

# Trophic rewilding can expand natural climate solutions

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## Supplementary Appendix 1

**Data sources and calculations of net ecosystem carbon balance (NECB). The calculations provide estimates presented in Table 1 of large wild vertebrate effects on the additional amount of atmospheric CO<sub>2</sub> that could be held in ecosystems through trophic rewilding.**

NECB is defined as the balance between net rate of carbon accumulation in ecosystems due to carbon fixation by plants and autotrophic and heterotrophic respiratory CO<sub>2</sub> emissions (net ecosystem productivity), as well as additional losses including CH<sub>4</sub> emissions directly from animals and soils and sediments of ecosystem (Chapin et al. 2006).

### Reference

Chapin, F.S. III. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* **9**, 1041-1050 (2006).

### Box 1: General calculation methods used to estimate respiratory CO<sub>2</sub> emissions by animal species

The literature does not provide direct measures of respiratory CO<sub>2</sub> release by wild animals. CO<sub>2</sub> release can be estimated using various allometric relationships relating energy metabolism, O<sub>2</sub> consumption and body mass (M) of animals. The following provides an overview of the general approach used to relate animal daily energy expenditure (aka field metabolic rates) to the daily amount of O<sub>2</sub> consumed while active. This is then used to obtain an indirect estimate of the amount of CO<sub>2</sub> released per animal per day.

Daily O<sub>2</sub> consumption at basal metabolic rate can be estimated as (Bishop 1999; Fig. 2):

$$\text{BMR}(\text{O}_2) \text{ Consumption (ml min}^{-1}\text{)} = 10.9 M(\text{kg})^{0.729} \quad (\text{B1})$$

This estimate must, however, be adjusted to account for the incremental increase above basal metabolism due to animal average daily activity (i.e., daily energy expenditure [DEE], aka active metabolic rate). However, to the best of our knowledge, the literature for terrestrial species only provides estimates of VO<sub>2max</sub> (maximum O<sub>2</sub> consumption at peak exercise) in relation to body mass (e.g. Bishop 1999), which would overestimate daily activity metabolism. The increment can be calculated using complementary approaches relating energy expenditure to body mass.

Daily energy expenditure (DEE), based on field metabolic rate measurements, can be related to body mass across a variety of vertebrate taxa using the following equations (Nagy et al. 1999; Table 2):

$$\text{Mammalian herbivores DEE (Kcal d}^{-1}\text{)} = 7.94 M(\text{g})^{0.646} \quad (\text{B2a})$$

$$\text{Mammalian carnivores DEE (Kcal d}^{-1}\text{)} = 2.23 M(\text{g})^{0.85} \quad (\text{B2b})$$

Where basal metabolic rate can be calculated according to Keliber's (1960) equation:

$$\text{BMR (Kcal d}^{-1}\text{)} = 70 M(\text{kg})^{0.75}$$

The increment can then be calculated as  $I = \text{DEE}/\text{BMR}$ . (B3)

This ratio can be used to scale daily BMR(O<sub>2</sub>) to DEE(O<sub>2</sub>) as

$$\text{DEE}(\text{O}_2) = I \times \text{BMR}(\text{O}_2) \quad (\text{B4})$$

This scaling assumes that the slope of the regression lines relating BMR(O<sub>2</sub>) to body mass and DEE(O<sub>2</sub>) body mass are parallel. We assume they are based on comparison of VO<sub>2max</sub> vs M and BMR(O<sub>2</sub>) vs M (Bishop 1999; Fig. 2).

Estimates of O<sub>2</sub> consumption can then be translated into CO<sub>2</sub> release using the respiratory quotient RQ, the ratio of CO<sub>2</sub> production to oxygen consumption during metabolism, which varies with diet and ranges from 1 for largely carbohydrate diets to 0.81 for protein diets (Kleiber 1960). Hence per-individual CO<sub>2</sub> released during daily energy expenditure is estimated as

$$\text{DEE}(\text{CO}_2) = \text{RQ} \times \text{DEE}(\text{O}_2) \text{ (ml min}^{-1}\text{)} \times 1.9 \times 10^{-3} \text{ g CO}_2 / \text{ml} \times 1440 \text{ min/d} \quad (\text{B5})$$

#### References

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Nagy, K.A., Girard, I.A. & Brown, T.K. Energetics of free-ranging mammals, reptiles and birds. *Ann. Rev. Nutr.* **19**, 247-277 (1999).

Kleiber, M. *The Fire of Life: An Introduction to Animal Energetics* (Wiley, 1961)

## Wildebeest in Serengeti savanna-woodland

By suppressing large-scale wildfires, restoring and protecting wildebeest populations and their grazing results in avoided emissions from burning of grasses. It further enhances the carbon sink via the release of organic carbon in dung that becomes incorporated in the soil pool (Holdo et al. 2009).

During the decade when wildebeest populations were at their lowest (1960's-1970's), the Serengeti was a net carbon source, releasing approximately 175 Mg C km<sup>-2</sup> yr<sup>-1</sup> (Holdo et al.; Fig 5B) =  $1.75 \times 10^8 \text{ g C km}^{-2} \text{ yr}^{-1} \times 3.66 \text{ (CO}_2 \text{ equivalency using a molar ratio of } 3.66 \text{ gCO}_2/\text{gC)} = 6.41 \times 10^8 \text{ g CO}_2 \text{ km}^{-2} \text{ yr}^{-1}$ . The total release for the entire 12,000 km<sup>2</sup> Serengeti area is estimated as  $6.41 \times 10^8 \text{ g CO}_2 \text{ km}^{-2} \text{ yr}^{-1} \times 1.2 \times 10^4 \text{ km}^2 = 7.7 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$ .

In recent decades (1990-200) the recovered wildebeest population ( $1.2 \times 10^6$  animals) has not only protected  $7.7 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$  from being emitted, it has resulted in an estimated additional annual storage of 20 Mg C km<sup>-2</sup> (Holdo et al. 2009: Fig. 5B) =  $2 \times 10^7 \text{ g C km}^{-2} \text{ yr}^{-1} \times 3.66 \text{ g CO}_2/\text{gC} \times 1.2 \times 10^4 \text{ km}^2 = 8.8 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1}$ .

This gives a total of  $8.6 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$ .

However, this does not account for CO<sub>2</sub> losses due to wildebeest respiration. Assuming an average wildebeest body mass of 175 kg (Subalusky et al. 2017), and using general methods outlined in Box 1, we estimated current population respiratory CO<sub>2</sub> release using equations B1-B5 to estimate per capita CO<sub>2</sub> release per day (DEE(CO<sub>2</sub>)). DEE(CO<sub>2</sub>) was then multiplied by 365 days and by wildebeest population size to estimate annual population CO<sub>2</sub> emissions, as follows:

From equation B1,  $\text{BMR}(\text{O}_2) = 470.5 \text{ ml min}^{-1}$

From equation B3,  $I = 5.75$ , where DEE was estimated using equation B2a.

From equation B4,  $\text{DEE}(\text{O}_2) = 5.75 \times 470.5 \text{ ml O}_2 \text{ min}^{-1} = 2705.4 \text{ ml min}^{-1}$

From equation B5, and assuming an  $RQ = 1 \text{ CO}_2/\text{O}_2$   
 $\text{DEE}(\text{CO}_2) = 2705.4 \text{ ml CO}_2 \text{ min}^{-1} \times 1440 \text{ min d}^{-1} \times 1.9 \times 10^{-3} \text{ g CO}_2/\text{ ml CO}_2$   
 $= 7402 \text{ g CO}_2 \text{ d}^{-1}$

Assuming a wildebeest population size of  $1.2 \times 10^6$  animals (Holdo et al. 2009), the annual release of  $\text{CO}_2$  by the population =  $7402 \text{ g CO}_2 \text{ d}^{-1} \times 365 \text{ d} \times 1.2 \times 10^6 \text{ animals}$   
 $= 3.24 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$

The budget also does not account for enteric methane release by wildebeest. Again, assuming a mean wildebeest body mass of 175 kg and using a body mass-methane emissions regression for ruminant ungulates developed from synthesis of empirical measures (Smith et al. 2015: Fig. 1) gives an average per capita wildebeest release of  $29.7 \text{ kg CH}_4 \text{ yr}^{-1}$ . Hence the estimated total methane release from the Serengeti wildebeest population =  $29.7 \text{ kg CH}_4 \text{ yr}^{-1} \times 10^3 \text{ g/kg} \times 1.2 \times 10^6 = 3.56 \times 10^{10} \text{ g CH}_4 \text{ yr}^{-1}$ . Using a conversion factor of 28x to account for  $\text{CH}_4$ 's carbon mass and higher heat trapping capacity relative to  $\text{CO}_2$  over a 100-year time horizon, gives  $\text{CO}_2\text{e}$  emission from methane =  $9.97 \times 10^{11} \text{ g yr}^{-1}$ .

### **Estimated net ecosystem carbon balance**

Together the population-mediated capture and storage of  $\text{CO}_2$  and population release of  $\text{CO}_2$  and  $\text{CH}_4$  leads to an estimated net  $\text{CO}_2$  storage of  $8.6 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1} - (3.24 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1} + 9.97 \times 10^{11} \text{ g CO}_2\text{e yr}^{-1}) = 4.4 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$ .

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## **Sea Otters in coastal kelp forests**

Sea otters, being top predators, influence kelp forest carbon capture and storage by controlling the abundance of their urchin prey that have a large grazing impact on kelp. This indirect effect of a top predator on plant biomass is known as a trophic cascade.

Sea otter trophic cascade effects were calculated in Wilmers et al. (2012, Table 1) for the region between southern British Columbia and the Aleutian Islands. Sea otters increase net primary productivity by  $243\text{-}875 \text{ g C m}^{-2} \text{ yr}^{-1}$  (or by a median value of  $559 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). Wilmers et al. (2012) consider several scenarios for the amount of biomass carbon captured by kelp that enters long-term deep ocean storage, ranging from 1% to 50%. Estimates suggest that generally 10% of NPP enters long-term storage (based on calculations of the fate of macroalgae in Krause-Jensen and Duarte 2016). However, the enhancement of kelp production due to sea otter

presence supports the build-up of the fish-based trophic chain and transfer of productivity to that trophic chain (Gregar et al. 2020). This could reduce kelp net primary productivity that potentially enters long-term storage by a factor of 10 (i.e. only 1% enters long term storage) (Gregar et al. 2020). Given the uncertainties with both endpoint estimates, we assume that a middle value between these endpoints (5%) represents a good first approximation. This gives a median net ecosystem storage effect of  $1.45 \times 10^6 \text{ t C yr}^{-1}$  (Wilmers et al. Table 2) or  $1.45 \times 10^{12} \text{ g C yr}^{-1} \times 3.66 \text{ gC /gCO}_2 = 5.3 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$ .

However, this does not account for CO<sub>2</sub> losses due to sea otter respiration. Assuming an average sea otter body mass of 27 kg (Lairdre et al. 2006), and using general methods outlined in Box 1, we estimated current population respiratory CO<sub>2</sub> release using equations B1-B5 to estimate per capita CO<sub>2</sub> release per day (DEE(CO<sub>2</sub>)). DEE(CO<sub>2</sub>) was then multiplied by 365 days and by sea otter population size to estimate annual population CO<sub>2</sub> emissions, as follows:

From equation B1,  $\text{BMR}(\text{O}_2) = 120.5 \text{ ml min}^{-1}$

From equation B3,  $I = 15.7$ , where DEE was estimated using equation B2b.

From equation B4,  $\text{DEE}(\text{O}_2) = 15.7 \times 120.5 \text{ ml O}_2 \text{ min}^{-1} = 1891.9 \text{ ml O}_2 \text{ min}^{-1}$

From equation B5, and assuming an  $\text{RQ} = 0.85 \text{ CO}_2/\text{O}_2$

$\text{DEE}(\text{CO}_2) = 0.85 \times 1893.9 \text{ ml CO}_2 \text{ min}^{-1} \times 1440 \text{ min d}^{-1} \times 1.9 \times 10^{-3} \text{ g CO}_2/\text{ml CO}_2$   
 $= 4399.8 \text{ g CO}_2 \text{ d}^{-1}$

Assuming 77,949 sea otters occur in the kelp zone of the focal region between Southern British Columbia and the Aleutian Islands (Doroff et al. 2011), then the annual population release is

$4399.8 \text{ g CO}_2 \text{ d}^{-1} \times 365 \text{ d} \times 77,949 \text{ animals} = 1.25 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1}$ .

### **Estimated net ecosystem carbon balance**

Subtracting respiration from ecosystem carbon store gives a net ecosystem carbon balance estimate of

$5.3 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1} - 1.25 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1} = 5.2 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1} = 0.0052 \text{ Gt CO}_2 \text{ yr}^{-1}$ .

Assuming the values for the range in carbon estimates (Table 1 and 2) represent 2 standard deviations (giving a coefficient of variation = 48%), then the estimated net ecosystem carbon balance = **0.0052 ± 0.0025 (1 SD) Gt CO<sub>2</sub> yr<sup>-1</sup>**.

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## Wolves in boreal forests

Effects of wolves on the boreal forest carbon balance (in g carbon), mediated through predator-prey interactions with moose that feed on boreal trees, was calculated in Wilmers and Schmitz (2016: page 3-4). This accounts for Net Ecosystem Productivity (NEP) which includes carbon uptake as net primary productivity, and carbon loss via heterotrophic (soil and moose) respiration.

Converting estimated NEP to CO<sub>2</sub> equivalency:  $4.6\text{--}9.9 \times 10^{13} \text{ g C yr}^{-1} \times 3.66 = 0.168\text{--}0.362 \text{ Gt CO}_2 \text{ yr}^{-1}$  (or an average  $0.265 \pm 0.137$  (1 SD) Gt CO<sub>2</sub> yr<sup>-1</sup>)

This estimate, however, does not include respiration release by wolves. Assuming an average wolf body mass of 45 kg (Hilderbrand and Golden 2012), and using general methods outlined in Box 1, we estimated current population respiratory CO<sub>2</sub> release using equations B1-B5 to estimate per capita CO<sub>2</sub> release per day (DEE(CO<sub>2</sub>)). DEE(CO<sub>2</sub>) was then multiplied by 365 days and by wolf abundance to estimate annual population CO<sub>2</sub> emissions, as follows:

From equation B1,  $\text{BMR}(\text{O}_2) = 174.8 \text{ ml min}^{-1}$

From equation B3,  $I = 16.5$ , where DEE was estimated using equation B2b.

From equation B4,  $\text{DEE}(\text{O}_2) = 16.5 \times 174.8 \text{ ml O}_2 \text{ min}^{-1} = 2884.2 \text{ ml O}_2 \text{ min}^{-1}$

From equation B5, and assuming an  $\text{RQ} = 0.85 \text{ CO}_2/\text{O}_2$

$\text{DEE}(\text{CO}_2) = 0.85 \times 2884.2 \text{ ml CO}_2 \text{ min}^{-1} \times 1440 \text{ min d}^{-1} \times 1.9 \times 10^{-3} \text{ g CO}_2/\text{ml CO}_2$   
 $= 6707.5 \text{ g CO}_2 \text{ d}^{-1}$

We assume, based on empirical synthesis, that wolves occur at average densities of 17.8 individuals / 1000 km<sup>2</sup> (Ripple and Beschta 2012: page 736). Scaling this to the entire  $1.89 \times 10^6$  km<sup>2</sup> boreal forest region gives a wolf population estimate of 33,642 animals.

The annual release by the boreal wolf population is then:

$6707.5 \text{ g CO}_2 \text{ d}^{-1} \times 365 \text{ d} \times 33,642 \text{ animals} = 8.24 \times 10^{10} \text{ g CO}_2 \text{ yr}^{-1}$ .

The estimate also does not include enteric methane release by moose. The mass of an average-sized moose is assumed to be 359 kg (Wilmers and Schmitz 2016). Using a body mass-methane emissions regression for ruminant ungulates developed from synthesis of empirical measures (Smith et al. 2015: Fig. 1) gives an average per capita moose release of 65.6 kg CH<sub>4</sub> yr<sup>-1</sup>. Assuming an average boreal forest moose density of 1.3 individual km<sup>-2</sup> in the presence of wolves (Wilmers and Schmitz 2016) gives an estimated total methane release from moose for the Canadian boreal region =  $1.3 \times 65.6 \text{ kg CH}_4 \text{ yr}^{-1} \times 10^3 \text{ g/kg} \times 1 \text{ km}^{-2} \times 1.89 \times 10^6 \text{ km}^2 = 1.61 \times$

$10^{11}$  g CH<sub>4</sub> yr<sup>-1</sup>. We multiply CH<sub>4</sub> by 28 to convert to CO<sub>2e</sub> which accounts for CH<sub>4</sub>'s carbon mass and higher heat trapping capacity relative to CO<sub>2</sub> over a 100-year time horizon. This gives an estimated release of  $4.51 \times 10^{12}$  g CO<sub>2e</sub> yr<sup>-1</sup>.

### **Estimated net ecosystem carbon balance**

Net carbon balance due to wolves becomes: NEP – wolf respiration – moose methane release

$$2.65 \times 10^{14} \text{ g CO}_2 \text{ yr}^{-1} - 8.24 \times 10^{10} \text{ g CO}_2 \text{ yr}^{-1} - 4.51 \times 10^{12} \text{ g CO}_{2e} \text{ yr}^{-1} = 2.60 \times 10^{14} \text{ g CO}_2 \text{ yr}^{-1} \\ = \mathbf{0.260 \pm 0.132 \text{ (1 SD) GtCO}_{2e} \text{ yr}^{-1}}$$

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## **Sharks in coral reef algal beds**

Sharks influence sediment carbon storage by limiting the spatial extent of herbivory and sediment bioturbation emanating outward from coral reefs (Atwood et al. 2018, Madin et al. 2019a).

At the Heron Island Lagoon in the Great Barrier Reef Marine Park (GBRMP), organic carbon storage in upper (0-5 cm) sedimentary depths is estimated to amount to 100 Mg ha<sup>-1</sup> when sharks are present and reduces to 39.8 Mg ha<sup>-1</sup> when sharks are absent (Atwood et al. 2018; Figure 4a) for a net effect due to sharks of 60.2 Mg ha<sup>-1</sup>. In lower (5-14 cm) sedimentary depths, organic carbon storage is estimated to amount to 100 Mg ha<sup>-1</sup> when sharks are present and reduces to 50.1 Mg ha<sup>-1</sup> when sharks are absent (Atwood et al. 2018; Figure 4b) with a net effect due to sharks of 49.9 Mg ha<sup>-1</sup>. This amounts to 110.1 Mg C ha<sup>-1</sup>. This is the total amount of storage over the past 100 years (Atwood et al. 2018) giving 1.10 Mg C ha<sup>-1</sup> yr<sup>-1</sup> =  $1.1 \times 10^6$  g C ha<sup>-1</sup> yr<sup>-1</sup> at a reef.

This does not account for CO<sub>2</sub> losses due to shark respiration. Average shark daily activity respiration rate (95 mg O<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>) was estimated from data synthesized in Bushell et al. (1989; Table 1) and Whitney et al. (2016; Table 3). Assuming an average body mass of the focal species in the reef (tiger, black-tipped Reef, and lemon sharks: Atwood et al. 2018) is 100 kg (Gallagher et al. 2014), gives a per individual average respiration rate of 9500 mg O<sub>2</sub> h<sup>-1</sup> which translates into  $9.5 \times 10^3$  mg O<sub>2</sub> h<sup>-1</sup> x 24 hr d<sup>-1</sup> x 365 d yr<sup>-1</sup> x 0.001 g/mg =  $8.3 \times 10^4$  g O<sub>2</sub> yr<sup>-1</sup>. Assuming an RQ = 0.85 (high protein diet) gives  $7.1 \times 10^4$  g CO<sub>2</sub> yr<sup>-1</sup> per individual.

## Estimated net ecosystem carbon balance

The entire GBRMP encompasses 2063 km<sup>2</sup> (Roelfsema et al. 2021). Assuming that Heron Island Lagoon is representative of the entire GBRMP (Atwood et al. 2018), and that average shark density on the reef is 6 individuals ha<sup>-1</sup> (Robbins et al. 2006; Fig. 2., Nadon et al. 2012; Fig. 4). then net ecosystem carbon balance for the region is:

$$[(1.1 \times 10^6 \text{ g C ha}^{-1} \text{ yr}^{-1} \times 3.66 \text{ gCO}_2/\text{gC}) - (6 \times 7.1 \times 10^4 \text{ g CO}_2 \text{ ha}^{-1} \text{ yr}^{-1})] \times 10^2 \text{ ha/km}^2 \times 2063 \text{ km}^2 = 7.4 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1} =$$

**0.00074 Gt CO<sub>2</sub> yr<sup>-1</sup> ± 0.00037** (1 SD) assuming 50% coefficient of variation).

Coral reefs worldwide conservatively cover a spatial extent of 3.01 x 10<sup>5</sup> km<sup>2</sup> (Li et al. 2020, Table 2). Assuming that processes in GBRMP are representative of coral reefs worldwide, this leads to a potential to store:

$$0.00074 \text{ Gt CO}_2 \text{ yr}^{-1} \times 3.01 \times 10^5 \text{ km}^2 / 2063 \text{ km}^2 = \mathbf{0.108 \pm 0.054} \text{ g CO}_2 \text{ yr}^{-1} \text{ (1 SD) assuming 50\% coefficient of variation).}$$

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## Muskox in arctic mire and wetland

Muskox impact arctic ecosystem carbon capture and storage through grazing and trampling. Grazing can alter the amount of CO<sub>2</sub> captured by vegetation and eventually stored as organic carbon in permafrost soils in the ecosystem. However, grazing and trampling can lead to



permafrost thawing that triggers anaerobic microbial decomposition of stored organic matter and the release of methane.

### ***CO<sub>2</sub> exchange***

Average Net Ecosystem Exchange of CO<sub>2</sub> (NEE) 2011-2013 (data: Falk et al. Table 4)

Control (with Muskox):	-340.6* mg CO <sub>2</sub> m <sup>-2</sup> h <sup>-1</sup>	average CV = 30%
Muskox Exclosure:	-281.6 mg CO <sub>2</sub> m <sup>-2</sup> h <sup>-1</sup>	average CV = 50%
Net difference:	-59 mg CO <sub>2</sub> m <sup>-2</sup> h <sup>-1</sup>	

\*(-) signifies net carbon uptake into ecosystem

Sampling season (=~ growing season) June-September = 100 d = 2400 h (Falk et al. Table 1).

Net ecosystem exchange (uptake) = -59 mg CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> x 2400 h = 141,600 mg CO<sub>2</sub> m<sup>-2</sup> = 141.6 g CO<sub>2</sub> m<sup>-2</sup>

Area of arctic mire or arctic wetland (Data: Reynolds 2019 Table 3 [CAVM habitat G4, W1, W2, W3])

483,000 km<sup>2</sup> = 4.83 x 10<sup>11</sup> m<sup>2</sup>

Muskox occupy ~ 60% of CAVM habitat G4, W1, W2, W3 habitat locations in the circumpolar arctic (Data: Cuyler et al. 2020 Fig. 1)

NEE = -141.6 g CO<sub>2</sub> m<sup>-2</sup> x 0.6 x 4.83 x 10<sup>11</sup> m<sup>2</sup> = 410.35 x 10<sup>11</sup> = -4.1 x 10<sup>13</sup> g CO<sub>2</sub> season<sup>-1</sup>

This will lead to an estimated 4.1 x 10<sup>13</sup> g CO<sub>2</sub> of avoided emissions = 0.041 Gt CO<sub>2</sub> ± 0.02 (assuming 50% coefficient of variation).

### ***CO<sub>2</sub> release***

The above estimate for NEE does not include estimates for direct CO<sub>2</sub> release from muskoxen individuals. Assuming an average body mass of 145 kg (Lawler and White 2003), and using general methods outlined in Box 1, we estimated current population respiratory CO<sub>2</sub> release using equations B1-B5 to estimate per capita CO<sub>2</sub> release per day (DEE(CO<sub>2</sub>)). DEE(CO<sub>2</sub>) was then multiplied by 365 days and by muskox population size to estimate annual population CO<sub>2</sub> emissions, as follows:

From equation B1, BMR(O<sub>2</sub>) = 410.3 ml min<sup>-1</sup>

From equation B3, I = 5.86, where DEE was estimated using equation B2a.

From equation B4, DEE(O<sub>2</sub>) = 5.86 x 410.3 ml O<sub>2</sub> min<sup>-1</sup> = 2404.4 ml O<sub>2</sub> min<sup>-1</sup>

From equation B5, and assuming an RQ = 1.0 CO<sub>2</sub>/O<sub>2</sub> (Lawler and White 2003, Fig 1)

DEE(CO<sub>2</sub>) = 1.0 x 2404.4 ml CO<sub>2</sub> min<sup>-1</sup> x 1440 min d<sup>-1</sup> x 1.9 x 10<sup>-3</sup> g CO<sub>2</sub>/ ml CO<sub>2</sub>  
= 6578.4 g CO<sub>2</sub> d<sup>-1</sup>

Assuming a population size of 126,285 individuals residing in circumpolar high arctic mire ecosystems (Cuyler et al. 2020), we arrive at a yearly CO<sub>2</sub> release of:

$$6578.4 \text{ g CO}_2 \text{ d}^{-1} \text{ individual}^{-1} \times 365 \text{ d} \times 126,285 \text{ individuals} = 3.03 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1}$$

### ***Methane exchange***

Muskox can cause methane release via changing soil biophysical conditions that enhance anaerobic microbial decomposition of organic matter and from enteric emissions as well as.

#### *Soil release:*

Average CH<sub>4</sub> Flux 2011-2013 (data: Falk et al. Figure 2)

Control (with Muskox): +3.33\* mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup>  
 Muskox Exclosure: +2.8 mg CH<sub>4</sub> m<sup>-2</sup> h<sup>-1</sup>  
 Net difference: +0.53 mg CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>

\*(+) signifies methane release from the ecosystem

$$\text{Net CH}_4 \text{ release} = 0.53 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1} \times 2400 \text{ h} = 1272 \text{ mg CH}_4 \text{ m}^{-2} \text{ season}^{-1}.$$

$$1272 \text{ mg CH}_4 \text{ m}^{-2} \text{ season}^{-1} \times 10^{-3} \text{ g/mg} \times 0.6 \times 4.83 \times 10^{11} \text{ m}^2 = 3.69 \times 10^{11} \text{ g CH}_4 \text{ season}^{-1}$$

Using a 28x conversion factor, we arrive at net CO<sub>2</sub>e emission = 1.03 x 10<sup>13</sup> g yr<sup>-1</sup>

#### *Animal release:*

Assuming a mean muskox body mass of 145 kg and using a body mass-methane emissions regression for ruminant ungulates developed from synthesis of empirical measures (Smith et al. 2015: Fig. 1) gives an average per capita muskox release of 24.2 kg CH<sub>4</sub> yr<sup>-1</sup>. Hence the estimated total methane release from the muskox population = 24.2 kg CH<sub>4</sub> yr<sup>-1</sup> x 10<sup>3</sup>g/kg x 126,285 = 3.06 x 10<sup>9</sup> g CH<sub>4</sub> yr<sup>-1</sup>. Using a 28x conversion factor, we arrive at a CO<sub>2</sub>e emission = 8.6 x 10<sup>10</sup> g yr<sup>-1</sup>.

The soil and animal CO<sub>2</sub>e release from methane together amounts to:

$$1.03 \times 10^{13} \text{ g yr}^{-1} + 8.6 \times 10^{10} \text{ g yr}^{-1} = 1.04 \times 10^{13} \text{ g yr}^{-1}$$

### **Estimated net ecosystem carbon balance**

NECB = NEE – muskox respiration – methane release (soil + animal)

$$4.1 \times 10^{13} \text{ g CO}_2 \text{ yr}^{-1} - 3.03 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1} - 1.04 \times 10^{13} \text{ g CO}_2 \text{ e yr}^{-1} = 3.03 \times 10^{13} \text{ g CO}_2 \text{ yr}^{-1}$$

$$= \mathbf{0.030 \text{ Gt CO}_2 \text{ yr}^{-1} \pm 0.015} \text{ (assuming 50\% coefficient of variation).}$$

### **References**

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## Global fish

The estimate was obtained from a published report providing a comprehensive, detailed carbon budget for marine fish ( $1.5 \pm 1.2$  Gt C (Pg C)  $\text{yr}^{-1}$ ; Saba et al. 2021; Abstract).

### Estimated net ecosystem carbon balance

$$1.5 \pm 1.2 \text{ Gt C yr}^{-1} \times 3.66 = \mathbf{5.50 \pm 4.40 \text{ Gt CO}_2 \text{ yr}^{-1}}$$

## References

Saba, G.K. et al. Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* **66**, 1639-1644 (2021).

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## Forest Elephants in Congo Basin Forest

Forest elephants enhance carbon capture and storage in tree biomass by dispersing seeds of carbon dense tree species in their dung and promoting seed germination in dung piles. As well, elephants forage on and trample understory vegetation thereby reducing plant competition with carbon dense tree species that make up the overstory.

Estimates of carbon capture and storage are presented for 79 tropical rainforest protected areas collectively covering a 537,733  $\text{km}^2$  area in the Congo basin and parts of East Africa (Berzaghi et al. 2022). The yearly net rate of change in carbon capture and storage in forest trees attributable to elephants is estimated to be (equation 8 in Berzaghi et al. 2022) 0.0754 tonnes C  $\text{ha}^{-1} \text{yr}^{-1}$  (SD 0.03 tC  $\text{ha}^{-1} \text{yr}^{-1}$ ) or 0.277 tCO<sub>2</sub>  $\text{ha}^{-1} \text{yr}^{-1}$  (SD 0.055 tCO<sub>2</sub>  $\text{ha}^{-1} \text{yr}^{-1}$ ). Carbon capture and storage in tree biomass for the landscape area covered by the protected areas is estimated to be  $537,772 \text{ km}^2 \times 100 \text{ ha/km}^2 \times 0.277 \text{ tCO}_2 \text{ ha}^{-1} \text{yr}^{-1} = 14,896,284 \text{ tCO}_2 \text{ yr}^{-1} = 1.489 \times 10^{13} \text{ gCO}_2 \text{ yr}^{-1} = 14.89 \text{ Tg CO}_2 \text{ yr}^{-1}$ .

However, elephants release CO<sub>2</sub> during respiration and release enteric methane.

### CO<sub>2</sub> release

We estimated current population respiratory CO<sub>2</sub> release using equations B1-B5 to estimate per capita CO<sub>2</sub> release per day (DEE(CO<sub>2</sub>)). DEE(CO<sub>2</sub>) was then multiplied by 365 days and by forest elephant population size to estimate annual population CO<sub>2</sub> emissions, as follows:

From equation B1,  $\text{BMR}(\text{O}_2) = 2512.4 \text{ ml min}^{-1}$ , assuming an average forest elephant = 1741.7 kg (White 1994).

From equation B3,  $I = 4.5$ , where DEE was estimated using equation B2a.

From equation B4,  $\text{DEE}(\text{O}_2) = 4.5 \times 2512.4 \text{ ml O}_2 \text{ min}^{-1} = 11305.8 \text{ ml O}_2 \text{ min}^{-1}$

From equation B5, and assuming an RQ = 1.0 CO<sub>2</sub>/O<sub>2</sub>  
DEE(CO<sub>2</sub>) = 1.0 x 11305.8 ml CO<sub>2</sub> min<sup>-1</sup> x 1440 min d<sup>-1</sup> x 1.9 x 10<sup>-3</sup> g CO<sub>2</sub>/ ml CO<sub>2</sub>  
= 30932.7 g CO<sub>2</sub> d<sup>-1</sup>

Assuming a population size of 99,000 (Berzaghi et al. 2022) gives an annual population CO<sub>2</sub> release of:

$$3.09 \times 10^4 \text{ g CO}_2 \text{ d}^{-1} \times 365 \text{ d yr}^{-1} \times 9.9 \times 10^4 \text{ animals} = 1.12 \times 10^{12} \text{ g CO}_2 \text{ yr}^{-1}$$

### *Methane release*

Berzaghi et al. (2022, page 3 **Carbon Sequestration and Valuation**) estimate that this population releases 0.012 Tg CH<sub>4</sub> yr<sup>-1</sup>. Using a conversion factor of 28x to account for biomass carbon and CH<sub>4</sub>'s higher heat trapping capacity relative to CO<sub>2</sub> gives CO<sub>2</sub>e = 0.336 Tg yr<sup>-1</sup>.

### **Estimated net carbon balance**

14.89 Tg CO<sub>2</sub> yr<sup>-1</sup> - 1.12 Tg CO<sub>2</sub> yr<sup>-1</sup> - 0.336 Tg CO<sub>2</sub>e yr<sup>-1</sup> = 13.43 Tg CO<sub>2</sub> yr<sup>-1</sup> = **0.013 Gt CO<sub>2</sub> yr<sup>-1</sup> ± 0.007 Gt CO<sub>2</sub> yr<sup>-1</sup>** (assuming 50% coefficient of variation based on above estimates).

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## **Bison in prairie grasslands**

Bison can alter carbon capture and storage by stimulating vegetation productivity and impacting soil respiration and carbon storage.

### *Accounting for CO<sub>2</sub> exchange in Net Primary Productivity*

#### **Tallgrass prairie:**

Average NPP during peak growing season (Knapp et al. Fig. 2)

Grazed NPP = 20 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> Coefficient of variation (CV) = 22%

Ungrazed NPP = 12.8 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> CV = 25%

Grazed NPP = 8.8 x 10<sup>-4</sup> g CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>

Ungrazed NPP = 5.7 x 10<sup>-4</sup> g CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>

Net difference = 3.1 x 10<sup>-4</sup> g CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>

Conversion: 60 sec/min x 60 min/hr x 12 hr/day growing x 100 days/season = 4.32 x 10<sup>6</sup> s/season

Grazed NPP = 3.1 x 10<sup>-4</sup> g CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> x 4.32 x 10<sup>6</sup> s/season = 13.4 x 10<sup>2</sup> g CO<sub>2</sub> m<sup>-2</sup>

Area of tallgrass available for restoration 35,475 km<sup>2</sup> (assuming 10% of area recovered over the next 100 years Data: Sanderson et al. 2008 Table 2).

Total tallgrass restoration area NPP =  $13.4 \times 10^2 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1} \times 10^6 \text{ m}^2 / \text{km}^2 \times 35,475 \text{ km}^2 = 4.75 \times 10^{13} \text{ g CO}_2 \text{ yr}^{-1}$ .

***Shortgrass prairie:***

Average NPP during peak growing season (Frank and McNaughton Fig. 2)

NPP difference between grazed and ungrazed plots = 89.1 g vegetation m<sup>-2</sup> per growing season.

NPP difference = 44.5 g C m<sup>-2</sup> per growing season (Assuming 50% carbon in biomass)

Area of shortgrass available for restoration 360,884 km<sup>2</sup> (assuming recovery of 16% Central shortgrass prairie, 1% Central and Southern mixed grasslands, 16% of Northern fescue grasslands, 31% of Northern mixed grasslands, and 15% of Southern shortgrass prairie over the next 100 years Data: Sanderson et al. 2008 Table 2)

Total shortgrass restoration area NPP =  $44.5 \text{ g C m}^{-2} \times 10^6 \text{ m}^2 / \text{km}^2 \times 360,884 \text{ km}^2 \times 3.66 \text{ g CO}_2 / \text{g C} = 5.8 \times 10^{13} \text{ g CO}_2 \text{ yr}^{-1}$ .

*Accounting for soil respiration*

Soil CO<sub>2</sub> release in grazed areas = 9.5 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (Johnson and Matchett 2001; Table 2).

Soil CO<sub>2</sub> release in ungrazed areas = 16 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (Johnson and Matchett 2001; Table 2).

Net difference = - 6.5 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (i.e., bison reduce soil carbon emissions).

Net soil emissions = - 6.5 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> = - 2.86 x 10<sup>-4</sup> g CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>

or - 2.86 x 10<sup>-4</sup> g CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> x 4.32 x 10<sup>6</sup> = -1.24 x 10<sup>3</sup> g CO<sub>2</sub> m<sup>-2</sup> y<sup>-1</sup>

(Conversion: 60 sec/min x 60 min/hr x 12 hr/day growing x 100 days/season (y) = 4.32 x 10<sup>6</sup> s/season (y)).

Assuming soil respiration is similar in tall and shortgrass prairie, then net soil carbon emissions for **tallgrass and shortgrass prairie** in the restoration area is calculated as:

$-1.24 \times 10^3 \text{ g CO}_2 \text{ m}^{-2} \text{ y}^{-1} \times 396,359 \text{ km}^2 \times 10^6 \text{ m}^2 / \text{km}^2 = - 4.91 \times 10^{14} \text{ g CO}_2 \text{ y}^{-1}$

Bison also release respiratory CO<sub>2</sub> and enteric methane.

Population respiratory CO<sub>2</sub> release was estimated using equations B1-B5 to estimate per capita CO<sub>2</sub> release per day (DEE(CO<sub>2</sub>)). DEE(CO<sub>2</sub>) was then multiplied by 365 days and by forest elephant population size to estimate annual population CO<sub>2</sub> emissions, as follows:

From equation B1, BMR(O<sub>2</sub>) = 989.7 ml min<sup>-1</sup>, assuming an average bison = 485 kg (White 1994).

From equation B3,  $I = 5.2$ , where DEE was estimated using equation B2a.  
 From equation B4,  $DEE(O_2) = 5.2 \times 989.7 \text{ ml } O_2 \text{ min}^{-1} = 5146.4 \text{ ml } O_2 \text{ min}^{-1}$   
 From equation B5, and assuming an  $RQ = 1.0 \text{ CO}_2/O_2$   
 $DEE(CO_2) = 1.0 \times 5146.4 \text{ ml } CO_2 \text{ min}^{-1} \times 1440 \text{ min d}^{-1} \times 1.9 \times 10^{-3} \text{ g } CO_2/\text{ml } CO_2$   
 $= 14080.6 \text{ g } CO_2 \text{ d}^{-1}$

Bison population density estimates range from 0.2 - 0.48 individuals  $\text{km}^{-2}$  (Fuller et al. 2007, Steenweg et al. 2016), or an average 0.34 individuals  $\text{km}^{-2}$ . Hence, over the 360,884  $\text{km}^2$  shortgrass + 35,475  $\text{km}^2$  tallgrass restoration area this could result between 134,762 additional animals. These individuals would annually release:

$$1.41 \times 10^4 \text{ g } CO_2 \text{ d}^{-1} \times 365 \text{ d yr}^{-1} \times 1.34762 \times 10^5 \text{ animals} = 6.93 \times 10^{11} \text{ g } CO_2 \text{ yr}^{-1}$$

#### *Methane release*

Per-individual methane efflux has been measured as 81  $\text{g } CH_4 \text{ d}^{-1}$  (95% CI 54-109) (Stoy et al. 2021). Bison density estimates ranges from 0.2 - 0.48 individuals  $\text{km}^{-2}$  (Fuller et al. 2007, Steenweg et al. 2016). Hence, over the 360,884  $\text{km}^2$  shortgrass + 35,475  $\text{km}^2$  tallgrass restoration area this could result between 79,271 – 190,252 additional animals. These animals would produce between  $6.4 \times 10^6$  -  $1.5 \times 10^7 \text{ g } CH_4 \text{ d}^{-1}$  or  $2.3 \times 10^9$  -  $5.5 \times 10^9 \text{ g } CH_4 \text{ yr}^{-1}$ . Converted this estimate to  $CO_2e$  by multiplying by 28 to account for  $CH_4$ 's higher heat trapping capacity relative to  $CO_2$  gives an estimate release of  $6.4 \times 10^{10}$  –  $1.5 \times 10^{11} \text{ g } CO_2e \text{ yr}^{-1}$ , or an average of  $1.07 \times 10^{11} \text{ g } CO_2e \text{ yr}^{-1}$ .

#### **Estimated net carbon balance**

$NPP_{\text{tallgrass}} + NPP_{\text{shortgrass}} - \text{soil respiration} - \text{animal respiration} - \text{animal methane release}$

$$4.75 \times 10^{13} \text{ g } CO_2 \text{ yr}^{-1} + 5.8 \times 10^{13} \text{ g } CO_2 \text{ yr}^{-1} - (-4.91 \times 10^{14} \text{ g } CO_2 \text{ yr}^{-1}) - 6.93 \times 10^{11} \text{ g } CO_2 \text{ yr}^{-1} - 1.07 \times 10^{11} \text{ g } CO_2e \text{ yr}^{-1}$$

$$= \mathbf{0.595 \pm 0.275 \text{ Gt } CO_2 \text{ yr}^{-1}} \text{ (assuming 50\% coefficient of variation).}$$

#### **References**

- Frank, D.A., McNaughton S.J. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* **96**, 157-161 (1993).
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 Stoy, P.C. et al. Methane efflux from an American bison herd. *Biogeosci.* **18**, 961–975 (2021).

## Baleen Whales

Baleen whales impact carbon capture and storage in the Southern Ocean via two major pathways: through carbon in biomass of whale carcasses that sink to the deep ocean and by stimulation of phytoplankton production resulting from the release in feces and urine that fertilize phytoplankton with limiting nutrients. Estimates for carcass sinking by Dufort et al. (2022, Results Page 4) suggest that restored Southern Ocean baleen whales could conservatively increase ocean carbon capture and storage by  $1.7 \times 10^{11} \text{ g C yr}^{-1} = 6.2 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1}$ . Estimates of effects of whales on phytoplankton carbon uptake are too uncertain to include in a budget (Dufort et al. 2022).

### Estimated net carbon balance

$1.7 \times 10^{11} \text{ g C yr}^{-1} \times 3.66 \text{ gCO}_2/\text{gC} = 6.2 \times 10^{11} \text{ g CO}_2 \text{ yr}^{-1} = \mathbf{0.00062 \text{ Gt CO}_2 \text{ yr}^{-1} \pm 0.0001}$   
 (assuming 25% coefficient of variation).

However, this estimate does not include CO<sub>2</sub> loss via respiration by the whale populations. Gunnufsen (2022, Page 44) estimated active VO<sub>2</sub> of an average humpbacked whale (M = 30,000 Kg) as 94 l O<sub>2</sub> min<sup>-1</sup>, noting that this represents 4.1 x BMR. This multiple of BMR for active metabolism compares favorably with data in Williams (2022, Fig. 4). This gives a per metabolic mass (per kg<sup>0.75</sup>) VO<sub>2</sub> = 41.2 ml O<sub>2</sub> min<sup>-1</sup>(Kg<sup>0.75</sup>)<sup>-1</sup>, or 5.93 x 10<sup>4</sup> ml O<sub>2</sub> d<sup>-1</sup>(Kg<sup>0.75</sup>)<sup>-1</sup>. We applied this to the five baleen species, assuming that such capita respiration scales linearly with metabolic body mass of baleen whales, based analysis of their on energetics and foraging efficiency (Goldbogen et al. 2019). Assuming an RQ of 0.9, daily VO<sub>2</sub> can be converted to annual per capita CO<sub>2</sub> release as 5.93 x 10<sup>4</sup> ml O<sub>2</sub> d<sup>-1</sup>(Kg<sup>0.75</sup>)<sup>-1</sup> x 0.9 x 1.9 x10<sup>-3</sup> g CO<sub>2</sub>/ml CO<sub>2</sub> x 365 d /yr = 3.71 x 10<sup>4</sup> gCO<sub>2</sub> (Kg<sup>0.75</sup>)<sup>-1</sup> yr<sup>-1</sup>.

This per capita estimate is scaled to the populations of the Southern Ocean in the following table.

Whale species	Mass (kg)	Mass (kg <sup>0.75</sup> )	Per individual CO <sub>2</sub> respiration (g yr <sup>-1</sup> )	Population size	Population CO <sub>2</sub> Respiration (g yr <sup>-1</sup> )
Fin	55000	3591.47	1.33 x 10 <sup>8</sup>	17337	2.31 x 10 <sup>12</sup>
Blue	110000	6040.11	2.24 x 10 <sup>8</sup>	1280	2.87 x 10 <sup>11</sup>
Humpback	30000	2279.51	8.46 x 10 <sup>8</sup>	6000	5.07 x 10 <sup>11</sup>
Minke	6000	681.73	2.53 x 10 <sup>7</sup>	162000	4.10 x 10 <sup>12</sup>
Right	45000	3089.65	1.15 x 10 <sup>8</sup>	926	1.06 x 10 <sup>11</sup>
				<b>Total Release</b>	<b>7.31 x 10<sup>12</sup></b>

where mean body mass (Mass) was obtained from Dufort et al. (2022) and population sizes were obtained from Tulloch et al. (2018).

The respiratory losses far exceed the estimated NECB due to carbon storage via sinking carcasses of these whale populations. This highlights that simply accounting for carbon in whale biomass would lead to the conclusion that whales are a net source of CO<sub>2</sub>. This underscores the imperative to better address uncertainties in estimates of Southern Ocean whale effects on phytoplankton production. Given that whales could enhance phytoplankton production to capture several Tg (aka 10<sup>12</sup> g) CO<sub>2</sub> yr<sup>-1</sup>, phytoplankton production could offset whale respiration losses resulting in net neutral to net positive effects on net ecosystem carbon balance (Dufort et al. 2022). Hence the above NECB estimate of 0.00062 Gt CO<sub>2</sub> yr<sup>-1</sup> ± 0.0001 is conservative.

### ***References***

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## Supplementary Appendix 2

**Description of potential effects on ecosystem properties and carbon storage if candidate animal species highlighted in Figure 1 were restored or protected through trophic rewilding.** Supporting references are provided after the explanations.

### **Arctic Yedoma: Caribou, Muskox, American Bison, Horses**

These herbivore species would primarily **protect carbon stores** in Yedoma permafrost soils. Their trampling and grazing would reduce shrub cover which in turn would enhance surface albedo. The higher albedo increases solar radiation reflectance back to the atmosphere and would reduce permafrost thawing and subsequent anaerobic microbial decomposition of soil organic matter which is released as CH<sub>4</sub>.

Their trampling would also increase soil compaction reducing microbial respiration and leaching of soil carbon storage pools.

#### **Reference:**

Macias-Fauria, M. et al. Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philos. Trans. R. Soc. B: Biol. Sci.* **375**, 20190122 (2020).

### **Arctic Tundra: Muskox**

This herbivore species would **protect carbon stores** in tundra soils. Its trampling and grazing would reduce shrub cover which in turn enhances surface albedo. The higher albedo would increase solar radiation reflectance back to the atmosphere reducing permafrost thawing and subsequent anaerobic microbial decomposition of soil organic matter which is released as CH<sub>4</sub>.

Its trampling would also increase soil compaction reducing microbial respiration and leaching of soil carbon storage pools.

It would also enhance **carbon capture and storage** through grazing which stimulates net primary production and increases carbon inputs to soil storage pools.

#### **Reference:**

Falk, J.M. et al. Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Env. Res. Lett.* **10**, 045001 (2015).

### **African Savanna: Wildebeest and other, diverse large grazing antelopes, White Rhino, Hippopotamus, African Buffalo, Zebra**

These herbivore species would **protect carbon stores** through grazing which reduces the spatial extent and intensity of wildfires thereby promoting carbon retention in vegetation and soil storage pools. Their trampling would further increase soil compaction reducing microbial respiration and leaching of soil carbon storage pools.

**Reference:**

Holdo, R.M. et al., A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biol.* **7**, e1000210 (2009).

Hyvarinen, O. et al. Megaherbivore impacts on ecosystem and Earth system functioning: the current state of the science. *Ecography* **44**, 1579-1594 (2021).

Dobson, A.P. et al. Savannas are vital but overlooked carbon sinks. *Science* **375**, 392.

**North American Grassland: American Bison, Elk**

These herbivore species would **enhance carbon capture** and storage through grazing that stimulates net primary production and increases carbon retention in vegetation and soils. They would further **protect carbon stores** via trampling that enhances soil compaction reduced soil respiration and carbon leaching.

**Reference:**

Frank, D. A., Kuns, M.M., Guido, D.R. Consumer control of grassland plant production *Ecology* **83**, 602–606 (2002).

Knapp A.K. et al. The keystone role of bison in North American Tallgrass prairie. *BioScience* **49**, 39-50 (1999).

**Argentinian Arid Alpine: Vicuña**

This herbivore species would **enhance carbon storage** via its spatial movement from lush feeding areas to dry grass habitat to avoid predators. This movement translocates organic carbon which is released as dung in the dry grass habitat soil storage pools. The dry conditions promote long-term storage due to decreased microbial activity and hence lower decomposition and soil respiration.

**Reference:**

Monk, J. *The biogeochemical legacy of the landscape of fear: pumas, vicuñas, and nutrient cycling in the high Andes*. PhD Dissertation, Yale University (2022).

**Indian Mountain Grassland: Bharal, Ibex, Yak**

These herbivore species would **protect carbon stores** through their trampling and grazing. This reduces soil microbial biomass and hence soil respiration. As a consequence the long-term stability of soil carbon storage is increased.

**Reference:**

Bagchi, S., Roy, S., Maitra, A. & Sran, ER.S. Herbivores suppress soil microbes to influence carbon sequestration in the grazing ecosystem of the Trans-Himalaya. *Agric. Ecosyst. Environ.* **239**, 199–206 (2017).

Naidu, D.G.T., Roy, S. & Bagchi, S. Loss of grazing by large mammalian herbivores can destabilize the soil carbon pool. *Proc. Natl. Acad. Sci. USA* **119**, e2211317119 (2022).

### **Australian Shrubland: Dingoes**

This carnivore species would **enhance carbon capture and storage** by preying on kangaroos. Predation and predation risk reduce the abundance and foraging activity of grazing kangaroos. This predator effect on herbivore prey in turn would enhance vegetation abundance and inputs to soil carbon storage pools.

#### **Reference:**

Morris T, Letnic M. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proc. R. Soc. B* 284: 20170111 (2017).

### **Coral Reef: Tiger, Black-tipped Reef and Lemon Sharks**

These carnivore species would **enhance carbon capture and storage** by preying on herbivorous coral reef fish. Predation and predation risk reduce grazing fish abundance and foraging effort which in turn would enhance primary production and inputs to sediment carbon storage.

These carnivore species would also **protect carbon stores**. Causing grazing fish to reduce their foraging effort would reduce sediment bioturbation by the grazing fish, reducing loss of organic carbon from sediment storage pool.

#### **Reference:**

Atwood, T.B. et al. Predators Shape Sedimentary organic carbon storage in a coral reef ecosystem. *Front. Ecol. Evol.* 6, 110 (2018).

### **Seagrass: Tiger sharks**

This carnivore species would **enhance carbon capture and storage** by preying on herbivorous sea turtles and dugongs. Predation and predation risk reduce turtle and dugong abundance and foraging effort which in turn would enhance primary production and inputs to sediment carbon storage.

This carnivore species would also **protect carbon stores**. Causing these herbivores to reduce their foraging effort would reduce sediment bioturbation, reducing loss of organic carbon from sediment storage pool.

#### **Reference:**

Atwood, T., Connolly, R., Ritchie, E. *et al.* Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Change* 5, 1038–1045 (2015).

### **Old- and New- world Tropical Forests: Forest Elephants, Old- and New-world primates, Tapirs, Black-fronted Piping Guan, Hornbills, Fruit bats**

These herbivore (browser and frugivore) species would **enhance carbon capture and storage** by dispersing seeds of consumed fruits. Because of their larger body sizes, they disperse larger seeds produced by more carbon-dense tree species found in the forest overstory. Dispersing these

seeds in their nutrient rich dung would promote the germination and establishment of carbon dense forest tree species across the landscape. Furthermore, foraging on understory vegetation would reduce competition with overstory trees, which would enhance net primary production and aboveground carbon storage by carbon dense canopy trees.

**Reference:**

- Berzaghi, F. et al. Financing conservation by valuing carbon services produced by wild animals. *Proc. Natl. Acad. Sci. USA* **119**, e2120426119 (2022).
- Osuri A.M. et al. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nat. Commun.* **7**, 11351 (2016).
- Culot, L., et al., Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. *Sci. Rep.* **7**, 7662 (2017).
- Chanthorn, W. et al. Defaunation of large-bodied frugivores reduces carbon storage in a tropical forest of Southeast Asia. *Sci. Rep.* **9**, 10015 (2019).

**Boreal Forest: Wolf**

This carnivore species would **enhance carbon capture and storage**. Reducing browsing moose abundance and foraging effort would in turn enhance primary production and organic matter inputs to soil carbon storage pools.

**Reference:**

- Wilmer, C.C., Schmitz, O.J. Effects of gray-wolf induced trophic cascades on ecosystem carbon cycling. *Ecosphere* **7(10)**:e01501 (2016).

**Boreal and temperate wetlands: Beaver**

This herbivore species would **enhance carbon storage**. By building dams that create aquatic reservoirs, the species' would engineer new ecosystem structures that collect organic matter debris from the surrounding landscape that sinks to sediment carbon storage pools.

**Reference:**

- Nummi, P., Vehkaoja M., Pumpanen J. & Ojala A. Beavers affect carbon biogeochemistry: both short-term and long-term processes are involved. *Mamm. Rev.* **48**, 298-311 (2018).

**Southern Ocean: Sperm whale; Blue whale, Fin whale, Humpback whale, Southern right whale, Antarctic Minke whale**

These carnivorous species would **enhance carbon capture and storage**. These species feed at ocean depth and return to the ocean surface to breath and release iron and nutrient rich fecal plumes in the surface waters (a process called the "whale pump"). This fertilization effect would stimulate surface ocean net primary productivity by phytoplankton. Eventually, some fraction of dead phytoplankton would evade microbial decomposition in the water column and sink to long-term storage in deep ocean sediments. In addition, carbon in sinking whale carcasses would add to deep ocean sediment carbon storage pools.

**Reference:**

- Dufort, A. et al. The collapse and recovery of carbon sequestration by baleen whales in the Southern Ocean. *Archimer* <https://doi.org/10.21203/rs.3.rs-92037/v1> (2022).
- Lavery, T.J. et al. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proc. R. Soc. B* **277**, 3527–3531 (2010).
- Pershing, A.J., et al. The impact of whaling on the ocean carbon cycle: Why bigger was better. *PLoS ONE* **5**, e12444 (2010).

**Gulf of Maine: Right whale, Humpback whale, Fin whale, Sei whale, Pilot whale, White-sided dolphin, Common dolphin, Harbor porpoise, Harbor seal, Gray seal**

These carnivorous species would **enhance carbon capture and storage**. These species feed at ocean depth and return to the ocean surface to breath and release iron and nutrient rich fecal plumes in the surface waters (a process called the “whale pump”). This fertilization effect would stimulate surface ocean net primary productivity by phytoplankton. Eventually, some fraction of dead phytoplankton would evade microbial decomposition in the water column and sink to long-term storage in deep ocean sediments. In addition, carbon in sinking whale carcasses would add to deep ocean sediment carbon storage pools.

**Reference:**

- Roman, J. & McCarthy, J.J. The whale pump: marine mammals enhance primary productivity in a coastal basin. *PLoS ONE* **5**: e13255 (2010).

**Beach: Sea Turtles**

These species would **enhance carbon capture and storage** by transporting nutrients obtained while feeding in the ocean and releasing them in waste while nesting on beaches. This fertilization input stimulates the production of coastal dune vegetation.

**Reference:**

- Hannan, L.B., Roth, J.D., Ehrhart, L.M., & Weishampel, J.F. Dune vegetation fertilization by nesting sea turtles. *Ecology* **88**, 1053-1058 (2007).
- Vander Zanden, H.B., Bjorndal, K. A., Inglett, P.W., & Bolten, A.B. Marine-derived nutrients from green turtle nests subsidize terrestrial beach ecosystems. *Biotropica* **44**, 294-301 (2012).

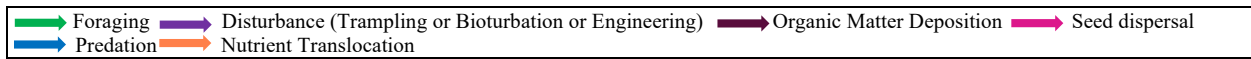
**Island semi-arid scrubland: Giant Tortoises**

This herbivore (grazer and frugivore) species would **enhance carbon capture and storage** Its foraging and defecation would promote nutrient release and seed dispersal across the landscape, enhancing the productivity of and carbon storage in aboveground vegetation.


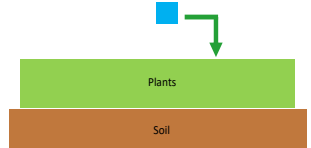

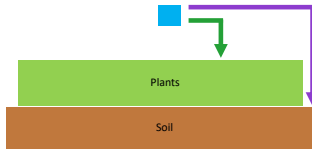
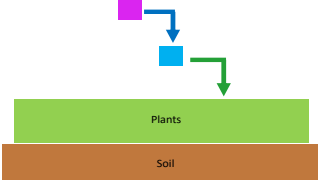
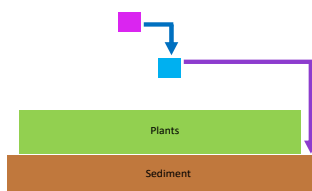
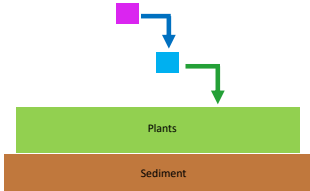
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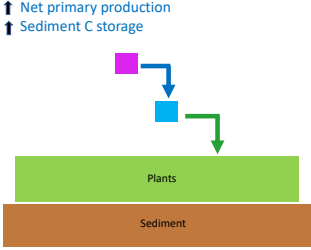
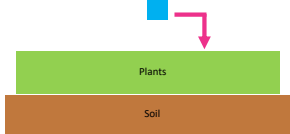
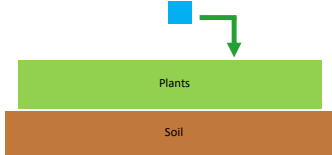
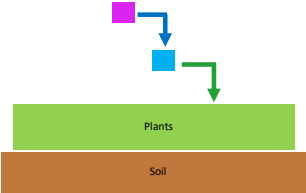
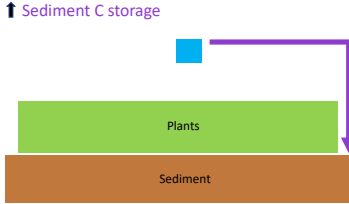
- Falcón, W., & Hansen, D. M. Island rewilding with giant tortoises in an era of climate change. *Phil. Trans. R. Soc. B* **373**, 20170442 (2018).
- Hunter, E. A., Gibbs, J. P., Cayot, L. J., & Tapia, W. Equivalency of Galápagos giant tortoises used as ecological replacement species to restore ecosystem functions. *Cons. Biol.* **27**, 701-709 (2013).

**Supplementary Table 1.** Ecosystems in which there is high potential to protect current carbon stores or enhance carbon capture and storage through trophic rewilding of large animal species. The table depicts the pathways through which the focal animal species can influence carbon capture and storage among different trophic compartments in ecosystems. Species and their potential to enhance carbon capture and storage were selected based on published studies that identified the animal functional roles within the ecosystem as described in the Supplemental Appendix 2

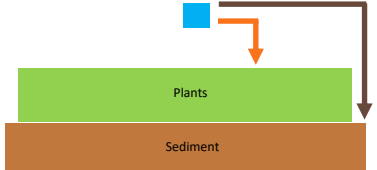
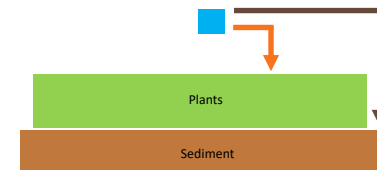
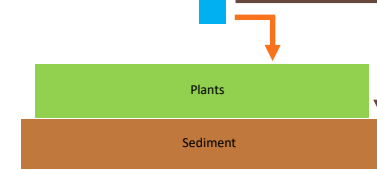
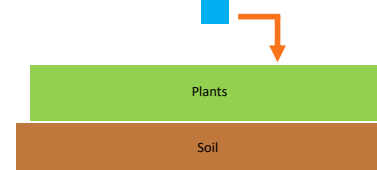
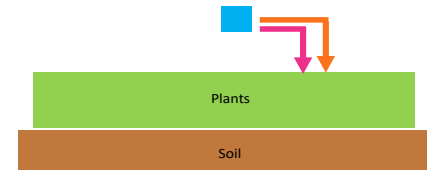


Ecosystem Type	Species	Functional Role
Arctic Yedoma	<ul style="list-style-type: none"> <li>Caribou,</li> <li>Muskox,</li> <li>American Bison,</li> <li>Horses</li> </ul>	<p>Protecting carbon stores</p> <ul style="list-style-type: none"> <li>↓ Shrub cover</li> <li>↑ Albedo/permafrost protection</li> <li>↑ Soil compaction</li> <li>↓ Soil CO<sub>2</sub> respiration</li> <li>↓ Soil CH<sub>4</sub> release</li> </ul>
Arctic Tundra	<ul style="list-style-type: none"> <li>Muskox</li> </ul>	<p>Protecting carbon stores</p> <ul style="list-style-type: none"> <li>↓ Shrub cover</li> <li>↑ Albedo/permafrost protection</li> <li>↑ Soil compaction</li> <li>↓ Soil CO<sub>2</sub> respiration</li> <li>↓ Soil CH<sub>4</sub> release</li> </ul> <p>Enhancing carbon capture and storage</p> <ul style="list-style-type: none"> <li>↑ Net primary production</li> </ul>
African savanna	<ul style="list-style-type: none"> <li>Wildebeest and other grazing antelopes, White Rhino, Hippo, African Buffalo, Zebra</li> <li>White Rhino, Elephant</li> </ul>	<p>Protecting carbon stores</p> <ul style="list-style-type: none"> <li>↓ Spatial extent and intensity of wildfires</li> <li>↑ Plant and soil C storage</li> </ul> <ul style="list-style-type: none"> <li>↑ Soil compaction</li> <li>↓ Soil CO<sub>2</sub> respiration</li> <li>↓ Soil C leaching</li> </ul>

<p>North American grassland</p>	<p>■ Bison, Elk,</p>	<div style="display: flex; justify-content: space-around;"> <div style="width: 45%;"> <p><b>Protecting carbon stores</b></p> <ul style="list-style-type: none"> <li>↑ Soil compaction</li> <li>↓ Soil CO<sub>2</sub> respiration</li> <li>↓ Soil C leaching</li> </ul>  </div> <div style="width: 45%;"> <p><b>Enhancing carbon capture and storage</b></p> <ul style="list-style-type: none"> <li>↑ Net primary production</li> <li>↑ Plant and Soil C storage</li> </ul>  </div> </div>
<p>Argentinian Arid Alpine</p>	<p>■ Vicuña</p>	<p style="text-align: center;"><b>Enhancing carbon capture and storage</b></p> <ul style="list-style-type: none"> <li>↑ Soil organic C inputs</li> </ul> 
<p>Indian mountain grassland</p>	<p>■ Bharal, Ibex, Yak</p>	<p style="text-align: center;"><b>Protecting carbon stores</b></p> <ul style="list-style-type: none"> <li>↓ Soil microbial biomass and CO<sub>2</sub> respiration</li> <li>↑ Stability of soil C storage</li> <li>↓ Soil microbial biomass and CO<sub>2</sub> respiration</li> <li>↑ Stability of soil C storage</li> </ul> 
<p>Australian Shrubland</p>	<p>■ Dingo (■ Kangaroos)</p>	<p style="text-align: center;"><b>Enhancing carbon capture and storage</b></p> <ul style="list-style-type: none"> <li>↑ Plant abundance</li> <li>↑ Plant and Soil C storage</li> </ul> 
<p>Coral Reef</p>	<p>■ Tiger, Black-tipped Reef, and Lemon Sharks (■ Herbivore fish)</p>	<div style="display: flex; justify-content: space-around;"> <div style="width: 45%;"> <p><b>Protecting carbon stores</b></p> <ul style="list-style-type: none"> <li>↓ Sediment C loss</li> </ul>  </div> <div style="width: 45%;"> <p><b>Enhancing carbon capture and storage</b></p> <ul style="list-style-type: none"> <li>↑ Net primary production</li> <li>↑ Sediment C storage</li> </ul>  </div> </div>

<p>Seagrass</p>	<p>■ Tiger sharks  ( ■ Dugongs, Sea turtles)</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Net primary production ↑ Sediment C storage</p> 
<p>Old- and New-world Tropical Forests</p>	<p>■ Elephants, Old- and New-world primates, Tapirs, Black-fronted Piping Guan, Hornbills, Fruit bats,  ■ Elephants</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Tree germination</p>  <p>↑ Net primary production</p> 
<p>Boreal Forest</p>	<p>■ Wolf  ( ■ Moose)</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Net primary production ↑ Plant and Soil C storage</p> 
<p>Boreal and temperate wetlands</p>	<p>■ Beaver</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Sediment C storage</p> 



<p>Southern Ocean</p>	<p>■ Sperm whale</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Net primary production ↑ Sediment organic C inputs</p> 
<p>Southern Ocean</p>	<p>■ Whales: Blue, Fin, Humpback, Southern Right, Antarctic Minke</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Net primary production ↑ Sediment organic C inputs</p> 
<p>Gulf of Maine</p>	<p>■ Whales and Dolphins: Right, Humpback, Fin, Sei, Pilot, White-sided, Common, Harbor porpoise, Seals: Harbor, Gray</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Net primary production ↑ Sediment organic C inputs</p> 
<p>Beach</p>	<p>■ Sea turtles</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Net primary production</p> 
<p>Island semi-arid scrubland</p>	<p>■ Giant tortoises</p>	<p>Enhancing carbon capture and storage</p> <p>↑ Plant germination ↑ Net primary production</p> 
<p> <span style="color: green;">→</span> Foraging     <span style="color: purple;">→</span> Disturbance (Trampling or Bioturbation or Engineering)     <span style="color: brown;">→</span> Organic Matter Deposition     <span style="color: pink;">→</span> Seed dispersal  <span style="color: blue;">→</span> Predation     <span style="color: orange;">→</span> Nutrient Translocation </p>		