (Chapin et al., 2002, 2006). Traditionally, net ecosystem carbon balance is estimated as

$$NECB = \text{Gross Primary Production} - \text{Ecosystem Respiration} - \text{Lateral Fluxes} \quad (9)$$

where Gross Primary Production is essentially gross carbon uptake by plants, Ecosystem Respiration comprises respiration by all trophic compartments (e.g., soil, plants, herbivores, predators; Chapin et al., 2006), and Lateral Fluxes comprise losses of C through mechanisms other than respiration (e.g., leaching to groundwater, methane emissions; Chapin et al., 2002). However, by only accounting for the effects of heterotrophs through respiration, Equation 9 does not account for the direct and indirect effects of animals on an ecosystem's trophic compartments, including net assimilation of C in animal biomass (secondary productivity that varies with plant and animal stoichiometry) and N and C release from animals (recycling feedbacks that also vary with animal stoichiometry) that promote Gross Primary Production, thereby missing important contributions to an ecosystem's C budget by these actors via the processes they mediate.

Hence, we expand on Equation 9 to integrate the effects of heterotrophs in the accounting of NECB. Broadly, we define NECB as the sum of Net Primary Production (NPP) and Net Heterotrophic Production (NHP):

$$NECB = NPP + NHP \quad (10)$$

These two components capture the combined anabolic and catabolic processes happening in an ecosystem, across all trophic compartments. Net Primary Production is the balance of the photosynthetic and respiratory processes that happen in the autotroph compartment of an ecosystem. If we imagine a terrestrial ecosystem, where primary producers are generally plants, we can then specify:

$$NPP = \text{Gross Plant Production} - \text{Plant Respiration} \quad (11)$$

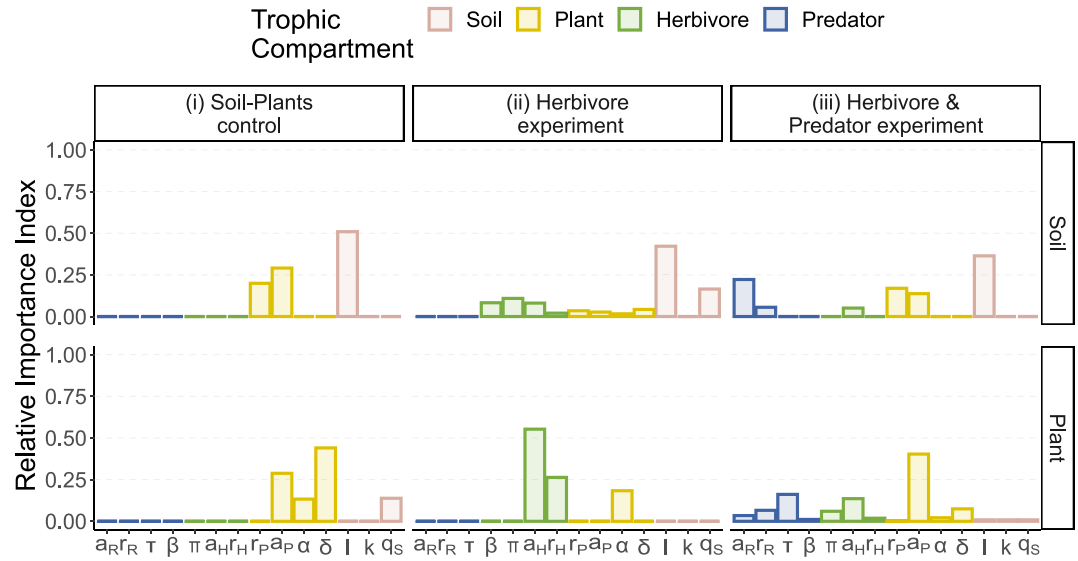
Conversely, Net Heterotrophic Production is the algebraic sum of all biomass-producing and respiratory processes taking place in the heterotrophic compartments of the ecosystem. These include (a) any trophic level above the autotrophs—e.g., herbivores, predators—but also (b) any trophic level involved in the decomposition pathways that recycle nutrients from waste and dead biomass and make them available to autotrophs once again—the so-called “brown food web”. In our case (Figure 1), depending on the modeling scenario, (a) is the herbivores and predators, and (b) is the soil. So, using the same terrestrial ecosystem example as Equation 11, for scenario (iii) we obtain:

$$\begin{aligned} NHP = & (\text{Predator Gross Production} - \text{Predator Respiration}) + \\ & (\text{Herbivore Gross Production} - \text{Herbivore Respiration}) + \\ & (\text{Soil Gross Production} - \text{Soil Respiration}) \end{aligned} \quad (12)$$

where Gross Production is measured as the C uptake rate by a given trophic compartment. Note that Equation 12 can accommodate more complex model formulations, for instance, models with trophic compartments for detritus, decomposer, or both. Equation 10 is conceptually comparable to Equation 9, but allows for debiting heterotroph respiration from heterotroph production. Accounting for both components of heterotrophic C effects allows us to explicitly measure the relative impact of different kinds of heterotrophs on NECB. When substituting the equilibrium values of  $\Phi_p^*$ ,  $\theta_p^*$ , and  $\gamma_S$  into Equations 11 and 12, NECB for scenario (i), an ecosystem without animals (i.e.,  $NECB_{-A}$ ), is calculated as:

$$NECB_{-A} = \alpha\Phi_p^* + \alpha\theta_p^* - 2\alpha\delta\theta_p^* - \gamma_S^* \quad (13)$$





**Figure 2.** Results of the sensitivity analyses run on equilibrium carbon stocks of the soil and plant trophic compartments in the model (i.e.,  $S_C^*, P_C^*$ ), for all modeling scenarios. As the length and complexity of the ecosystem's trophic food chain increase from scenario (i) [left panels] to scenario (iii) [right panels], animal-mediated processes—uptake,  $a_i$  and recycling  $r_i$  in particular—become increasingly important. In turn, these processes shape ecosystem productivity (Figure 4) and C sequestration (Figure 5) capacity. **Top row.** With no animals in the ecosystem, abiotic and plant-mediated processes drive soil C content [left panels]. With herbivores, herbivore-mediated processes drive a substantial share of soil [green bars, middle panels]. With predators, the effect of animal-mediated processes combined on soil C content is comparable to that of abiotic processes [for example,  $a_R, r_R, a_H$  versus  $I$ , right panels]. **Bottom row.** When herbivores are left unchecked, herbivores are the main driver of plants' C content [green bars, middle panels]. In the presence of predators [right panels], trophic cascade dynamics limit animal-mediated control of plant C which is mostly shaped by the plants' own nutrient uptake from the soil.

Likewise, we can further substitute the equilibrium values  $\Phi_H^*$  and  $\theta_H^*$  into Equations 11 and 12, to get the value of NECB for scenario (ii), when the ecosystem contains herbivores but not predators (i.e.,  $NECB_H$ ):

$$NECB_H = \alpha(\Phi_P^* + \theta_P^*) + \beta(\Phi_H^* + \theta_H^*) - 2\alpha\delta\theta_P^* - 2\beta\pi\theta_H^* - \gamma_S^* \quad (14)$$

Finally, when the ecosystem has both herbivores and predators (scenario (iii)), we derive the value of NECB (i.e.,  $NECB_A$ ) by additionally substituting in Equations 11 and 12 the equilibrium values of  $\Phi_R^*$  and  $\theta_R^*$ :

$$NECB_A = \alpha(\Phi_P^* + \theta_P^*) + \beta(\Phi_H^* + \theta_H^* + \Phi_R^* + \theta_R^*) - 2\alpha\delta\theta_P^* - \beta(2\pi\theta_H^* + 2\tau\theta_R^*) - \gamma_S^* \quad (15)$$

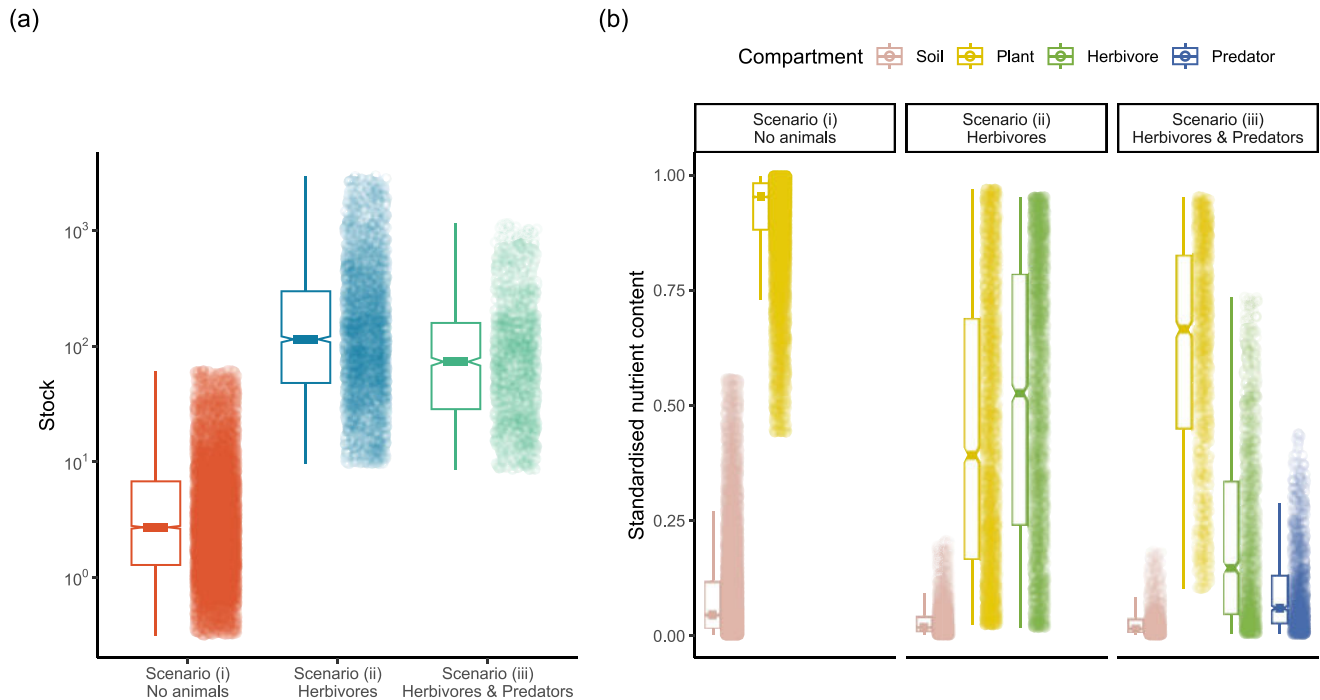
Text S1 in Supporting Information S1 presents the full derivation of Equations 13–15.

## 4. Results

Introducing animals into the ecosystem model (Figure 1) leads to an extensive rewiring of trophic pathways, consistent with a shift from pervasive bottom-up to top-down control (Figure 2). While this trophic rewiring influences the dynamics of both elements—C and N—tracked by the model, here we focus on C. Further, in the following, we focus only on changes to the C content of soil and plants trophic compartments as these are the main pools used in conventional C cycle modeling and carbon accounting (we refer the interested reader to the Supplementary Code document in our online repository (Rizzuto et al., 2023) for results pertaining to N dynamics in the ecosystem, as well as those on C and N dynamics in the herbivore and predator trophic compartments).

### 4.1. Animal Presence Rewires the Ecosystem's Trophic Pathways

When animals are absent from the ecosystem (scenario (i) in Figure 1), results of our sensitivity analysis align with insights from conventional carbon cycle models in that primary producers drive carbon dynamics of both soil and plant trophic compartments through uptake (parameter  $a_p$ ), recycling ( $r_p$ ), and respiration ( $\delta$ ; Figure 2).

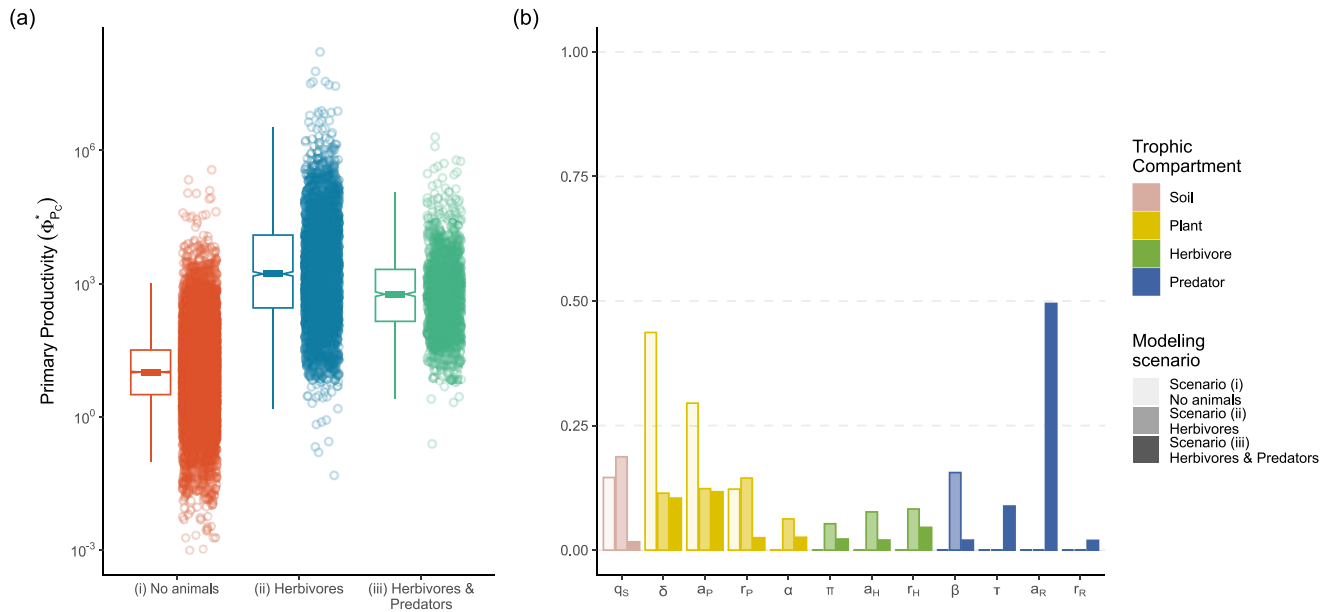


**Figure 3.** Ecosystem carbon content and distribution among trophic compartments, across the three modeling scenarios. **Panel (a):** introducing animals—either herbivores or herbivores and predators—leads to an overall increase in the absolute amounts of carbon in the ecosystems. Animal presence leads to a 1–2 orders of magnitude increase in the ecosystem content of C compared to the control scenario (i) where animals are absent from the ecosystem (red vs. blue, green boxplots). However, we observe differences in the ecosystem C content even among the two experimental scenarios (ii) and (iii). When the ecosystem includes only herbivores (blue), the increase in C content w.r.t. scenario (i) is larger—two orders of magnitude—than when predators are also present in the system (green). In this panel, the thick line inside the box is the median, and the top and bottom hinges are the first and third quantiles. Whiskers extend from the top and bottom hinges to no further than 1.5 times the interquartile range. Points beyond the whiskers are deemed outliers. Note the  $\log_{10}$  scale of the y-axis. **Panel (b):** C content of each trophic compartment standardized to total C in the ecosystem, across modeling scenarios. Increasing trophic complexity leads to a redistribution of C along the food chain. In scenario (i), left panel, most ecosystem C appears stored in plants. When herbivores are present in the system, but not predators (scenario (ii), middle panel), C is almost equally distributed between plants and herbivores. In the scenario that includes herbivores and predators (scenario (iii), right panel), plants again are the larger repository for ecosystem C. Note the minimal contribution to C storage of the soil compartment across all scenarios.

Further, inorganic inputs into the soil ( $I$ ) have a disproportionately large influence on soil C dynamics compared to all other parameters, underscoring the influence of N-limitation on ecosystem dynamics (pink bars in left panels of Figure 2). In scenario (ii), a tri-trophic system with herbivores at the top of the food chain, we see an important rearrangement of which parameters drive ecosystem stocks and fluxes of C (Figure 2, middle panel). While N-limitation ( $I$ ) still plays a major role in controlling carbon cycling, herbivore-mediated processes—i.e., uptake ( $a_H$ ), recycling ( $r_H$ ), and respiration ( $\pi$ )—appear to overtake plant-mediated processes in their contribution to soil C dynamics (green bars in middle panel, top row of Figure 2). Further, these herbivore-mediated processes act as the main drivers of plant C content in this scenario (green bars in middle panel, bottom row of Figure 2). Finally, in scenario (iii)—where the ecosystem also comprises predators (Figure 2, right panels)—we observe a further upward shift of control for soil C dynamics. Beyond the role of soil inorganic N inputs ( $I$ ), predator-mediated processes captured by their uptake ( $a_R$ ) and recycling ( $r_R$ ) rates are among the main drivers of soil C content in this scenario (blue bars in top right panel, Figure 2). Plant recycling ( $r_P$ ) and uptake ( $a_P$ ) rates also contribute to shaping C stocks in the soil (yellow bars in top right panel, Figure 2). Finally, the same predator-mediated processes, alongside herbivore-mediated ones (i.e.,  $a_H$ ,  $\pi$ ), appear to be key drivers of plant C content in this scenario (compare blue, green, and yellow bars in the bottom right panel, Figure 2).

Further differences emerge across modeling scenarios in how the ecosystem behaves toward capturing and storing atmospheric C (Figure 3). The ecosystem appears to reach its highest C capture potential in scenario (iii), when herbivores but not predators are present in the system. Compared to scenario (i), the ecosystem in the herbivores-only scenario sequesters two orders of magnitude more atmospheric C (Figure 3a). Scenario (iii), with both herbivores and predators, shows a somewhat reduced sequestration of atmospheric C—although still one order of magnitude higher than the ecosystem without any animals (scenario (i); Figure 3a). Alongside these changes in





**Figure 4.** Effects of herbivores' presence and absence on primary productivity. **Panel (a):** difference in median primary productivity among the three scenarios. Animal presence—whether comprising only herbivores (blue) or herbivores and predators (green)—leads to a two orders of magnitude increase in the median primary productivity of the ecosystem. Notably, presence of predators (scenario (iii), green) leads to somewhat lower median primary productivity compared to scenario (ii) where only herbivores are present in the system. Note the  $\log_{10}$  scale of the y-axis. All other specifications as in Figure 3a. **Panel (b):** relative parameter importance as determined using a sensitivity analysis on the values of primary productivity. When animals are absent (scenario (i)), plants shape primary productivity through their respiratory ( $\delta$ ), growth ( $a_p$ ), and recycling ( $r_p$ ) processes (yellow transparent bars). For scenario (ii) and (iii), control of primary productivity rests with herbivores and predators, respectively. When the ecosystem comprises only herbivores (light-colored bars), animal stoichiometry ( $\beta$ , blue) plays a key role in shaping primary productivity. Other herbivore-mediated processes ( $a_H$ ,  $r_H$ ,  $\pi$ , green) also shape primary productivity while plant- and soil-mediated processes appear to exert less control on primary productivity compared to scenario (i). In scenario (iii), when the ecosystem contains herbivores and predators, it is the latter trophic compartment that control primary productivity (solid blue bars)—almost entirely through its consumptive processes ( $a_R$ ). Note that  $\beta$  is shown in blue in scenario (ii) but refers to the herbivore in this case, as the predator is absent from this scenario.

absolute C content, we also observe changes in the location of C storage in the ecosystem (Figure 3b). While in scenario (i) most ecosystem C appears stored in the plant compartment, in scenario (ii) we find comparable shares of ecosystem C in both plants and herbivores (yellow vs. green boxplots; Figure 3b). Conversely, in scenario (iii), plants again make up the largest portion of C stored in the system, followed by herbivores and predators—thus showing that herbivores and predators can control C storage despite having much lower biomass representation in the ecosystem than plants (Figure 3b). The soil compartment does not appear to store significant amounts of C across all three scenarios (Figure 3b).

#### 4.2. Animals Increase Biomass Turnover, Boosting Primary Productivity

The increased sequestration of atmospheric C by the ecosystem when animals are present appears also due to a two-fold increase in primary productivity in scenarios (ii) and (iii) compared to scenario (i) (Figure 4a). C:N Stoichiometry of plants ( $\alpha$ ) and especially animals ( $\beta$ ) plays a much larger role in shaping primary productivity when herbivores are present (scenario (ii)). The importance of these parameters diminishes when predators are present in scenario (iii) and is null in scenario (i) (Figure 4b). As well, the animals' functional response parameters—uptake ( $a_H$ ,  $a_R$ ), recycling ( $r_H$ ,  $r_R$ ), and respiration ( $\pi$ ,  $\tau$ ) rates (green and blue bars in Figure 4b)—also become important because they partially subsume the influence of plant- and soil-mediated processes (pink and yellow bars in Figure 4b). Notably, in scenario (iii), the predators' own uptake rate ( $a_R$ ) and hence their control over herbivores becomes the single most important driver of primary productivity (Figure 4b).

Partial derivatives of primary productivity with respect to the uptake and recycling rates of both herbivores ( $\frac{\partial \Phi_p^*}{\partial a_H}$  and  $\frac{\partial \Phi_p^*}{\partial r_H}$ , respectively) and predators ( $\frac{\partial \Phi_p^*}{\partial a_R}$  and  $\frac{\partial \Phi_p^*}{\partial r_R}$ ) provide some insights in how their influence plays out. In scenario (ii), with no predators, the herbivores' uptake rate has an overall dampening effect on primary productivity (Figure S2a in Supporting Information S1), reducing primary productivity. Some values of  $a_H$ , however,

have the opposite effect and lead to an increase in primary production (shown in blue in Figure S2a in Supporting Information S1). Conversely, herbivores' recycling rate  $r_H$  substantially increases primary productivity, leading to an overall increase in the plant's productivity (Figure S2b in Supporting Information S1)—although again, some parameter values have the opposite, negative effect (shown in red in Figure S2b in Supporting Information S1).

In scenario (iii), with both herbivores and predators present in the model, the predators' uptake rate ( $a_R$ ) has mostly a negative influence on primary productivity (Figure S3a in Supporting Information S1)—similar to the effects of  $a_H$  in scenario (ii). Again, we find that a small number of  $a_R$  values have the opposite effect, increasing primary productivity instead (in blue in Figure S3a in Supporting Information S1). Likewise, the predators' recycling rate ( $r_R$ ) leads to an increase in primary productivity (Figure S3b in Supporting Information S1), much like the recycling rate of herbivores in scenario (ii)—but, again, with a few values having the opposite, dampening effect (in red in Figure S3b in Supporting Information S1). Conversely, herbivore-mediated uptake (Figure S3c in Supporting Information S1) in scenario (iii) appears to elicit an increase in primary productivity (Figure S3c in Supporting Information S1)—which contrast with its effect in scenario (ii). Herbivore-mediated recycling maintains a positive, if much reduced, influence on primary productivity in scenario (iii) (Figure S3d in Supporting Information S1).

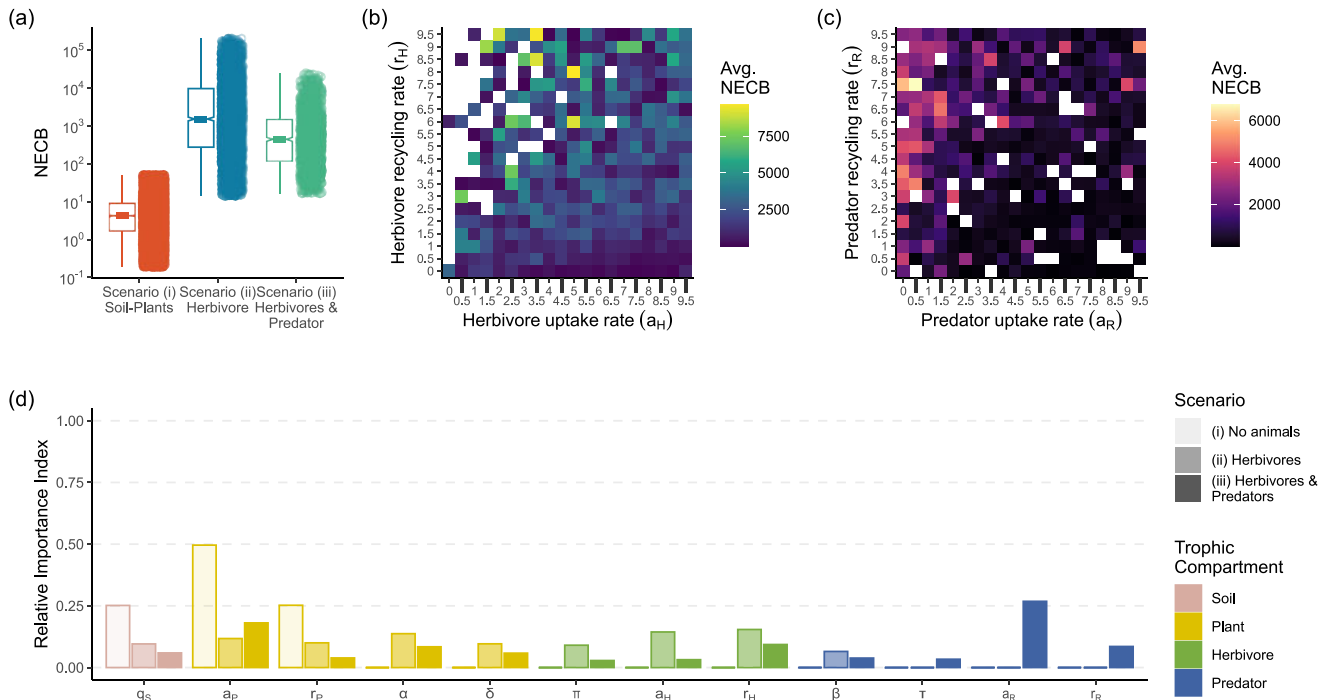
### 4.3. Animal Influence on Net Ecosystem Carbon Balance

Modeling scenarios comprising animals—either only herbivores (scenario (ii)) or herbivores and predators (iii)—had higher median values of NECB overall compared model scenario (i), where no animals are present in the system (Figure 5a). In particular, scenario (ii) shows an almost 3-fold increase in NECB compared to scenario (i) (red vs. blue boxplots; Figure 5a), mirroring the increase in primary productivity observed for the plant compartment in the same scenario (Figure 4a). Scenario (iii), with both herbivores and predators, shows a smaller, 2-fold increase in NECB compared to the no-animals scenario (red vs. green boxplots; Figure 5a). Again, in both animal presence scenarios, the increase in NECB appears driven by parameters related to the functional response of the animals, in particular their recycling ( $r_H$ ,  $r_R$ ) and uptake ( $a_H$ ,  $a_R$ ) rates (Figure 5d). However, we found no substantial differences between scenario (ii) and scenario (iii) in how the uptake and recycling rates of the food chain's top level influences NECB. In scenario (ii), where herbivores are the top of the food chain, their influence appears maximized for low values of  $a_H$  and high values of  $r_H$ . Conversely, in scenario (iii), the influence of the top trophic compartment (predators) appears highest for very low values of uptake rate ( $a_R$ ) and intermediate values of recycling rates ( $r_R$ ). Further, and notably, the C:N stoichiometry of plants ( $\alpha$ ) appears to substantially influence NECB only in the modeling scenarios that include animals—and more so in scenario (ii), where only herbivores are present in the ecosystem than scenario (iii). These differences between scenarios (ii) and (iii) underlie the role of food web length and complexity in shaping ecosystem functioning.

## 5. Discussion

We provide a general framework to account for animal effects on ecosystem carbon cycling and balance. Our framework unites a compartment-style ecosystem model common in community ecology (Daufresne & Loreau, 2001a, 2001b; Loreau, 2010) to a carbon budget model common in biogeochemistry (Chapin et al., 2002, 2006), thus laying the foundation for a zoogeochimical theory for carbon cycling (*sensu* Schmitz et al., 2018). Our modeling reveals that ignoring animals when accounting for ecosystem carbon balance could not only result in *quantitatively* inaccurate estimates of ecosystem carbon storage (Figures 4a and 5a), but could also overlook the *qualitatively* different ways in which carbon cycling is controlled when animals are absent compared to when they are present (Figure 2, Figure 4b, Figure 5d). The latter has important implications for managing ecosystem carbon storage through nature-based climate change solutions that focus merely on plants and soils regardless of the presence of animals.

Animal presence restructures the ecosystem's trophic food web and rewires the ecosystem carbon cycle (Figure 1). Consistent with earlier modeling, we found that introducing herbivores and predators has cascading trophic effects that can influence plant growth and carbon accumulation in soil stocks (Figure 3; de Mazancourt et al., 1998; Leroux & Loreau, 2010; Loreau, 2010). In our modeling these effects further lead to higher storage of atmospheric carbon in plant biomass in the presence of animals than in their absence (Figure 3a). This cascading effect influences the distribution of C stocks in the ecosystem (Figure 3b) by shifting control of C cycling from lower to higher trophic compartments (Figure 2). This *qualitatively* different set of ecosystem C cycling controls



**Figure 5.** Summary of results of the analyses on Net Ecosystem Carbon Balance (NECB) using Equation 10. **Panel (a):** NECB estimates across the three modeling scenarios. As with primary productivity (Figure 4a), animal presence leads to a two-fold increase in NECB, compared to the control scenario (i). Note, however, that when the food chain comprises a predator foraging on the herbivore, the increase in NECB is somewhat lower (scenario (iii), green) than when herbivores are alone in the ecosystem (scenario (ii), blue). Note the  $\log_{10}$  scale on the y-axis. All other specifications as in Figure 3a. **Panel (b):** average estimates for NECB with increasing values of herbivores' uptake ( $a_H$ , x-axis) and recycling ( $r_H$ , y-axis) rates in scenario (ii). Ecosystems populated by herbivores with relatively low values of uptake rate ( $0.5 \leq a_H \leq 5$ ) and relatively high values of recycling rate ( $6 \leq r_H \leq 9.5$ ) show heightened values of NECB (yellow cells, top left quadrant). **Panel (c):** average estimates for NECB with increasing values of predators' uptake ( $a_R$ ) and recycling ( $r_R$ ) rates in scenario (iii). The preponderance of high average NECB values toward the left side of the plot suggests higher predator recycling rates ( $r_R$ ) are a key driver of this ecosystem process. **Panel (d):** relative parameter importance in estimating NECB from Equation 10 across the three modeling scenarios. When animals are absent from the ecosystem (transparent bars), the plant's attack rate ( $a_p$ ) is the single most important driver of NECB. Plant recycling rate ( $r_H$ ) also plays a significant, if smaller, role on par with the soil leaching rate ( $q_s$ ). In ecosystems with herbivores but no predators (light-colored bars, scenario (ii)), no clear dominant parameter stands out. Parameters capturing the effects of herbivory— $a_H$ ,  $r_H$ —appear to elicit relatively stronger influence on NECB than their plant-mediated counterparts ( $a_p$ ,  $r_p$ ) in this scenario. Plant C:N ratio,  $\alpha$ , appears to play a similarly important role, possibly hinting at dietary trade-offs faced by herbivores. Several other parameters,  $a_p$ ,  $r_p$ ,  $\pi$ ,  $\delta$ , appear to contribute to shaping NECB estimates when herbivores are present. Notably, soil leaching ( $q_s$ ) appears much less relevant for NECB when herbivores are present. Finally, when predators are present in the ecosystem (scenario (iii), solid bars), their uptake rate ( $a_R$ ) is the single most important driver of NECB—closely followed by the plants' uptake rate ( $a_p$ ), hinting at the key role played by the trophic cascade mediated by predators in this scenario.

results from the presence of a suite of direct, consumptive effects—captured, for instance, by animal uptake rates  $a_i$  ( $i \in [H, R]$ )—and indirect, non-consumptive processes (i.e., recycling,  $r_i$ , and respiration,  $\pi$ ,  $\tau$ ) that supersede their plant-mediated counterparts (parameters  $a_p$  and  $r_p$ ; Figure 2). In turn, this leads to (a) a short-circuiting of the recycling pathways that replenish the carbon and nitrogen soil pools (DeAngelis, 1992) and (b) the creation of conditions for increased plant nutrient uptake and growth by removing plant biomass (i.e., grazing optimization, Figure 4a; *sensu* Hilbert et al., 1981; de Mazancourt et al., 1998). Animal control also partially plays out by limiting the influence of key physical environmental factors (Figure 2), such as inorganic nutrient inflow ( $I$ ) or leaching loss ( $q_s$ ) from the soil. Thus, our model's results offer initial theoretical support for empirical descriptions of the pervasive influences that animals can have on an ecosystem's ability to capture and sequester atmospheric C, and on its overall carbon budget (Schmitz et al., 2014, 2018).

The animal-caused qualitative changes to the structure of the ecosystem's trophic food web in turn *quantitatively* alter key ecosystem processes. Estimates for both primary production and net ecosystem carbon balance (NECB) appear generally higher with herbivores or with herbivores and predators in the ecosystem than without (Figures 4a and 5a, respectively). This increased production and cycling of C is consistent with trophic dynamic theory specifying that higher primary productivity is necessary to support trophic levels above primary producers (i.e., the ecosystem exploitation hypothesis; Oksanen et al., 1981). Moreover, the magnitude of modeled animal

effects is consistent with the magnitude of effects measured in natural ecosystems (Schmitz & Leroux, 2020; Schmitz et al., 2018). However, animal influence does not act only in one direction. Primary production appears to respond in contrasting ways to the consumptive and non-consumptive influences exerted by herbivores in scenario (ii), when the ecosystem does not comprise a predator compartment (Figure S2 in Supporting Information S1). As expected, herbivore consumption of plant biomass (parameter  $a_H$ ) leads to a reduction of primary production for most parameter sets (shown in gray in Figure S2a in Supporting Information S1). However, a non-trivial number of parameter sets leads to an increase of primary production when herbivores are present (blue dots in Figure S2a in Supporting Information S1). In a similar way, recycling of nutrient from the herbivore compartment (parameter  $r_H$ ) generally increases primary production, but a sizable subset of parameter sets reduces it (red dots in Figure S2b in Supporting Information S1). The balance of these two processes and the environmental context in which they take place are key for their outcome. Further, as plants' and animals' stoichiometry (parameters  $\alpha$  and  $\beta$ , respectively) influences both processes, our results offer further support to the advancement of the burgeoning field of zoogeochemistry (*sensu* Schmitz et al., 2018). Empirical evidence supports these contrasting outcomes (Pringle et al., 2023; Subalusky & Post, 2019): while herbivores often limit or reduce net primary production (Tanentzap & Coomes, 2012), in some contexts they can enhance it—for instance, as do the hippopotamuses of the Mara River (Subalusky et al., 2015, 2018) or the ungulate assemblages in several grassland ecosystems in Africa, Eurasia, and North America (Forbes et al., 2019; Frank & McNaughton, 1993; McNaughton, 1979; Schoenecker et al., 2022). Similarly, in scenario (iii), predators' uptake ( $a_R$ ) plays a dampening role on primary productivity while predators' recycling ( $r_R$ ) increases it—with some exceptions as was the case with herbivores in scenario (ii) (Figure S3, panels (a)–(b) in Supporting Information S1, contrast blue and red dots). In this scenario, herbivore-mediated processes have little to no influence on primary productivity, further strengthening our interpretation of an upward shift of C cycling control as the food chain lengthens. Again, environmental context may be key to balance the outcomes of these two predator-mediated processes—as shown, for example, for wolves and elks in the plains of the USA versus wolves and moose in the boreal forests (Wilmers & Schmitz, 2016), or with different functional types of predators within ecosystem (Schmitz, 2009; Schmitz et al., 2017).

As with primary productivity, there is no single directional effect of animal presence on NECB. Animal presence predominantly increases NECB (Figure 5a) and partially limits plant control over this process (compare transparent, light, and solid bars in Figure 5b). However, the way animal influence plays out depends on the scenario considered. In scenario (ii), where herbivores are at the top of the food chain, varying levels of herbivore uptake ( $a_H$ ) and recycling ( $r_H$ ) rates can have varying effects on NECB estimates (Figure 5d) which depend on specific parameter combinations. This outcome is consistent with empirical evidence that herbivores can enhance or limit carbon capture, but the effects are highly case- and study-specific (see review in Pringle et al., 2023). Even species that are phylogenetically similar can have different effects on carbon dynamics. Forest elephants (*Loxodonta cyclotis*) in the rainforests of the Congo Basin, in central Africa, enhance carbon storage by primary producers through foraging effects and other types of indirect disturbance (e.g., debarking, trampling; Berzaghi et al., 2023). Elsewhere in Africa, high densities of bull savanna elephants (*L. africana*) lead to reduction in aboveground carbon gains in the subtropical savanna of Kruger National Park (Davies & Asner, 2019). While a region of parameter space can be identified where low  $a_H$  values and high  $r_H$  values appear to result in higher NECB (upper left quadrant of Figure 5b) more consistently, we still observe high variability between the outcomes of specific parameter pairs. Further studies should explore this relationship, taking advantage of empirical data when available, to offer further clarity. In scenario (iii), conversely, the influence of predator uptake ( $a_R$ ) and recycling ( $r_R$ ) rates appears to be more consistent (Figure 5c), with higher values of NECB found for high levels of  $r_R$  and low levels of  $a_R$ —again hinting at the key role played by that indirect, animal-mediated recycling pathway that short-circuits the return of C to the soil pools.

Together with a growing body of empirical evidence (see Pringle et al., 2023; Schmitz et al., 2018; Schmitz et al., 2023), our model shows that any effort to accurately account for the uptake, cycling, and storage of carbon in ecosystems should include animal contributions. Simply accounting for animal-mediated processes via heterotrophic respiration does not return a complete picture of an ecosystem's carbon balance and indeed appears to underestimate it—as shown by the results of our modeling scenarios (ii) and (iii) comprising animals (in blue and green in Figures 4 and 5; see also Rastetter et al., 2022). Empirical evidence (Berzaghi et al., 2019; Don et al., 2019; Doughy et al., 2016; Holdo et al., 2009; Leroux et al., 2020; Malhi et al., 2016; Sitters et al., 2020),

and now theoretical evidence (Figure 3) increasingly challenges the assumption that an ecosystem's biomass-dominant compartments (plant, microbes) can subsume the effects of animals on the carbon cycle.

Beyond the risk of inaccurately estimating an ecosystem's carbon budget, the model results have important implications for any management effort aimed at enhancing ecosystem carbon storage in the presence of animals using conventional means. For example, simply increasing primary producers' biomass via planting and cultivation could be using the wrong lever to achieve its goals. Instead, and perhaps counterintuitively, protecting and building the biomass of animal populations can instigate feedback loops—through the consumptive and recycling pathways highlighted above—that can influence and potentially enhance an ecosystem's primary production and net carbon balance. While much remains to be clarified (Kristensen et al., 2022; Pringle et al., 2023; Schmitz et al., 2018), theoretical and empirical evidence increasingly supports reorienting our efforts to develop nature-based climate change solutions that explicitly incorporate animals (Berzaghi et al., 2022; Malhi et al., 2022; Schmitz et al., 2023; Schmitz & Sylvén, 2023).

We offer our model as a scaffolding to provide general insights on the role of animals in ecosystem carbon cycling and balance. The exact amounts of carbon captured and stored in an ecosystem will depend on the assemblage of animal, plant, and microbial species comprising a given ecosystem and on its geophysical conditions—e.g., soil composition, temperature, moisture, etc. The interplay between these factors will have a decided effect on mechanisms and rates of carbon uptake via photosynthetic capture and assimilation, consumptive transfer, and accumulation in animal (herbivore and carnivore) biomass, microbial processes, and on the rates of autotrophic (plant) and heterotrophic (microbial and animal) release of carbon into the atmosphere. It follows that applying the modeling framework we describe here to a particular ecosystem will require gathering and substituting model parameter values for functions which explicitly incorporate physiological mechanisms and whose values vary across the domain of biophysical conditions present in the ecosystem, as is done with conventional carbon cycle models that exclude animals (Piao et al., 2013; Zaehle et al., 2014) and with animal-driven models in certain ecosystems (Dangal et al., 2017; Rastetter et al., 2022). Indeed, empirical knowledge to quantify animal-mediated processes and thus parameterize the model for specific systems already exists for several ecosystems and animal species (reviewed in Pringle et al., 2023) and could allow our model to inform restoration and management efforts aimed at leveraging animal contributions to increase ecosystem carbon capture and storage (e.g., through trophic rewilding; *sensu* Schmitz et al., 2023; Schmitz & Sylvén, 2023).

We present a simple model rooted in the trophic compartment formalization—consistent with previous modeling efforts. This approach implicitly assumes that the many species comprising a trophic compartment are all functionally equivalent (Schmitz & Leroux, 2020). That is, the model does not differentiate between a hare and an elephant as both can be described as “herbivores.” Yet, ecosystems contain diverse assemblages of species that may share some characteristics (e.g., diet type) but not others (e.g., hind- vs. fore-gut fermentation) and thus need not be assumed to be functionally equivalent (Schmitz & Leroux, 2020). While helpful in reducing the mathematical complexity of the model and maintaining its analytical tractability, assuming complete functional equivalence limits our ability to disentangle the role of individual species' traits in enabling their influence on ecosystem processes. As well, and consequently, it also constrains the usefulness of this type of model in exploring the relationship between ecosystem functioning and animal biodiversity. A possible way to address this limitation and dissect functional differences among multiple species within a trophic compartment would be to expand our model framework to incorporate functional traits of animals—i.e., the morphological (e.g., bird beak shape), behavioral (e.g., group vs. solitary living), or physiological (e.g., ruminant vs. non-ruminant) attributes that drive an organism's biogeochemical function (*sensu* Schmitz & Leroux, 2020). Our model uses a linear (type I) functional response to represent both plant uptake of nutrients from the soil and animal (herbivore and predator) consumption of biomass, in order to blend animal ecology with conventional biogeochemical model characterization of elemental flux among trophic compartments in ecosystems. However, more complex functional responses may be worth exploring to develop a more complete picture of animal control on carbon cycling. In addition, our model assumes all plants (herbivores) are palatable to herbivores (predators). However, in many ecosystems, several plant and herbivore species evade consumption with gross morphology, life history, or chemical traits that make them unpalatable (Pastor & Cohen, 1997). Future models should incorporate resource palatability as an important axis mediating animal effects on carbon cycling. Finally, our framework does not explicitly model microbial activities connected to the carbon cycle—respiration and production—subsuming them into the soil compartment (Figure 1). Dissecting the organic and inorganic components of soil—for instance, by adding a detritus and decomposers trophic compartments to the model—would shed light on the



interactions between the above- and below-ground food webs, their individual and combined effects on ecosystem carbon cycling, and on their synergistic or antagonistic nature (Kristensen et al., 2022; Losada et al., 2023; Naidu et al., 2022).

Carbon capture, cycling, and storage are essential ecosystem processes to help arrest climate change. Historically, models used to quantify these processes have excluded animals from their frameworks by reasoning that animals make up a small portion of an ecosystem's total biomass and this limits their influence of carbon dynamics. Increasingly, empirical evidence shows that this is not the case. Rather, animal influences permeate all aspects of ecosystem carbon budgets. Here, we develop an ecosystem carbon model that accounts for animal control of ecosystem carbon dynamics by focusing on herbivores. We show that (a) animal presence rewires the ecosystem's trophic food web and qualitatively changes how its carbon cycle plays out, concentrating control in the top trophic compartment; (b) this re-arrangement of the carbon cycle leads to quantitative changes in key ecosystem processes involved in the ecosystem's carbon budget; and (c) generalizing animal effects across different conditions and scenarios can be challenging as animal control and influence on ecosystem carbon cycle vary with context. Together, these results lend further support to calls for integrating estimates of animal influences on ecosystem carbon services in existing models of carbon cycling at multiple spatio-temporal scales and to the development of nature-based solutions that leverage animal contributions to mitigate climate change, such as, trophic rewilding.

## Appendix A: Model Equilibria and Feasibility Conditions

Here, we report the equilibria and feasibility conditions for each of the three modeling scenarios listed in Section 2.

### A1. Scenario (i)—An Ecosystem With Soil and Plants but No Animals

*Equilibria:* The model without herbivores has two equilibria: one where all state variables values are positive and thus biologically meaningful (i.e., “feasible” equilibrium), and one where they are not. The solutions for these equilibria are:

Feasible Equilibrium

$$S_N^* = \frac{I}{k} \quad (\text{A1})$$

$$S_C^* = \frac{kr_P}{a_P I} \quad (\text{A2})$$

$$P_N^* = \frac{q_S}{a_P \alpha - a_P \alpha \delta} \quad (\text{A3})$$

Non-feasible equilibrium

$$S_N^* = \frac{I}{k} \quad (\text{A4})$$

$$S_C^* = 0 \quad (\text{A5})$$

$$P_N^* = 0 \quad (\text{A6})$$

*Feasibility conditions:* In the feasible equilibrium, all state variables are  $>0$  when  $\alpha > 0$ ,  $0 < \delta < 1$ ,  $r_P > 0$ ,  $q_S > 0$ ,  $k > 0$ ,  $I > 0$ , and  $a_P > 0$ .

### A2. Scenario (ii)—An Ecosystem With Soil, Plants, and Herbivores

*Equilibria:* The model with herbivores has three equilibria: one where all state variables are  $>0$  and thus biologically meaningful, and two where they are not.

Feasible equilibrium:

$$S_N^* = \frac{I}{k} \quad (\text{A7})$$



$$S_C^* = \frac{kr_H r_P (\alpha + (\pi - 1)\beta - \alpha\delta)}{a_H I q_S + a_P I (\pi - 1) r_H \beta} \quad (\text{A8})$$

$$P_N^* = \frac{r_H}{a_H} \quad (\text{A9})$$

$$H_N^* = \frac{r_P (a_H q_S + a_P r_H \alpha (\delta - 1))}{a_H (a_H q_S + a_P (\pi - 1) r_H \beta)} \quad (\text{A10})$$

The two non-feasible equilibria are,

Case 1:

$$S_N^* = \frac{I}{k} \quad (\text{A11})$$

$$S_C^* = 0 \quad (\text{A12})$$

$$P_N^* = 0 \quad (\text{A13})$$

$$H_N^* = 0 \quad (\text{A14})$$

Case 2: Note that this is equivalent to the feasible equilibrium for scenario (i), reported in Equations A1 to A3:

$$S_N^* = \frac{I}{k} \quad (\text{A15})$$

$$S_C^* = \frac{kr_P}{a_P I} \quad (\text{A16})$$

$$P_N^* = \frac{q_S}{a_P \alpha - a_P \alpha \delta} \quad (\text{A17})$$

$$H_N^* = 0 \quad (\text{A18})$$

*Feasibility conditions:* The feasible equilibrium produces positive stocks for all state variables when  $\alpha > 0$ ,  $\beta > 0$ ,  $a_H > 0$ ,  $a_P > 0$ ,  $I > 0$ ,  $k > 0$ ,  $r_H > 0$ ,  $r_P > 0$ , and

1.  $0 < \pi < 1$ , and either
  - $a_H(a_H q_S + a_P(\pi - 1)r_H \beta) < 0$  and either
    - \*  $\delta \geq 1$ , and  $q_S > 0$
    - \*  $\beta > \frac{\alpha(\delta - 1)}{(\pi - 1)}$ ,  $a_H(a_H q_S + a_P r_H \alpha (\delta - 1)) > 0$ ,  $0 < \delta < 1$
  - $0 < \delta < 1$ ,  $\beta < \frac{\alpha(\delta - 1)}{(\pi - 1)}$ ,  $a_H(a_H q_S + a_P r_H \alpha (\delta - 1)) < 0$ , and  $a_H(a_H q_S + a_P(\pi - 1)r_H \beta) > 0$
2.  $\pi \geq 1$ ,  $q_S > 0$ ,  $0 < \delta < 1$ , and  $a_H(a_H q_S + a_P r_H \alpha (\delta - 1)) < 0$

Note that, given the constraints on the values of  $\delta$ ,  $\pi$ , and  $\tau$  (Table 2), feasibility condition #2 can never be realized for the parameter space considered here. Likewise, feasibility condition #1 cannot be realized for  $\delta \geq 1$ .

### A3. Scenario (iii)—An Ecosystem With Soil, Plants, Herbivores, and Predators

*Equilibra:* Of the five model equilibria that exist for this scenario, four include one or more state variables = 0 and are thus not biologically meaningful. The remaining one with all state variables >0 is the one we used in the analyses.

Feasible equilibrium:

$$S_N^* = \frac{I}{k} \quad (A19)$$

$$S_C^* = \frac{k(a_R r_P + a_H r_R)}{a_P a_R I} \quad (A20)$$

$$P_N^* = -\frac{a_R q_S r_P + a_H q_S r_R + a_P r_H r_R \beta (\pi - \tau)}{a_P (a_R r_P \alpha (\delta - 1) + a_H r_R \beta (\tau - 1))} \quad (A21)$$

$$H_N^* = \frac{r_R}{a_R} \quad (A22)$$

$$R_N^* = -\frac{a_H a_R q_S r_P + a_H^2 q_S r_R + a_H a_P (\pi - 1) r_H r_R \beta + a_P a_R r_H r_P \alpha (\delta - 1)}{a_P a_R (a_R r_P \alpha (\delta - 1) + a_H r_R \beta (\tau - 1))} \quad (A23)$$

The four non-feasible equilibria are,

Case 1:

$$S_N^* = \frac{I}{k} \quad (A24)$$

$$S_C^* = \frac{k r_H r_R \beta (\tau - \pi)}{a_R I q_S} \quad (A25)$$

$$P_N^* = 0 \quad (A26)$$

$$H_N^* = \frac{r_R}{a_R} \quad (A27)$$

$$R_N^* = -\frac{r_H}{a_R} \quad (A28)$$

Case 2:

$$S_N^* = \frac{I}{k} \quad (A29)$$

$$S_C^* = 0 \quad (A30)$$

$$P_N^* = 0 \quad (A31)$$

$$H_N^* = 0 \quad (A32)$$

$$R_N^* = 0 \quad (A33)$$

Case 3: Note that this is equivalent to the feasible equilibrium for scenario (ii), reported in Equations A7 to A10:

$$S_N^* = \frac{I}{k} \quad (A34)$$

$$S_C^* = \frac{k r_H r_P (\alpha + (\pi - 1) \beta - \alpha \delta)}{a_H I q_S + a_P I (\pi - 1) r_H \beta} \quad (A35)$$

$$P_N^* = \frac{r_H}{a_H} \quad (A36)$$

$$H_N^* = -\frac{r_P(a_H q_S + a_P r_H \alpha(\delta - 1))}{a_H(a_H q_S + a_P(\pi - 1)r_H \beta)} \quad (\text{A37})$$

$$R_N^* = 0 \quad (\text{A38})$$

Case 4: Note that this is equivalent to the feasible equilibrium for scenario (i), reported in Equations A1 to A3.

$$S_N^* = \frac{I}{k} \quad (\text{A39})$$

$$S_C^* = \frac{k r_P}{a_P I} \quad (\text{A40})$$

$$P_N^* = \frac{q_S}{a_P \alpha - a_P \alpha \delta} \quad (\text{A41})$$

$$H_N^* = 0 \quad (\text{A42})$$

$$R_N^* = 0 \quad (\text{A43})$$

*Feasibility conditions:* The feasible equilibrium reported above results in positive stocks for all state variables when  $\alpha > 0$ ,  $\beta > 0$ ,  $r_R > 0$ ,  $r_P > 0$ ,  $a_R > 0$ ,  $a_H > 0$ ,  $I > 0$ ,  $k > 0$ ,  $q_S > 0$ ,  $r_H > 0$ , and either of

1.  $\pi > 0$ ,  $a_H r_R \beta (a_H (\pi - 1) r_R \beta + a_R r_P \alpha (\delta - 1)) < 0$ ,  $\delta > 0$ , and
  - $\alpha < \frac{a_H r_R \beta}{a_R r_P \delta - a_R r_P}$ , or
  - $\delta \leq 1$ , and either
    - $a_P > 0$ ,  $\tau > 0$ ,  $a_P + \frac{a_H q_S (a_R r_P + a_H r_R)}{r_H (a_H (\pi - 1) r_R \beta + a_R r_P \alpha (\delta - 1))} < 0$ ,  $a_H r_R \beta (a_R r_P \alpha (\delta - 1) + a_H r_R \beta (\tau - 1)) < 0$ , or
    - $a_P + \frac{a_H q_S (a_R r_P + a_H r_R)}{r_H (a_H (\pi - 1) r_R \beta + a_R r_P \alpha (\delta - 1))} > 0$ ,  $a_H r_R \beta (a_R r_P \alpha (\delta - 1) + a_H r_R \beta (\tau - 1)) > 0$
2.  $a_P > 0$ ,  $\delta > 1$ ,  $\pi + \frac{a_R r_P \alpha (\delta - 1)}{a_H r_R \beta} \geq 1$ ,  $\tau > 0$ ,  $\alpha < \frac{a_H r_R \beta}{a_R r_P \delta - a_R r_P}$ ,  $a_H r_R \beta (a_R r_P \alpha (\delta - 1) + a_H r_R \beta (\tau - 1)) < 0$ ,
3.  $a_P > 0$ ,  $\pi + \frac{a_R r_P \alpha (\delta - 1)}{a_H r_R \beta} \geq 1$ ,  $\delta > 0$ ,  $\tau > 0$ ,  $a_H r_R \beta (a_R r_P \alpha (\delta - 1) + a_H r_R \beta (\tau - 1)) < 0$ ,  $\delta \leq 1$

Note that, given the constraints on the values of  $\delta$ ,  $\pi$ , and  $\tau$  (Table 2), feasibility condition #2 can never be realized for the parameter space considered here.

## Appendix B: Derivation of the Differential Assimilation Rate for Carbon by Herbivores

Here, we derive the expressions for the term  $W_{CH}[H_N, H_C]$  in the model (Table 1), the fraction of assimilated C that herbivore release over time as a function of their content of C and N. In our model, herbivores are N-limited; that is, herbivores eliminate excess C obtained through diet from their system via respiration (Daufresne & Loreau, 2001b; Leroux et al., 2012). Note that, in our model, Equations 5 and 6 are related through parameter  $\beta$ —the animals' C:N ratio—according to the following equation:

$$\frac{dH_C}{dt} = \beta \frac{dH_N}{dt} \quad (\text{B1})$$

It follows that,

$$\alpha \Phi_H - (\beta \theta_H + W_{CH}[H_N, H_C]) = \beta (\Phi_H - \theta_H) \quad (\text{B2})$$

Expanding the term in parentheses on the left hand side of the equation, and isolating the  $W_{CH}[H_N, H_C]$ , we get:

$$-W_{CH}[H_N, H_C] = \beta \Phi_H - \beta \theta_H - \alpha \Phi_H + \beta \theta_H \quad (\text{B3})$$

$$W_{CH}[H_N, H_C] = (\alpha - \beta)\Phi_H \quad (\text{B4})$$

And, finally, substituting the formula for  $\Phi_H$  (Table 1) in Equation B4, we get the formula for  $W_{CH}[H_N, H_C]$  as shown in Table 1:

$$W_{CH}[H_N, H_C] = (\alpha - \beta)a_H P_N H_N \quad (\text{B5})$$

## Data Availability Statement

All code used in our analyses is available through an online repository available via Rizzuto et al. (2023) Code and data for Rewiring the carbon cycle: a theoretical framework for animal-driven ecosystem carbon sequestration. <https://doi.org/10.6084/m9.figshare.23688855>.

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